ALPINE AND CLIFF ECOSYSTEMS
IN THE NORTH-CENTRAL ROCKY MOUNTAINS

by

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Ken Andrew Aho

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ABSTRACT

Data collection and analysis for managed wild lands is vital to their effective stewardship. To address this I gathered and analyzed data for largely undocumented alpine and cliff ecosystems located in the North-Central Rocky Mountains. This information should aid in decision-making processes for regional land managers and increase the overall ecological understanding of these systems.

This manuscript includes detailed community analyses of alpine vegetation and its environment on andesitic-volcanic substrates in the Washburn Range and the Northern Absarokas. It also places the Washburn Range and Northern Absarokas into a regional non-volcanic context by comparing them to alpine areas in the Beartooth Mountains.

Cliff communities were studied to record common species and to describe variation with respect to water and substrate gradients. An understanding of both alpine and cliff systems is important given the growing presence of exotic mountain goats (*Oreomnos americanus*) in the region, and concerns over the impact of global climate change to the Greater Yellowstone Ecosystem, particularly in alpine areas.

I also present here a number of original methods which should be of interest to ecologists. These include (1) methods for identifying appropriate vegetation classification methods, and finding the correct number of data clusters in datasets, (2) methods for studying important environmental parameters on rock surfaces, and (3) a new protocol for efficiently determining soil water potentials.

CHAPTER 1

INTRODUCTION

Overview

This dissertation was created to address the lack of ecological information for alpine environments in the North-Central Rocky Mountains and Greater Yellowstone Ecosystem (Fig. 1.1). A lack of information is of concern for several reasons. First, the Greater Yellowstone Ecosystem (GYE), including regions in Yellowstone National Park, is inhabited by rapidly expanding populations of exotic mountain goats (*Oreomnos americanus*). Exotic mountain goat impacts on alpine vegetation in Olympic National Park have been decidedly negative, as both threatened endemic plant species and overall alpine plant diversity have been reduced by their presence (Houston et al. 1994). In addition, while the net effects of global warming on terrestrial vegetation communities is difficult to gauge, alpine communities are likely to be particularly negatively affected. In the Greater Yellowstone Ecosystem treelines are expected to move up in elevation, decreasing alpine area size, and reducing alpine diversity (Weaver 2001, Romme and Turner 1990). This work provides long term plots, baseline information and an ecological context to quantify the impacts of mountain goats, climate change, and other factors over time.

Chapters 2 through 5 of the dissertation describe the alpine vegetation and environments of the North-Central Rocky Mountains (Fig. 1.1). While others have studied alpine ecology in the Northern Rockies (e.g. Johnson and Billings 1962, Cooper et al. 1997, Pemble 1965, and Thilenius and Smith 1985) no previous ecological research has been conducted on the alpine vegetation of the volcanic Washburn Range (Chapters 2 and 3), or the Northern Absaroka Volcanics (Chapter 4). Chapter 5 incorporates volcanic alpine information from Chapters 2-4 in combination with data from alpine limestone and granite mountains in the Beartooths to evaluate variation in alpine vegetation with respect to local (e.g. topography) and regional (e.g. climate, substrate) factors. Such scale concerns have never been directly and quantitatively addressed for alpine vegetation in the Rocky Mountains. Chapter 6, which describes the ecology of sub-alpine cliffs was written to address to the lack of regional information on this topic, and because invasive mountain goats inhabit and impact the communities of both the general alpine and sub-alpine cliff areas (Fig. 1.1).

Chapters 7-10 describe original methods used in the dissertation. Chapter 7 is concerned with cluster analysis, and quantifying what constitutes legitimate data clusters. Its findings provide tools to identify communities discussed in Chapters 3, 4 and 5. Chapter 8 details methods for describing rock surface environments and provides a foundation for conclusions concerning cliff substrate characteristics discussed in Chapter 6. Chapter 9 describes methods for calibrating and using gypsum block water sensors used in quantifying soil water conditions in Chapters 2 through 5.

Please note that chapters in this dissertation are intended to be stand alone publishable documents with complete methods, bibliographies etc. While this hopefully allows the reader to fully understand individual chapters he/she is interested in, it also results in unavoidable repition particularly in methods sections of Chapters 3, 4, and 5.

Consideration for Alpine Ecosystems

Alpine plant communities occupy islands separated by a low altitude sea. Thus island equilibrium theory (MacArthur and Wilson 1963, 1967), which predicts that the probability of extinction increases with decreasing island area and increasing isolation, is relevant in studying alpine environments (Hadley 1987, Bruun and Moen 2003, Chapter 3). Geographic isolation causes high rates of alpine endemism within spheres of consistently demanding environmental pressure (Körner 2003). Indeed, the unique ecological stresses of these environments (e.g. intense solar radiation fluctuations, cold, high winds, and ice) play a large role not only in determining community composition, but in preserving biodiversity, since mitigation of environmental stress reduces alpine plant diversity (Nilsson et al. 2002).

It follows that alpine plant communities in this dissertation should be viewed as islands within a much larger Rocky Mountain alpine archipelago which has existed and evolved for at least 140 Million years (Billings 2000). In island communities diversity is maintained by integrated patches which provide avenues for immigration and shunts for extinction (Levins 1969, 1970, Hubbell 2001). Thus, while habitat destruction reduces local island viability by decreasing area, it also reduces the integrity of the entire Rocky Mountain alpine.

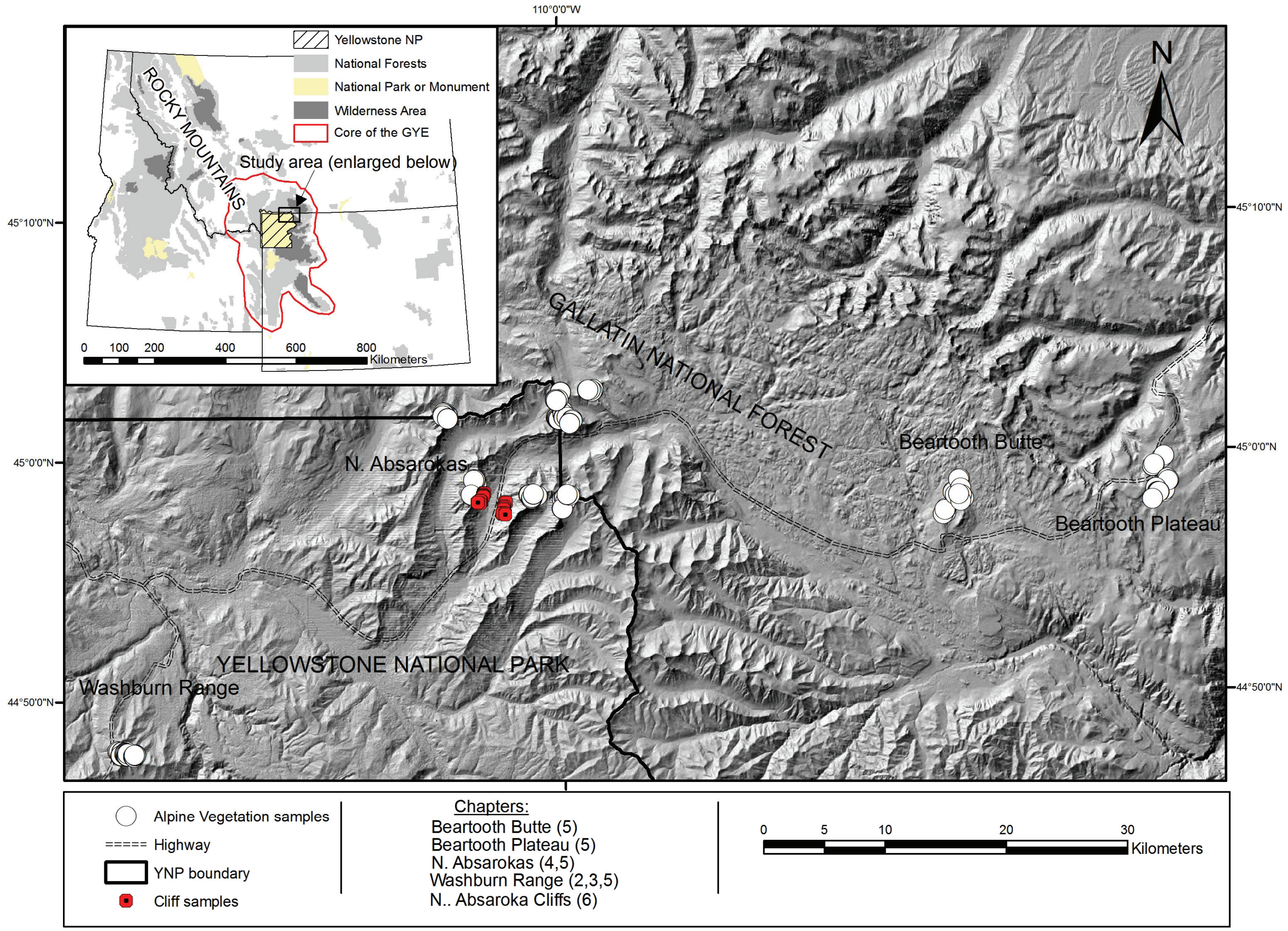

Figure 1.1. Study area locations dealt with in Chapters 2 through 6. The GYE consists of protected federal lands directly adjoining and including Yellowstone National Park (cf. Reese 1991). The North-Central Rocky Mountains encompass a similar region, i.e. regions in the Rockies bounded by the Windriver Range to the south and the Big Belt and Crazy Mountains to the north (Howard and Williams 1972).

Conservation

Along with distinct community properties, e.g. facilitation and feedback loops (Bruno et al. 2003, Callaway and Walker 1997, Callaway et al. 2002), high rates of endemism (Körner 2003), and the unique specificity of alpine communities to their environments (Nilsson et al. 2002), the importance of studying the alpine is emphasized by its vulnerability to human impacts. These include global warming (Romme and Turner 1990, Gottfried et al. 1998), increased U.V. radiation (Caldwell et al. 1982, Billings 1984), introduction of non-native species (Houston et al. 1994, Hess et al. 1999), and general loss of habitat through both fragmentation (Grabherr 1982, Billings 2000), and sub-alpine encroachment (Grabherr 1995). It is difficult to overvalue the importance of alpine systems, or to overestimate the negative consequences of their degradation and loss.

Literature cited

Billings, W. D. 1984. Effects of solar ultraviolet-B radiation on plants an vegetation as ecosystem components, pp. 206-217 in Causes and effects of changes in the stratospheric ozone: update 1983. National Academy Press, Washington D.C.

Billings, W. D. 2000. Alpine Vegetation of North America. pp. 537- 572. *In* North American Terrestrial Vegetation 2nd edition, Barbour, M. D. and Billings, W. D. eds. Cambridge Univ. Press, Cambridge.

Bruno, J. F., Stachowicz, J. J., and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. Trends in ecology and evolution. In press

Bruun, H. H., and J. Moen. 2003. Nested communities of alpine plants on isolated mountains: relative importance of colonization and extinction. Journal of Biogeography. 30: 297-303.

Caldwell, M. M., Robberecht, R., and W. D. Billings. 1982. Differential Photosynthetic inhibition by ultraviolet radiation in species from the arctic-alpine zone. Arctic and Alpine research. 14: 195-202.

Callaway, R. M., and L. R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology. 78: 1958-1965.

Callaway, R. M., Brooker, R. W., Choler, P., Kikvidze, Z., Lortie, C. J., Michalet, C., Paolini, L., Pugnaire, F. I., Newingham, B., Aschehoug, E. T., Armass, C., Kikodze, D., and B. J. Cook. 2002. Positive interactions of alpine plants increase with stress. Nature 417: 844-848.

Cooper, S. V., Lessica, P., and D. Page-Dumroese. 1997. Plant community classification for alpine vegetation on the Beaverhead National Forest, Montana. Gen. Tech. Rep. INT-GTR -362. Ogden UT: U.S. Department of Agriculture, Forest Service Intermountain Research Station. 61 pgs.

Gottfried, M., Pauli, H., and G. Grabherr. 1998. Prediction of vegetation patterns at the limits of plant life: a new view of the Alpine-Nival ecotone. Alpine and Arctic Research. 30: 207-221.

Grabherr, G. 1982. The impact of trampling by tourists on a high altitudinal gradient in the Tyrolean Alps. Vegetation. 48: 209-217.

Grabherr, G. 1995. Patterns and current changes in alpine plant diversity, pp 167-181 in F. S. Chapin and C. Körner (eds.), Arctic and alpine biodiversity, Springer-Verlag, New York Jones C.G.,

Hadley, K. S. 1987. Vascular alpine distributions within the central and southern Rocky Mountains, U.S.A. Arctic and Alpine research. 19(3): 242-251.

Hess, S. C., Banko, P. C., Brenner, G. J., and J. D. Jacobi. 1999. Factors related to the recovery of subalpine woodlands on Mauna Kea, Hawaii. Biotropica. 31(2): 212-219:

Houston, D., Schreiner, E., and B. Moorhead. 1994. Mountain goats in Olympic National Park: Biology and management of an introduced species. Scientific Monographs MNP/NROLYM/NRSM-94-25.

Howard, A. D., and J. D. Williams. 1972. Physiography. *In* Geologic altas of the Rocky Mountain region. Rocky Mountain association of geologists. Denver, CO.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton and Oxford, UK.

Johnson, P. L., and W. D. Billings. 1962. The alpine vegetation of the Beartooth plateau in relation to crypopedogenic processes and patterns. Ecological Monographs (32): 105-135.

Körner, C. 2003. Alpine plant life: Functional plant ecology of high mountain Ecosystems, 2nd edition. Springer-Verlag, Berlin. 338 pgs.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America. 15: 237-240.

Levins, R. 1970. Extinction. In: Lectures on mathematical analysis of biological patterns, pp. 123-138. Annals of the New York Academy of Sciences, Vol. 231.

MacArthur, R. H., and E. O. Wilson. 1963. An insular theory of island zoogeography. Evolution. 17: 373-387.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, USA.

Nilsson, M. C., Wardle, D. A., Zackrisson, O., and A. Jaderlund. 2002. Effects of the alleviation of ecological stresses on an alpine tundra community over an eight year period. Oikos. 97: 3-17.

Pemble, R. H. 1965. A survey of distribution patterns in the Montana alpine flora. Masters Thesis, University of Montana, Missoula. 146 pages.

Reese, R. 1991. Greater Yellowstone, the national park and associated wildlands, Montana geographic series No. 6. American and world geographic publishing, Helena MT, USA.

Romme, W. H., and M. G. Turner. 1990. Implications of Global Climate Change for Biogeographic patterns in the Greater Yellowstone Ecosystem. Conservation Biology. 5(3): 573-585.

Thilenius, K. F., and D. R. Smith. 1985. Vegetation and Soils of an Alpine Range In the Absaroka Mountains, Wyoming. USDA Forest Service General Technical Report RM-121, 18 pgs. Rocky Mountain Forest and Range Experiment Station, Fort Collins Colo.

Weaver, T. 2001. Whitebark pine in its environment. Pgs. 41-73, *In* D Tomback, S Arno, and R Keane eds. Whitebark pine communities: ecology and restoration. Island press, Washington DC. 440 pgs.

CHAPTER 2

INDICATOR SPECIES FOR WATER AND TEMPERATURE CONDITIONS IN ALPINE ECOSYSTEMS (NORTH-CENTRAL ROCKY MOUNTAINS)

Introduction

Water and temperature are major controls of vegetation distributions in alpine environments (Billings1999). As a result most descriptions of alpine communities speculate about water and temperature requirements of types identified and described (Johnson and Billings 1962, Douglas and Bliss 1977, Willard 1979, Komárková 1980, Urbanczyk and Henderson 1994, Cooper et al. 1997, many more). While these studies probably correctly identify general water and temperature conditions, the characterizations are nonetheless qualitative. For instance, quantitative descriptions, such as the length of warm or moist seasons, are rarely made.

Similarly, little quantitative information exists concerning individual alpine plant distributions on soil water and temperature gradients, particularly in the Northern Rocky Mountains. Soil water distributions have been described for selected species in Colorado (Ehleringer and Miller 1975 [5 spp.], Isard 1986 [1 spp.], Walker et al. 1994 [3 spp.], Humpheries et al. 1996 [18 spp.]), and Southern Wyoming (Oberbauer and Billings 1981 [29 spp.]). Distributions of alpine plants on soil temperature gradients are poorly documented in North America, although the effect of growing season length on snowbank distributions has been studied in Colorado (Galen and Stanton 1995 [6 spp.]), and semi-qualitative heat and drought tolerance categories have been established for a number of alpine species in Coastal British Columbia (Klinka et al. 1989).

We quantitatively related alpine species distributions at one well sampled location to soil water and soil temperature conditions. We had three objectives: 1) determine environmental indicator species for the North-Central Rockies, 2) calibrate species so that they could be used to quantify environmental conditions for alpine communities including those described in the past (e.g. Komárková 1979, Cooper et al. 1997, etc.), and 3) provide a general method for evaluating of soil moisture and temperature conditions at other sites.

Study Area

Our studies were conducted in the alpine environments of Mount Washburn (3124m), Yellowstone National Park (YNP), WY, USA (44º 48'N, 110º 26'W). Long term climate information has been recorded at Canyon WY., 600m below and 10 km south of the Washburn summit. At Canyon average temperatures (max/min) in July are 22.3º/3.1ºC while those in December are -4.7º/-16.6ºC (Chapter 3). Precipitation is consistent through the year (≅ 20mm month^{-1}; Chapter 3). Within the Washburn alpine itself, warmest air temperatures (≅ 17.5ºC) occur during late July/early August (≅ Julian day 210), and summer precipitation is consistent but low (0.75 mm day^{-1}; Chapter 3). Surface of the Washburn Range consists largely of rocks and soils derived from Eocene volcanoes (47-49 MYBP) of the Absaroka Volcanic Supergroup. The dominant formation (Langford) consists of light colored lava flows and alluvial facies composed of hornblende and pyroxene andesite fragments (Smedes and Prostka 1972; Chapter 3).

Methods

Vegetation Sampling

Twenty-two plots were established to represent the alpine vegetation of Washburn and its water and temperature gradients. Five major physical environments were selected for sampling. These were talus, south slopes, ridgetops, north slopes, and snowbank sites (Chapter 3). Each of the five environments was sampled at four sites along a slight altitudinal gradient (Elev. 3124m – 3032m). Two additional plots were installed at one site to represent cliff base runnels (Chapter 3). Within each site, vegetation of each of the five environments was sampled with two randomly located replicates. Each replicate consisted of ten 20 x 50cm frames placed at one meter intervals along a ten meter sampling tape oriented parallel to the topographic contour. The vegetation in each frame was characterized by listing the plant species present and visually estimating the cover of each (Daubenmire 1959). Vegetation data were gathered in the first weeks of July 2000 and 2001. Nomenclature follows Dorn (1992). Voucher specimens are deposited in the Yellowstone National Park herbarium (YELLO) in Gardiner MT.

Measuring Soil Moisture and Temperature

To measure soil water and temperature conditions we installed sensors at 15 cm depth at all 22 plots and read them periodically over five growing seasons, 2000-2004. Moisture sensors were Bouyoucos gypsum blocks manufactured by Beckman

Instruments (PO Box 3100, 2500 Harbor Boulevard, Fullerton, CA.). Moisture readings were made with a Delmhorst KS-D1 digital soil moisture (electric resistance) meter. Resistance readings were converted to water potentials using methods described in Chapter 9. Temperature sensors were thermocouples manufactured using methods described in Taylor and Jackson (1986), and read by an Omega HH-25TC thermocouple thermometer (www.Omega.com).

We separately modeled seasonal soil water and temperature patterns at all 22 plots. To describe the drying of soils from early spring (wet) to late summer (dry) we curve-fit soil water potentials (Ψ) against time (Julian day 175-235; i.e. June 24-August 23), with sigmoidal equations (Chapter 3; Appendix B.2). To describe the seasonal change in soil temperature from spring (cool) to summer (warm) to autumn (cool) we fit soil temperature against time (Julian day 180 to 280; i.e. June 29 to October 7) using unimodal quadratic equations (Chapter 3; Appendix B.3). Soil water and temperature models were both effective in describing seasonal variability in soil conditions (For soil water: $\overline{r^2} = 0.9$, $\overline{p} < 0.02$, for soil temperature: $\overline{r^2} = 0.7$, $\overline{p} < 0.002$; Chapter 3).

We indexed the length of moist and warm seasons from the soil water and temperature models. The moist season was designated as the number of days in which Ψ was above -0.12 MPa (i.e. -1.2 bars). This response occurred annually at all sites from dry ridges to wet snowbanks and generally presaged a dramatic drying trend (Chapter 3). The warm season was represented as the number of days when soil temperature was above 10ºC. The relatively high threshold (cf. 0°C, Weaver 1994) was used because sites generally reached this temperature in the middle of the summer. Moist and warm season indices are intended to parallel, but not equal, the physiological threshold of species studied.

Analysis

We described the distribution of species along temperature and water gradients both categorically, by relating species responses to gradient segments, and continuously, by regressing plant cover against environmental continua (i.e. days with water stress or days with warm soils). Of the 81 species found in our plots we limited our analysis to the 59 which occurred within at least 5% of the plots.

Categorical Analysis To categorically describe species distributions, moisture and temperature gradients were divided into segments and species responses among the segments were compared. Category widths across gradients were chosen to equalize sample size among categories, and to demonstrate the full range of variation in the Washburn environment

The soil water gradient (i.e. summer days when $\Psi > -0.12$ MPa) was divided into four 8 day periods (Table 2.1). The first three categories represented dry (< 8 days, 16 sites), mesic (8-16 days, 11 sites), and wet (16-24 days, 11 sites) 'treatments'. The fourth category consisted of two wet talus sites with more than 24 days of soil water potential above (wetter than) -0.12 MPa.

The soil temperature gradient (i.e. summer days with soil temperature exceeding 10° C) was partitioned into four 20 day periods (Table 2.1). These categories represented frigid (< 20 days, 16 sites), cool (20-40 days, 10 sites), warm, (40-60 days, 12 sites) and relatively hot (> 60 days, 12 sites) 'treatments' (Table 2.1).

Species affinity to segments of the water/temperature gradients was expressed with four measures: fidelity, constancy, cover, and indicator species analysis scores (Dufrêne and Legendre 1997). Fidelity is the percentage of time that a species occurs in a particular gradient segment compared to occurrences across the entire gradient. Constancy is the percentage of samples in a category which contain the species of interest. Cover is the average percentage of ground covered by the species of interest across all samples within a category. Indicator species analysis (ISA) combines fidelity and cover to calculate indicator values (Dufrêne and Legendre 1997). *P*-values for ISA values were obtained by randomizing treatment assignments 1000 times with Monte Carlo procedures (cf. McCune and Grace 2002).

Table 2.1. Description of soil water and temperature categories

Name of treatment		Range of days in gradient		Number of sites (n=40 total)	
Moisture	Temperature	Moist.[1]	Temp.[2]	Moist.	Temp.
D = Dry	F = Frigid	<8	<20	16	6
M = Mesic	C = Cold	≥8 & <16	≥20 & <40	11	10
W = Wet	W = Warm	≥16 & <24	≥40 & <60	11	12
WT = Wet talus	H = Hot	≥24	≥60	2	12

[1] Number of summer days (Julian day 175-235) with $\Psi > -0.12$ MPa.
[2] Number of summer days (Julian day 180-280) when soil temperature exceeded 10° C.

Non-Parametric Regression Models In addition to categorical responses we analyzed the continuous relationship between species cover and moisture/ temperature gradients using nonparametric regression (NPR). Our NPR models used a local mean estimator within a Gaussian-weighted kernel window (Bowman and Azzalani 1997, pg. 49). While not a direct measure of gradient specificity, the width of an optimal kernel window (OKW) allows some measure of the preference of a species for particular portions of a gradient (McCune 2004). This is true since a narrow kernel window is optimal for modeling rapid response changes. Thus, for unimodal shaped responses, a small OKW indicates that the species responds markedly to a specific portion of a gradient (i.e. has a narrow tolerance range), while a large OKW suggest that the species is a generalist and/or is unaffected by the range of gradient values.

Soil water and temperature NPR regressions were created for all 59 species using 100 evenly placed steps across the expalantory gradient. At each step kernel widths were tested in intervals of 5% of the total data range in an automated procedure to find optimal tolerance (McCune 2004). Intervals narrower than 5% resulted in overfitted curves that poorly described general distribution patterns. A single optimum kernel width was fixed for all windows across the gradient. This approach allows a better estimate of spread around an optimum (i.e. tolerance) than adaptive kernel models (Scott 1992). To protect against estimating a response in a region of the predictor space with insufficient data, 5% of predictor data was required for each response estimate.

We measured NPR model adequacy using the "cross-r^2" statistic which evaluates the size of the residual sum of squares (RSS) with respect to the total sum of squares (TSS) (Eq. 2.1; Antoine and McCune 2004). Because the calculation incorporates a cross-validation procedure, the cross-r^2 statistic differs from a traditional r^2 since RSS may be greater than TSS, allowing negative values to occur.

$$crossR^2 = 1 - \frac{RSS}{TSS} = 1 - \frac{\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}{\sum_{i=1}^{n}(y_i - \bar{y}_i)^2} \qquad (2.1)$$

where $\hat{y}_i$ = the fitted value for the model, and y_i = is the observed value.

Software NPR models were created using the program Hyperniche (McCune 2004). All other statistical analyses were conducted in R (R core development team 2005) using base and labdsv (Roberts 2005) libraries.

Results

Categorical Analysis

An ordered table of species responses by category can be used to show variations in distribution along the water and temperature gradients with some species preferring intermediate conditions, some preferring extreme conditions, and still others appearing multimodal or indiscriminant (Braun-Blanquet 1964). To demonstrate this we tabled species fidelity, constancy, cover and indicator score *p*-values against soil water availability (Table 2.2) and soil temperature (Table 2.3). We ordered species so that those indicating dry conditions were in the upper rows of Table 2.2 while those indicating wet conditions were at the bottom. Similarly, species are listed by preference for cold to hot conditions in Table 2.3. The sorting was done with respect to fidelity using a program written in the R language (SORTID; Appendix A.1).

Forty-three of the fifty-nine species studied were significant ISA indicators of a moisture treatment. Sixteen indicated dry conditions (D); six indicated mesic conditions (M); twenty indicated wet conditions (W); and one species indicated the wet talus (WT) treatment (Table 2.2). One species, *Phlox pulvinata,* occurred in sites at the transition between dry and mesic treatments and was a significant indicator of both conditions (Table 2.2; Appendix A.2).

Forty-five species were ISA significant indicators of temperature. Twenty-two species were indicators of frigid (F) conditions; fourteen indicated cold (C) conditions; six species indicated of warm (W) conditions; and three species indicated hot (H) conditions (Table 2.3). Two species were significant indicators of two temperature treatments. *Potentilla diversifolia* and *Luzula spicata* occurred mostly at the transition between frigid and cold treatments and indicated both conditions (Table 2.3; Appendix A.3).

NPR Modeling

Species response curves were generally unimodal in shape (cf. Whittaker 1956), but occasionally displayed multiple modes or essentially flat responses (Appendix A.2, 2.C). While cross-r^2 values were generally low (Tables 2.2, 2.3), NPR moisture and temperature models seem to adequately describe distributions for the 59 species studied. The strength of inference in NPR models is demonstrated by a high level of agreement with categorical results; i.e. NPR peaks were in accordance with maximum categorical responses (Table 2.4, Fig. 2.1). Fidelity, constancy and cover were also highly correlated with each other (Table 2.5).

Discussion

Indicators of Soil Water

We identified species indicating short to long durations of available water in surface soils. Recall that our season length classes were based on the number of days when topsoil water potential was below -0.12 MPa from Julian day 175 to 235; dry (<8 days), mesic (8-16 days), wet (16-24 days), and wet talus (>24 days). The periods measured probably represent the actual conditions experienced by shallow rooted plants, such as graminoids. On the same sites taprooted plants, those drawing water from deeper horizons, may have longer growing seasons.

Dry Indicators The driest alpine locations on Mt. Washburn occur on snow-free and densely vegetated north-facing slopes, rocky south facing slopes, and ridgetops. These environments are dry for different reasons. South facing slopes and ridgetops receive less water (are wind-swept) and lose more water due to higher radiation driven evaporation (Chapter 3). In contrast, short periods of moisture availability on densely vegetated north-facing lee slopes is probably due to desiccation of topsoil by the plants themselves, since these sites are initially well watered by wind deposited snow (cf. Körner 2003, pg. 132).

Dry site indicators on turf include *Besseya wyomingensis, Carex elynoides, Carex obtusata, Oxytropis lagopus, Poa cusickii* and *Poa rupicola.* On south slopes and ridgetops dry indicators include: *Eriogonum ovalifolium,* and *Oxytropis borealis.* Species growing at both locations include *Erigeron rydbergii, Potentilla ovina, Selaginella densa,* and *Smelowskia calycina* (Table 2.2).

Mesic Indicators Several species perform best at intermediate soil water conditions. These included *Antennaria microphylla, Draba incerta, Erigeron compositus, Poa pattersonii,* and *Senecio canus* (Table 2.2). These species either do not physiologically tolerate relatively extreme conditions and/or have a competitive advantage at intermediate positions on the water gradient.

Wet Indicators Wet sites on Washburn occur under or near late melting snowbanks and in talus areas. While snowbank sites dried by autumn talus sites generally did not, suggesting that plants that occupy talus are limited by other factors, e.g. substrate instability, lack of surface soil, or lack of nutrients (cf. Körner 2003).

Wet indicators at snowbank sites included: *Achillea millefolium, Agoseris glauca, Androsace septentrionalis, Antennaria media, Artemisia scopulorum, Aster alpigenus, Aster foliaceus* var. *apricus, Carex paysonis, Carex phaeocephala, Draba crassifolia, Epilobium anagallidifolium, Erigeron simplex, Lewisia pygmaea, Pedicularis cystopteridifolia, Penstemon procerus, Polygonum bistortoides, Salix arctica, Sibbaldia procumbens, Stellaria monantha,* and *Veronica wormskjoldii* (Table 2.2). Wet talus indicators included *Elymus scribneri*. *Ranunculus eschscholtzii* commonly occurred on both snowmelt and wet talus sites (Table 2.2).

Euryhydric Species and Species with Multiple Modes Several species had broad tolerances and appeared with equal abundance across the gradient (Table 2.2). These include *Festuca brachyphylla, Luzula spicata, Myosotis alpestris, Poa alpina*, and *Potentilla diversifolia*. Still other species appeared to have well multiple separated optima across the water gradient. These included: *Lomatium cous*, *Phlox multiflora*, and *Trisetum spicatum* (Table 2.2).

Indicators of Soil Temperature

We also identified species associated with short and long warm temperature seasons; i.e. the number of days when soil temperature is above 10ºC between Julian days 180 and 280. Recall that our temperature classes were frigid (< 20 days), cool (20-40 days), warm (40-60 days) and relatively hot (> 60 days). Because of the depth of sensors (15 cm), the temperature index should be well correlated with the actual growing season of shallow rooted graminoids.

Low Temperature Indicators Coldest soils were at north-facing areas, particularly late snowmelt sites. These areas were kept cold by low incident radiation and meltwater from snowbanks. Indicators included *Artemisia scopulorum, Aster alpigenus, Carex paysonis, Carex phaeocephala, Erigeron simplex, Mertensia alpina, Pedicularis cystopteridifolia, Penstemon procerus, Potentilla diversifolia, Saxifraga rhomboidea, Sibbaldia procumbens, Stellaria monantha,* and *Veronica wormskjoldii* (Table 2.3). Note that while annuals *Androsace septentrionalis* and *Draba crassifolia* appear to be low temperature (and wet soil) indicators (Tables 2.2, 2.3), both species grow in diverse sites below the alpine, and may favor snowbank locations because regular disturbance from snowmelt increases available microsites for seed bank germination, and decreases density dependent competition (Reynolds 1984).

Intermediate Temperature Indicators Many species performed best near the center of the temperature gradient (i.e. C and W treatments). Cooler intermediate temperature indicators included *Achillea millefolium, Agoseris glauca, Arenaria congesta, Myosotis alpestris,* and *Poa rupicola*. Warmer intermediate temperature indicators included *Astragalus kentrophyta, Erigeron rydbergii, Eriogonum ovalifolium, Oxytropis lagopus, Selaginella densa* and *Smelowskia calycina*.

High Temperature Indicators Warmest soils on Washburn occurred on ridgetops (with early/long exposure to radiation) and under steep south facing talus (with high levels of radiation). For ridgetops higher soil temperatures may be misleading since, relative to other sites, the leaf surface temperatures may be significantly lowered by high winds (Geiger et al. 2003, Körner 2003). Warm site indicators on ridgetops were often prostrate/cushion plants e.g. *Draba incerta, Erigeron compositus,* and *Lomatium cous.* More upright plant indicated often warm talus e.g. *Elymus scribneri, Poa pattersonii,* and *Senecio canus* (Table 2.3). Differences in physiognomy are surely due to presence/lack of wind in these environments, rather than temperature differences.

Eurythermic Species, and Species with Multiple Modes Several species had particularly broad tolerances and appeared largely unaffected by the temperature gradient. These included: *Arenaria obtusiloba, Carex elynoides, Carex obtusata, Cerastium arvense, Phlox pulvinata, Polemonium viscosum, Potentilla ovina, Sedum lanceolatum*, and *Trisetum spicatum* (Table 2.3). Still other species appeared to have well separated multiple modes. These included *Lomatium cous* and *Phlox multiflora,* which also had multiple modes along the moisture gradient, along with *Poa rupicola, Cerastium arvense, Carex elynoides*, and *Lupinus argenteus* (Appendix A.3, Table 2.3).

Interactions Between Water and Temperature Gradients

Site moisture and temperature were unassociated at the study site ($r^2 = 0.023$, $p = 0.349$; Chapter 3). As a result distributions of most species were generally explained by one factor, rather than both. Exceptions mostly include wet/cold (snowmelt) indicators. This is true because only late melt specialists are tolerant of both very short growing seasons, and the low temperatures (meltwater soils) of late summer (Billings and Bliss 1959, Billings 2000).

Application

Ecologists have often compared communities/ecosystems with respect to qualitative measures of water/temperature hypothesized to control their composition, structure, and function (e.g. Holdridge 1947). Quantitative analyses include moisture calibration for a number of alpine species in the Colorado Rockies (e.g. Ehleringer and Miller 1975, Isard 1986, Walker et al. 1994, Humpheries et al. 1996). Our work provides similarly useful environmental information for alpine communities in the North-Central Rocky Mountains.

To describe the water and temperature environment at a site one can list indicators present and note the environmental conditions they predict (Tables 2.2, 2.3). If dissenting species are present, one should comment on within-plot variability (if any) which may account for their co-occurrence. Multiple concurring indicators and an absence of dissenters may allow general site description without quantitative temperature or moisture sampling.

Alternatively, if one wants a more formal description of the environment of a site, one may assign a numeric indicator value to each species according to the location of its optimum on the water/temperature gradients. The assignment might be on the basis of presence/absence measure (e.g. fidelity) or a composite indicator (e.g. ISA, which combines fidelity and cover). To illustrate, we provide Table 2.6 which assigns environmental category values (EC) to species depending on which water or temperature category their maximum ISA scores occurred in. For water categories, D = 0, M = .5, and W = 1, for temperature categories F = 0, C = .0.25, W = 0.75, H = 1. Note that in our example the WT water category was dropped since it is poorly represented.

Using the EC values, indicator values averaged across species (providing a composite environmental description) and their standard errors (which measure of indicator concurrence) are easily calculated. Note that abundance (cover) responses can also be taken into consideration by weighting species EC values by their recorded abundance at a site of interest (cf. Ellenberg 1979, Jongman et al. 1995, Eq. 2.2).

$$Wght.Avg = (EC_1 y_1 + EC_2 y_2 + ... + EC_m y_m)/(y_1 + y_2 + ... + y_m) \qquad (2.2)$$

Where $y_1, y_2, ..., y_m$ are abundance responses of species 1…*m* at a site of interest

<u>Considerations</u>

Using our strategy one prefers narrower tolerance indicator species to species with broader tolerances or multimodal distributions. To account for this, species whose optimal kernel width (OKW) is greater than two standard deviations above a standardized mean (i.e. *z*-score > 2), whose ISA *p*-values are greater than 0.2, and/or whose distributions appear multimodal, are noted in Table 2.6.

The absence of an indicator species provides little information about the environment of a site since this may be due to conditions such as inadequate dispersal or removal by a predator/pathogen. In contrast, while environmental quality may be indicated by the presence of one species (Klinka et al. 1989), our confidence rises with the presence of several concurring indicators (Odum 1971). Thus, for confident environmental description, we recommend that several concurring indicators (≥ 3) be present. Similarly, in the characterization of a community rather than a site, one should limit indicator species used to those with high constancy (e.g. >30%) to insure against false indications of accidental "ephemeral" species.

Because the range of most of the indicator species is wide (in some cases circumboreal or circumpolar; Table 2.6) it should be possible to evaluate conditions at widely separated locations in the Northern Rockies. Such application gives rise to concerns about the confounding effects of ecotypes. The similarity in temperatures of widely separated alpine sites (Weaver 1990) offers the hope that differentiation of regional temperature ecotypes is slight. Differences in summer rainfall patterns between Colorado, Southern Montana, and Canada (Walter et. al 1975) could generate races with variable amounts of drought tolerance within the North-Central Rockies. If so, a drought resistant ecotype calibrated in the Greater Yellowstone Ecosystem north might suggest drier than actual conditions in the south.

Table 2.2. Species distributions on a soil water gradient (i.e. number of days between Julian Day 175-235 with $\Psi > -0.12$ MPa), as shown by categorical and NPR analyses. Categories are D = dry (< 8 days), M = mesic ($8 \leq$ days < 16), W = wet ($16 \leq$ days < 24), WT = wet talus (> 24 days). Species are sorted from 'hydrophobic to hydrophilic' with respect to fidelity using the function SORTID (Appendix A.1). Maximum ISA categories for each species are indicated with shaded cells.

		Fidelity (%)[1]				Constancy (%)[2]				Cover (%)[3]				ISA *p*-values[4]				NPR models[5]		
		D	M	W	WT	D	M	W	WT	D	M	W	WT	D	M	W	WT	Mx rsp[6]	OKW[7]	Xr.sq[8]
Dry	*Oxytropis borealis**	100	0	0	0	25	0	0	0	1.1	0	0	0	<0.01	.	.	.	7.4	1.6	-0.02
	*Carex elynoides**	86	14	0	0	75	18	0	0	5.9	2.1	0	0	<0.01	.	.	.	7.1	1.6	0.12
	*Selaginella densa**	78	22	0	0	88	36	0	0	9.6	7.9	0	0	<0.01	0.98	.	.	6.1	1.6	0.13
	*Oxytropis lagopus**	70	30	0	0	44	27	0	0	1.1	0.2	0	0	0.01	.	.	.	6.1	1.6	0.14
	Carex obtusata	69	31	0	0	56	36	0	0	2	4.7	0	0	0.28	0.21	.	.	11.8	3.2	0.01
	*Potentilla ovina**	75	17	8	0	56	18	9	0	1.7	0.6	+	0	<0.01	.	.	.	6.1	1.6	0.04
	*Smelowskia calycina**	62	38	0	0	50	45	0	0	0.8	0.5	0	0	0.04	0.41	.	.	6.1	3.2	0.04
	*Poa rupicola**	67	25	8	0	100	55	18	0	8	1.8	+	0	<0.01	.	.	.	6.7	1.6	0.20
	*Erigeron rydbergii**	57	43	0	0	50	55	0	0	1.9	1.2	0	0	0.05	0.29	.	.	6.1	1.6	0.10
	*Eriogonum ovalifolium**	71	14	14	0	31	9	9	0	0.3	+	+	0	0.02	.	.	.	6.1	1.6	0.05
	*Poa cusickii**	62	19	19	0	62	27	27	0	1.5	0.2	0.2	0	<0.01	.	.	.	6.1	1.6	0.04
	*Besseya wyomingensis**	64	14	21	0	56	18	27	0	1.1	0.3	0.2	0	0.01	.	.	.	7.4	1.6	0.02
	Astragalus kentrophyta	42	58	0	0	31	64	0	0	2	0.9	0	0	0.29	0.25	.	.	6.1	1.6	0.01
	*Astragalus alpinus**	59	24	18	0	62	36	27	0	2.1	1.3	+	0	0.02	.	.	.	10.5	3.2	0.04
	*Phlox pulvinata**	52	39	4	4	75	82	9	50	5.1	5	0.1	0.2	0.03	0.04	.	.	6.1	3.2	0.19
	*Senecio canus**	38	62	0	0	19	45	0	0	0.4	0.8	0	0	.	0.01	.	.	12.4	3.2	-0.03
	Lomatium cous†*	55	30	5	10	69	55	9	100	1.8	0.6	+	0.8	<0.01	.	.	0.50	6.1	4.7	0.03
	Polemonium viscosum	50	29	21	0	44	36	27	0	2.6	1.1	+	0	0.09	.	.	.	8.0	1.6	0.00
	Mertensia alpina	46	31	23	0	38	36	27	0	2.3	0.4	0.4	0	0.11	.	.	.	6.1	7.9	-0.05
	All moss (mostly *T. ruralis*)*	48	26	26	0	69	55	55	0	3.4	1.2	1.5	0	0.16	.	.	.	6.1	25.2	-0.05
	Arenaria obtusiloba	45	30	24	0	94	91	73	0	3.4	3.7	0.9	0	0.06	0.12	.	.	13.1	1.6	0.16
	*Sedum lanceolatum**	45	30	24	0	94	91	73	0	2.1	1.7	0.2	0	0.01	0.42	.	.	13.1	1.6	0.13
	Saxifraga rhomboidea	50	20	30	0	31	18	27	0	0.4	0.1	0.2	0	0.32	.	0.90	.	6.1	25.2	-0.06
	*Poa pattersonii**	36	43	21	0	31	55	27	0	0.5	2.1	0.3	0	.	0.01	.	.	12.7	3.2	-0.01
	Potentilla diversifolia	46	21	33	0	69	45	73	0	6	2.8	5.8	0	0.25	.	0.27	.	24.4	7.9	-0.05
	Festuca brachyphylla	38	33	29	0	56	73	64	0	1	0.6	1.4	0	.	.	0.32	.	24.4	7.9	-0.06
	Phlox multiflora†	42	25	33	0	31	27	36	0	0.5	0.8	0.4	0	.	0.74	.	.	13.1	1.6	0.02
	*Cerastium arvense**	42	28	28	3	94	91	91	50	6.8	3	1.9	1.1	0.01	.	.	.	6.1	4.7	0.01
	Lupinus argenteus	47	12	41	0	50	18	64	0	2	2.2	3.6	0	.	.	0.09	.	26.9	4.7	-0.04
	Luzula spicata	41	23	36	0	56	45	73	0	1.4	1.1	0.9	0	0.53	.	0.67	.	6.1	25.2	-0.05
Mesic	*Myosotis alpestris*	43	29	14	14	19	18	9	50	+	1.6	+	0.2	.	0.51	.	.	13.1	1.6	0.20
	*Antennaria microphylla**	0	100	0	0	0	27	0	0	0	0.4	0	0	.	<0.01	.	.	12.4	3.2	-0.05
	*Draba incerta**	0	100	0	0	0	27	0	0	0	+	0	0	.	<0.01	.	.	12.7	3.2	-0.04
	*Erigeron compositus**	27	53	13	7	25	73	18	50	0.5	0.6	+	+	.	0.03	.	.	6.1	4.7	-0.01
	Arenaria congesta†	33	33	33	0	12	18	18	0	+	0.6	0.2	0	.	0.38	.	.	24.7	1.6	-0.04

Table 2.2. cont.

		Fidelity (%)[1]				Constancy (%)[2]				Cover (%)[3]				ISA *p*-values[4]				NPR models[5]		
		D	M	W	WT	D	M	W	WT	D	M	W	WT	D	M	W	WT	Mx rsp[6]	OKW[7]	Xr.sq[8]
Mesic ↑	*Trisetum spicatum*	29	36	29	7	25	45	36	50	0.4	1.2	0.3	0.2	.	0.11	.	.	13.1	1.6	0.13
	Agoseris glauca *	40	0	60	0	25	0	55	0	0.3	0	0.8	0	.	.	<0.01	.	27.9	4.7	0.02
	*Achillea millefolium**	21	37	42	0	25	64	73	0	0.8	1.5	2.5	0	.	0.42	0.03	.	26.0	7.9	-0.02
	*Androsace septentrionalis**	33	0	67	0	12	0	36	0	+	0	0.1	0	.	.	0.03	.	26.6	6.3	-0.04
	*Polygonum bistortoides**	23	15	62	0	19	18	73	0	0.2	0.6	1.7	0	.	.	<0.01	.	24.7	4.7	0.06
	Poa alpina	20	30	40	10	12	27	36	50	0.1	0.3	0.3	0.2	.	0.63	0.36	0.88	37.7	25.2	-0.05
	*Elymus scribneri**	9	45	27	18	6	45	27	100	+	0.5	0.7	1.2	.	0.25	0.51	0.04	16.8	3.2	-0.03
	*Penstemon procerus**	11	22	67	0	6	18	55	0	+	0.1	0.7	0	.	.	<0.01	.	26.6	6.3	0.06
	*Carex paysonis**	9	18	73	0	6	18	73	0	+	+	27.5	0	.	.	<0.01	.	26.6	3.2	0.51
	*Artemisia scopulorum**	17	0	83	0	6	0	45	0	+	0	1.7	0	.	.	<0.01	.	26.9	6.3	0.07
	*Stellaria monantha**	11	11	78	0	6	9	64	0	+	+	0.5	0	.	.	<0.01	.	26.6	4.7	0.30
	*Carex phaeocephala**	0	12	88	0	0	9	64	0	0	0.3	1.1	0	.	.	<0.01	.	22.5	1.6	0.32
	*Antennaria media**	0	0	100	0	0	0	36	0	0	0	0.3	0	.	.	<0.01	.	27.2	6.3	0.05
	*Aster alpigenus**	0	0	100	0	0	0	36	0	0	0	0.5	0	.	.	<0.01	.	24.7	6.3	0.03
	*Aster foliaceus v. apricus**	0	0	100	0	0	0	36	0	0	0	1.9	0	.	.	<0.01	.	27.9	4.7	0.14
	*Draba crassifolia**	0	0	100	0	0	0	36	0	0	0	+	0	.	.	<0.01	.	23.1	1.6	0.43
	*Epilobium anagallidifolium**	0	0	100	0	0	0	36	0	0	0	0.2	0	.	.	<0.01	.	18.4	1.6	0.21
	*Erigeron simplex**	0	0	100	0	0	0	73	0	0	0	1.4	0	.	.	<0.01	.	24.1	4.7	0.23
	*Lewisia pygmaea**	0	0	100	0	0	0	36	0	0	0	+	0	.	.	<0.01	.	18.7	1.6	0.06
	Pedicularis	0	0	100	0	0	0	27	0	0	0	+	0	.	.	0.02	.	17.8	3.2	0.08
	*Salix arctica**	0	0	100	0	0	0	27	0	0	0	0.7	0	.	.	<0.01	.	24.7	1.6	0.35
	*Sibbaldia procumbens**	0	0	100	0	0	0	45	0	0	0	2.6	0	.	.	<0.01	.	17.8	3.2	0.07
	*Veronica wormskjoldii**	0	0	100	0	0	0	27	0	0	0	0.7	0	.	.	0.01	.	17.8	3.2	0.00
Wet ↓	*Ranunculus eschscholtzii*	0	0	67	33	0	0	18	50	0	0	+	0.2	.	.	0.06	0.06	37.7	15.8	-0.04
		Avg. Fidelity (%)				Avg. Constancy (%)				Ttl. Cover (%)				No. of significant indicators				NPR averages		
		D	M	W	WT	D	M	W	WT	D	M	W	WT	D	M	W	WT	Mx rsp	OKW	Xr.sq
		34	23	41	2	32	29	33	9	82	57	65	4.1	16	6	20	1	16.0	5.1	0.07

[1] Fidelity is the percentage of time that a species occurs in a particular gradient segment compared to occurrences across the entire gradient. [2] Constancy is the proportion of samples in a segment which are occupied by the species. [3] Cover is the average cover of the species on samples within the gradient segment. Cover values > 0% but ≤ 0.1% are denoted with a "+". [4] ISA combines fidelity and cover. ISA *p*-values indicate the probability of randomly obtaining an indicator score as high as the one observed over 1000 iterations. ISA *p*-values for each species were calculated as one treatment vs. the other three combined treatments. Thus it is possible for a species to be a significant indicator of more than one treatment. If a species was a better indicator of the other three combined treatments than the tested treatment, its *p*-value is not included above. An asterisk "*" indicates that the species significantly ($p \leq 0.05$) indicates at least one water category. [5] NPR models the association between species cover and environmental continua. [6] The number of days with soil water potential > -0.12 MPa when maximum cover occurred (i.e. higher number = greater preference for wet soils). [7] Optimal kernel width (OKW) describes tolerance. Smaller OKWs = narrower tolerance; this interpretation is not valid for multimodal species indicated with †. [8] See methods for cross-r^2 explanation.

Table 2.3. Species distributions on a soil temperature gradient (i.e. number of days between Julian Day 180-280 with soil temperature > 10ºC), as shown by categorical and NPR analyses. Categories are F = frigid (< 20 days), C = cold (20 ≤ days < 40), W = warm (40 ≤ days < 60), and H= relatively hot (> 60 days). Species sorted from frigid to hot soil preference with respect to fidelity using the function SORTID (Appendix A.1). Maximum ISA categories for each species are indicated with shaded cells.

		Fidelity (%)[1]				Constancy (%)[2]				Cover (%)[3]				ISA *p*-values[4]				NPR models[5]		
		F	C	W	H	F	C	W	H	F	C	W	H	F	C	W	H	Mx rsp[2]	OKW[3]	Xr.sq[4]
	*Artemisia scopulorum**	83	17	0	0	83	10	0	0	3.1	+	0	0	<0.01	.	.	.	0.0	15.6	0.30
	*Draba crassifolia**	75	25	0	0	50	10	0	0	+	+	0	0	<0.01	1.00	.	.	0.0	23.4	0.09
	*Veronica wormskjoldii**	67	33	0	0	33	10	0	0	1.2	+	0	0	0.02	.	.	.	0.0	23.4	0.06
	*Androsace septentrionalis**	67	17	17	0	67	10	8	0	0.2	+	+	0	<0.01	.	.	.	0.0	19.5	0.07
Frigid	*Aster alpigenus**	50	50	0	0	33	20	0	0	0.6	0.1	0	0	0.02	0.57	.	.	0.0	23.4	0.04
	*Carex phaeocephala**	50	38	12	0	67	30	8	0	1.5	0.5	+	0	<0.01	0.44	.	.	0.0	23.4	0.07
↑	*Pedicularis cystopteridifolia**	67	0	33	0	33	0	8	0	+	0	+	0	0.03	.	0.70	.	0.0	43.0	-0.04
	*Salix arctica**	33	67	0	0	17	20	0	0	0.2	0.7	0	0	1.00	0.05	.	.	21.1	7.8	-0.01
	*Erigeron simplex**	50	25	25	0	67	20	17	0	2.1	+	0.1	0	<0.01	.	.	.	0.0	15.6	0.36
	*Penstemon procerus**	33	44	22	0	50	40	17	0	0.6	0.4	0.2	0	0.05	0.14	.	.	0.0	35.1	-0.02
	*Stellaria monantha**	44	33	11	11	67	30	8	8	0.7	0.1	+	+	<0.01	0.83	.	.	0.0	15.6	0.27
	*Saxifraga rhomboidea**	40	40	10	10	67	40	8	8	1.2	0.2	+	+	<0.01	0.64	.	.	0.0	15.6	0.25
	*Mertensia alpina**	38	38	15	8	83	50	17	8	2.1	1	0.4	1.6	<0.01	0.57	.	.	0.0	62.5	-0.06
	Antennaria media	25	50	25	0	17	20	8	0	0.1	0.1	+	0	0.71	0.16	.	.	0.0	43.0	-0.04
	*Epilobium anagallidifolium**	50	0	50	0	33	0	17	0	0.3	0	+	0	0.03	.	0.47	.	0.0	31.2	-0.02
	*Sibbaldia procumbens**	40	20	40	0	33	10	17	0	4.2	+	0.3	0	0.03	.	.	.	0.0	23.4	0.05
	*Carex paysonis**	45	18	27	9	83	20	25	8	26.3	6	7.1	+	<0.01	.	.	.	0.0	19.5	0.15
	*Polygonum bistortoides**	38	31	23	8	83	40	25	8	2.7	0.8	0.3	0.1	<0.01	0.62	.	.	0.0	15.6	0.21
	*Poa alpina**	30	50	0	20	50	50	0	17	0.5	0.6	0	0.1	0.08	0.02	.	.	0.0	23.4	0.01
	*Potentilla diversifolia**	25	42	25	8	100	100	50	17	8.2	7.8	3.5	1.9	0.02	<0.01	.	.	0.0	15.6	0.06
	*Astragalus alpinus**	24	47	18	12	67	80	25	17	1.4	3.1	0.3	0.5	0.34	<0.01	.	.	21.9	7.8	0.04
	*Lupinus argenteus**	35	24	29	12	100	40	42	17	5.5	3.4	2.1	0.2	<0.01	0.68	.	.	0.0	3.9†	0.09
	All moss (mostly *T. ruralis*)*	26	35	30	9	100	80	58	17	10.3	1.3	0.7	+	<0.01	.	.	.	0.0	19.5	0.16
	Lewisia pygmaea	25	25	50	0	17	10	17	0	+	+	+	0	0.22	.	0.36	.	0.0	62.5	-0.05
	*Luzula spicata**	27	36	18	18	100	80	33	33	1.8	1.9	0.4	0.9	0.03	0.04	.	.	0.0	27.3	-0.04
	*Besseya wyomingensis**	14	50	29	7	33	70	33	8	0.7	1.5	0.4	+	0.95	<0.01	.	.	35.9	3.9	0.19
	*Arenaria congesta**	0	67	33	0	0	40	17	0	0	0.8	+	0	.	<0.01	.	.	37.5	3.9	0.05
	Agoseris glauca *	20	40	20	20	33	40	17	17	+	0.8	0.2	0.2	.	0.03	.	.	23.4	11.7	0.01
↓	*Carex elynoides**	14	43	29	14	33	60	33	17	5.9	5.9	1.8	+	0.61	0.03	.	.	36.7	3.9†	0.10
	*Oxytropis borealis**	50	0	0	50	33	0	0	17	1.8	0	0	0.6	<0.01	.	.	0.50	0.0	23.4	-0.04
Cold	*Trisetum spicatum*	29	21	21	29	67	30	25	33	1.3	0.6	0.1	0.7	0.06	.	.	0.85	78.1	3.9	0.02
	Aster foliaceus v. apricus	0	50	50	0	0	20	17	0	0	1.4	0.5	0	.	0.06	0.54	.	24.2	15.6	0.00
	*Poa cusickii**	12	25	56	6	33	40	75	8	0.5	0.5	1.8	+	.	.	<0.01	.	42.2	3.9	0.02
	Potentilla ovina	17	25	42	17	33	30	42	17	1.8	1.3	0.8	0.1	0.58	0.62	0.66	.	0.0	46.9	-0.05
	*Cerastium arvense**	17	28	33	22	100	100	100	67	3.8	8.6	2.1	2.7	0.86	<0.01	.	.	35.1	3.9†	0.21

Table 2.3. cont.

		Fidelity (%)^1				Constancy (%)^2				Cover (%)^3				ISA p-values^4				NPR models^5		
		F	C	W	H	F	C	W	H	F	C	W	H	F	C	W	H	Mx rsp^2	OKW^3	Xr.sq^4
Warm ↑	*Poa rupicola**†	12	33	38	17	50	80	75	33	2.9	7.2	2.3	2.5	.	0.01	.	.	34.4	3.9	0.04
	Carex obtusata	15	31	31	23	33	40	33	25	0.5	5.2	1.7	0.7	.	0.16	.	.	25.8	15.6	-0.04
	*Achillea millefolium**	16	37	16	32	50	70	25	50	0.9	3	1	0.8	.	0.02	.	.	24.2	11.7	0.04
	Arenaria obtusiloba	18	24	33	24	100	80	92	67	1.6	3.7	2.9	2	.	0.41	0.41	.	78.1	62.5	-0.06
	Polemonium viscosum	21	21	29	29	50	30	33	33	3.6	0.9	0.3	1.6	0.13	.	.	0.88	0.0	62.5	-0.06
	*Ranunculus eschscholtzii**	33	0	33	33	17	0	8	8	0.1	0	+	+	0.05	.	.	.	0.0	62.5	-0.05
	Sedum lanceolatum	12	30	33	24	67	100	92	67	+	1.9	2	0.9	.	0.12	0.16	.	31.2	11.7	0.04
	Festuca brachyphylla	17	25	29	29	67	60	58	58	2.4	0.6	0.6	0.9	0.15	.	.	.	0.0	19.5	0.01
	*Myosotis alpestris**	0	57	14	29	0	40	8	17	0	1.8	+	+	.	0.01	.	.	25.8	3.9	0.18
	*Selaginella densa**	6	33	44	17	17	60	67	25	+	6.1	12	3	.	0.49	0.01	.	53.1	3.9	0.40
	*Erigeron rydbergii**	0	36	50	14	0	50	58	17	0	0.9	2.3	0.7	.	0.74	<0.01	.	54.7	3.9	0.10
	Phlox pulvinata	9	26	39	26	33	60	75	50	3.5	5.4	4.2	1.1	.	0.36	0.17	.	0.0	54.7	-0.05
	*Phlox multiflora**†	0	50	17	33	0	60	17	33	0	1.3	+	0.7	.	<0.01	.	0.60	25.8	3.9	0.26
	*Smelowskia calycina**	8	15	46	31	17	20	50	33	+	0.1	1.1	0.3	.	.	0.03	.	42.2	3.9	0.04
	Eriogonum ovalifolium	0	29	43	29	0	20	25	17	0	+	0.4	+	.	.	0.13	.	55.5	3.9	0.18
	*Oxytropis lagopus**	0	10	70	20	0	10	58	17	0	0.2	1.3	0.2	.	.	<0.01	.	55.5	3.9	0.12
	Lomatium cous†	0	30	25	45	0	60	42	75	0	1.7	0.3	1.4	.	0.18	.	0.06	78.1	3.9	0.02
	*Poa pattersonii**	7	14	36	43	17	20	42	50	+	0.1	0.6	2.1	.	.	.	0.04	78.1	7.8	0.23
	*Astragalus kentrophyta**	0	17	50	33	0	20	50	33	0	0.3	2.8	0.4	.	.	<0.01	.	42.2	3.9	0.01
	Erigeron compositus	0	20	33	47	0	30	42	58	0	0.4	0.3	0.7	.	.	.	0.06	78.1	7.8	0.01
	Antennaria microphylla	0	33	0	67	0	10	0	17	0	0.2	0	0.2	.	0.83	.	0.22	78.1	62.5	-0.06
	Senecio canus	0	12	38	50	0	10	25	33	0	+	0.4	0.8	.	.	0.62	0.10	78.1	7.8	0.09
	*Elymus scribneri**	0	0	36	64	0	0	33	58	0	0	0.5	0.9	.	.	0.66	<0.01	64.8	3.9	0.10
↓ Hot	*Draba incerta**	0	0	33	67	0	0	8	17	0	0	+	+	.	.	.	0.03	78.1	23.4	-0.03

	Avg. Fidelity (%)				Avg. Constancy (%)				Ttl. Cover (%)				No. of significant indicators				NPR averages		
	F	C	W	H	F	C	W	H	F	C	W	H	F	C	W	H	Mx rsp	OKW	Xr.sq
	24	29	27	22	40	37	30	21	107	91	60	32	22	14	6	3	24.4	20.2	0.07

[1] Fidelity is the percentage of time that a species occurs in a particular gradient segment compared to occurrences across the entire gradient. [2]Constancy is the proportion of samples in a segment which are occupied by the species. [3]Cover is the average cover of the species on samples within the gradient segment; cover values > 0% but ≤ 0.1% are denoted with a "+". [4]ISA combines fidelity and cover. ISA p-values indicate the probability of randomly obtaining an indicator score as high as the one observed over 1000 iterations. ISA p-values for each species were calculated as one treatment vs. the other three combined treatments. Thus it is possible for a species to be a significant indicator of more than one treatment. If a species was a better indicator of the other three combined treatments than the tested treatment, its p-value is not included above. An asterisk "*" indicates that the species significantly ($p \leq 0.05$) indicates at least one temperature category. [5]NPR models the association between species cover and environmental continua. [6] The number of days with soils warmer than 10º C when maximum species cover occurred (i.e. higher number = greater preference for warm/hot soils). [7]Optimal kernel width (OKW) describes tolerance. Smaller OKWs = narrower (more specific) tolerance; this interpretation is not valid for multimodal species indicated with †. [8]See methods for cross-r^2 explanation.

Table 2.4. Agreement of NPR maximum responses[1] with categorical response maxima across 59 species. That is, the percent of time NPR maxima (e.g. high point in curve in Fig. 2.1) occurred in the same category (section of gradient) that maximum fidelity, constancy and cover responses occurred in. *P*-values for agreement of categorical responses with NPR are also indicated[2].

	Moisture		Temperature	
	%Agreement with NPR	*p*-value	%Agreement with NPR	*p*-value
Fidelity	75.9	<0.001	72.3	<0.001
Constancy	74.1	<0.001	90.9	<0.001
Cover	88.2	<0.001	83.1	<0.001
ISA score	86.2	<0.001	89.7	<0.001

[1] NPR maxima were assigned to the category whose mean value they were closest to.

[2] *P*-values are type-I errors for tests of the H_0 "The agreement of NPR models with categorical responses is no greater than expected by chance". *P*-values were obtained with a Monte-Carlo randomization of categorical assignments using 1000 iterations.

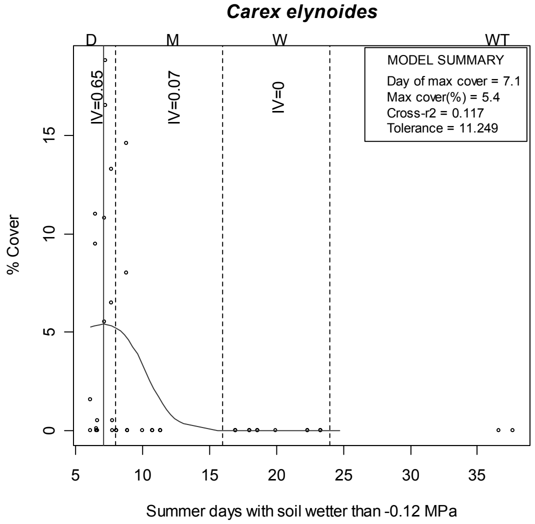

Figure 2.1. Cover response of a dry site indicator (*Carex elynoides*) to moist days ($\Psi > -0.12$ MPa) in the summer. A strong concurrence between continuous (NPR) and categorized (ISA) treatments is shown. IV = ISA scores. The vertical solid line indicates the predicted optimum number of moist days for *C. elynoides* growth. For a complete summary of all species models see Appendices 2.B and 2.C.

Table 2.5. Comparison of fidelity, constancy and cover responses of the 59 species to each other. Correlations and *p*-values are from Spearman sign rank tests. The upper triangle (light gray) contains temperature comparisons. The bottom triangle (darker gray) contains moisture comparisons.

Fidelity	$r_s = 0.68$; $p < 0.001$	$r_s = 0.60$; $p < 0.001$	$r_s = 0.79$; $p < 0.001$
$r_s = 0.86$; $p < 0.001$	Constancy	$r_s = 0.88$; $p < 0.001$	$r_s = 0.93$; $p < 0.001$
$r_s = 0.85$; $p < 0.001$	$r_s = 0.93$; $p < 0.001$	Cover	$r_s = 0.88$; $p < 0.001$
$r_s = 0.92$; $p < 0.001$	$r_s = 0.94$; $p < 0.001$	$r_s = 0.92$; $p < 0.001$	ISA score

Conclusions

Our soil moisture and temperature indices are based on a thorough analysis of one site in the North-Central Rockies using both multiple categorical criteria (i.e. fidelity, constancy, cover, and ISA analysis) which describe species affinities for segments of these gradients, and NPR regressions which describe tolerance, the specific point of peak abundance, and the number of modes. On both the water and temperature gradients, we determined species largely restricted to extreme and intermediate conditions. Most species are widespread throughout the region, and thus can be used as indicators of soil conditions on alpine sites throughout the North-Central Rocky Mountains. Our calibrated species allow description of soil temperature and moisture conditions for alpine communities described in the past, and provide complementary environmental data for future studies at sites where soil instrumentation and continuous data collection may be difficult.

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Table 2.6. Distribution information for indicator species and data for creating water and temperature index responses. Shaded cells indicate where *EC* values are questionable due to large NPR tolerances, high ISA *p*-values, and/or multimodality.

	Distrib.			Soil water			Soil temp		
	Lat. (° N)		Notes[1]	*EC*[2]	*OKWz*[3]	ISA.*p*-val	*EC*[2]	*OKWz*[3]	ISA.*p*-val
Achillea millefolium	70	30		1	0.47	0.03	0.25	-0.46	0.02
Agoseris glauca	70	30		1	-0.06	<0.01	0.25	-0.46	0.03
all Mosses (mostly *T. ruralis*)				0	3.34	0.16	0	-0.04	<0.01
Androsace septentrionalis	70	30	A	1	0.20	0.03	0	-0.04	<0.01
Antennaria media	70	30		1	0.20	<0.01	0.25	1.22	0.16
Antennaria microphylla	70	30		0.5	-0.32	<0.01	1	2.27	0.22
Arenaria congesta	60	30		0.5	-0.58†	0.38	0.25	-0.88	<0.01
Arenaria obtusiloba	70	20	A	0	-0.58	0.06	NA[4]	2.27	0.41
Artemisia scopulorum	50	30		1	0.20	<0.01	0	-0.25	<0.01
Aster alpigenus	50	30		1	0.20	<0.01	0	0.17	0.02
Aster foliaceus var. *apricus*	60	30		1	-0.06	<0.01	0.25	-0.25	0.06
Astragalus alpinus	70	40	A	0	-0.32	0.02	0.25	-0.67	<0.01
Astragalus kentrophyta	60	30		0.5	-0.58	0.25	0.75	-0.88	<0.01
Besseya wyomingensis	60	40		0	-0.58	0.01	0.25	-0.88	<0.01
Carex elynoides	50	20		0	-0.58	<0.01	0.25	-0.88†	0.03
Carex obtusata	70	20	A,R	0.5	-0.32	0.21	0.25	-0.25	0.16
Carex paysonis	60	30		1	-0.32	<0.01	0	-0.04	<0.01
Carex phaeocephala	70	20		1	-0.58	<0.01	0	0.17	<0.01
Cerastium arvense	70	20		0	-0.06	0.01	0.25	-0.88†	<0.01
Draba crassifolia	70	20	A	1	-0.58	<0.01	0	0.17	<0.01
Draba incerta	70	30	R	0.5	-0.32	<0.01	1	0.17	0.03
Elymus scribneri	55	20		1	-0.32†	0.04	1	-0.88	<0.01
Epilobium anagallidifolium	70	20		1	-0.58	<0.01	0	0.59	0.03
Erigeron compositus	70	20	A	0.5	-0.06	0.03	1	-0.67	0.06
Erigeron rydbergii	50	43	L,R	0	-0.58	0.05	0.75	-0.88	<0.01
Erigeron simplex	50	30		1	-0.06	<0.01	0	-0.25	<0.01
Eriogonum ovalifolium	60	20		0	-0.58	0.02	0.75	-0.88	0.13
Festuca brachyphylla	70	20		1	0.47	0.32	0	-0.04	0.15
Lewisia pygmaea	65	20		1	-0.58	<0.01	0.75	2.27	0.36
Lomatium cous	55	30		0	-0.06†	<0.01	1	-0.88†	0.06
Lupinus argenteus	60	20		1	-0.06	0.09	0	-0.88†	<0.01
Luzula spicata	70	20		0	3.34	0.53	0	0.38	0.03
Mertensia alpina	60	20	R	0	0.47	0.11	0	2.27	<0.01
Myosotis alpestris	70	35	A	0.5	-0.58	0.51	0.25	-0.88	0.01
Oxytropis borealis	70	20		0	-0.58	<0.01	0	0.17	<0.01
Oxytropis lagopus	50	43	L,R	0	-0.58	0.01	0.75	-0.88	<0.01
Pedicularis cystopteridifolia	48	43	L,R	1	-0.32	0.02	0	1.22	0.03
Penstemon procerus	70	20		1	0.20	<0.01	0	0.80	0.05
Phlox multiflora	50	20		0.5	-0.58†	0.74	0.25	-0.88†	<0.01
Phlox pulvinata	50	20		0.5	-0.32	0.03	0.75	1.85	0.17
Poa alpina	70	20		1	3.34	0.36	0.25	0.17	0.02
Poa cusickii	70	20		0	-0.58	<0.01	0.75	-0.88	<0.01
Poa pattersonii	70	20		0.5	-0.32	0.01	1	-0.67	0.04
Poa rupicola	70	20		0	-0.58	<0.01	0.25	-0.88†	0.01
Polemonium viscosum	60	20		0	-0.58	0.09	0	2.27	0.13
Polygonum bistortoides	60	20		1	-0.06	<0.01	0	-0.25	<0.01
Potentilla diversifolia	70	20		NA[4]	0.47	0.25	0.25	-0.25	<0.01
Potentilla ovina	65	25		0	-0.58	<0.01	0	1.43	0.58
Ranunculus eschscholtzii	70	20		1	1.77	0.06	0	2.27	0.05
Salix arctica	70	40	A	1	-0.58	<0.01	0.25	-0.67	0.05
Saxifraga rhomboidea	60	25	R	0	3.34	0.32	0	-0.25	<0.01
Sedum lanceolatum	70	20		0	-0.58	0.01	0.25	-0.46	0.12
Selaginella densa	70	20		0	-0.58	<0.01	0.75	-0.88	0.01
Senecio canus	60	25		0.5	-0.32	0.01	1	-0.67	0.1
Sibbaldia procumbens	70	20	A	1	-0.32	<0.01	0	0.17	0.03
Smelowskia calycina	70	30	A	0	-0.32	0.04	0.75	-0.88	0.03
Stellaria monantha	70	20	A	1	-0.06	<0.01	0	-0.25	<0.01
Trisetum spicatum	70	20		0.5	-0.58	0.11	0	-0.88	0.06
Veronica wormskjoldii	70	20	A	1	-0.32	0.01	0	0.17	0.02

Table 2.6 cont.

[1]Notes: L = Locally endemic to the Greater Yellowstone Ecosystem, R = not present on coastal cordilleras, A = Arctic-alpine, North American to partly or wholly circumpolar . [2]*EC* = Environmental category; for water: 0=D, 0.5=M, 1=W, for temperature: 0=F, 0.25=C, 0.75=W, 1=H. Thus *EC* numbers increase with wetter or warmer soils. [3] Tolerance *z*-score, i.e. the number of standard deviations an optimal kernel width is from a standardized mean; across all models within a gradient type. [4]ISA score tie between two categories. †=Multimodal.

Literature cited

Antoine, M. E., and B. McCune. 2004. Contrasting fundamental and realized niches with epiphytic lichen transplants in old growth *Pseudotsuga* forests. Bryologist 107: 163-173.

Billings, W. D. 2000. Alpine Vegetation of North America. pp. 537- 572. *In* North American Terrestrial Vegetation 2nd edition, Barbour, M. D. and Billings, W. D. eds. Cambridge Univ. Press, Cambridge.

Billings, W. D., and L. C. Bliss. 1959. An snowbank alpine environment and its effects on vegetation, plant development, and productivity. Ecology 40(3): 388-397.

Bowman A. W., and A. Azzalini. Applied smoothing techniques for data analysis. The kernel approach with S-plus illustrations. Clarendon Press, Oxford, UK.

Braun-Blanquet, J. 1964. Pflanzenoziologia. Grundüge der Vegetationskunde. 3. Aufl. Berlin. Wien. Springer Verlag, New York, USA.

Cooper, S. V., Lessica, P., and D. Page-Dumroese. 1997. Plant community classification for alpine vegetation on the Beaverhead National Forest, Montana. Gen. Tech. Rep. INT-GTR -362. Ogden UT: U.S. Department of Agriculture, Forest Service Intermountain Research Station. 61 pgs.

Daubenmire, R. 1959. A canopy coverage method of vegetation analysis. Northwest Science. 33: 43-64.

Dorn, R. D. 1992. Vascular Plants of Wyoming. Mountain West Publishing. Cheyenne WY.

Douglas, G. W., and L. C. Bliss. 1977. Alpine and high subalpine plant communities of the North Cascades range, Washington and British Columbia. Ecological Monographs. 47: 113-150.

Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetric approach. Ecological Monographs. 67(3): 345-367.

Ehleringer, J. R., and P. C. Miller. 1975. Water relations of selected plant species in the alpine tundra, Colorado. Ecology. 56: 370-380.

Ellenberg, H. 1979. Ziegerwerte der Gefässpflanzen Mittleeuropas. Scripta Geobotanica 9, Göttingen, 121 pgs.

Galen, C. and M. L. Stanton. Responses of snowbed species to changes in growing season length. Ecology. 76(5) 1546-1558.

Gauslaa, Y. 1984. Heat resistance and energy budget in different Scandinavian plants. Holarctic ecology. 7:1-78.

Geiger, R., R. H. Aeon & P. Todhunter. 2003. The Climate Near the Ground. 6th edition. Rowman and Littlefield. Lanham, MD., U.S.A.

Hill, M. O. 1979. TWINSPAN—A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. *Ecology and Systematics.* Cornell University, Ithaca, NY, US.

Holdridge, L. R. 1947. Determination of the world plant formations from simple climatic data. Science. 105: 367-368.

Humpheries, H., Coffin, D., and W. K. Laurenroth. 1996. An individual based model of alpine plant distributions. Ecological Modelling. 84: 99-126.

Isard, S. A. 1986. Factors influencing soil moisture and plant community distribution on Niwot Ridge, Front Range, Colorado, U.S.A. Arctic and alpine research. 18(1): 83-96.

Johnson, P. L., and W. D. Billings. 1962. The alpine vegetation of the Beartooth Plateau in relation to cryptogenic processes and patterns. Ecolog. Monogr. 32: 105-135.

Jongman, R. H. G., ter Braak, C. F. G., and O. F. R. van Tongern. 1995. Data analysis In Community and landscape ecology. Cambridge University Press. Cambridge, UK.

Klinka, K., Krajina, V. J., Ceska, A., and Am. M. Scage. 1989. Indicator species of coastal British Columbia. UBC Press Vancouver.

Komárková, V. 1979. Alpine vegetation of the Indian Peaks area, Front Range Colorado Rocky Mountains. PhD dissertation University of Colorado, Boulder. 591 pgs.

Komárková, V. 1980. Classification and ordination in the Indian Peaks area, Colorado Rocky Mountains. Vegetatio. 42: 149-163.

Körner, C. 2003. Alpine plant life: Functional plant ecology of high mountain ecosystems, 2nd edition. Springer-Verlag, Berlin. 338 pgs.

Lackschewitz, K. H. 1994. Beartooth alpine flora, pgs. 105-113. *In*: Anderson, B. (ed.) Beartooth Country: Montana’s Absaroka and Beartooth Mountains. Unicorn Publishing, Helena MT.

McCune, B. 2004. Nonparametric regression for habitat modeling http://www.pcord.com/NPMRintro.pdf.

McCune B., and J. B. Grace. 2002. Analysis of ecological communities. MJM software design, Glendale Beach, Oregon.

Oberbauer, S. F., and W. D. Billings. 1981. Drought tolerance and water use by plants along an alpine topographic gradient. Oecologia. 50: 325-331.

Odum, E. P. 1971. Fundamental of ecology. WB Saunders Company. Philidelphia, PA. USA.

R Development Core Team. 2005. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Reynolds, D. N. 1984. Populational dynamics of three annual species of alpine plants in the Rocky Mountains. Oecologia. 62: 250-255.

Roberts, D. 2005. Vegetation classification in R, for labdsv ver. 1.1-1, vegetation ecology package. http://labdsv.nr.usu.edu/tutorial.html

Scott, D. W. 1992. Multivariate density estimation. John Wiley and Sons, New York, USA.

Smedes, H. W., and Protska, H. J. 1972. Stratigraphic framework of the Absaroka Volcanic Supergroup in the Yellowstone National Park region: U.S.G.S. Prof. Pap. 720-C, US Gov. Print. Office, Wash. DC, 33 pgs.

Stewart, J. 203. Calculus: early transcendentals. Thompson Learning Inc.

Taylor, S. T., and R. D. Jackson. 1986. Temperature. In, pp. 927-941. A. Klute ed. Methods of soil analysis, part 1, physical and mineralogical methods, 2nd edition. Soil Science Society of America Inc. Madison, WI.

ter Braak, C. J. F., and L. G. Barendregt 1986. Weighted averaging of species indicator values: its efficiency in environmental calibration. Mathematical biosciences. 78: 57-72.

ter Braak, C. J. F., and C. W. N. Looman. 1986. Weighted averaging, logistic regression and the Gaussian response model. Vegetatio. 65: 3-11.

Tichy, L. 2002. JUICE, software for vegetation classification. Journal of vegetation science. 13: 451-453.

Urbanczyk, S. A., and D. A. Henderson. 1994. Classification and ordination of alpine plant communities, Sheep Mountain, Lemhi County, Idaho. Madrono. 41(3): 205-223.

Walker, M. D., Webber, P. J., Arnold, E. H., and D. Ebert-May. 1994. Effects of interannual climate variation on aboveground phytomass in alpine vegetation. Ecology. 75(2): 393-408.

Walter, H.; Harnickell, E.; Mueller-Dombois, D. 1975. Climate diagram maps of the individual continents and the ecological climatic regions of the earth. Springer-Verlag. New York. USA.

Weaver, T. 1990. Climates of subalpine pine woodlands. p 72-79 *in* W Schmidt and K McDonald ed 1990 Proceedings-- Symposium on whitebark pine ecosystems: ecology and management of a high mountain resource. USDA Forest Service General Tech Report INT-270. Ogden UT.

Weaver, T. 1994. Vegetation distribution and production in Rocky Mountain climates--with emphasis on whitebark pine. 11 pgs *in* W Schmidt and K Holtmeier eds. 1994. Stone pines and their environments: the status of our knowledge. USDA Forest Service Gen Tech Rept INT-GTR-309. Proceedings of an international workshop 5-11 Sept 1992, San Moritz Switzerland.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs. 26: 1-80.

Willard, B. E. 1979. Plant Sociology of alpine tundra, Trail Ridge, Rocky Mountain National Park, Colorado. Quarterly of the Colorado school of mines. 74: 4.

CHAPTER 3

ALPINE COMMUNITIES, ECOLOGY, AND FLORA OF MOUNT WASHBURN, (YELLOWSTONE NATIONAL PARK, USA)

Introduction

Mount Washburn, a peak in central Yellowstone National Park, is both a site of long-standing scientific interest (Shultz 1969, Richmond et al. 1978, Tomback et al. 2001), and probably the most frequently climbed volcanic summit in the Rocky Mountains. In spite of this, its alpine ecology and flora are undocumented; though descriptions exist for neighboring alpine areas in the Beartooths (Johnson and Billings 1962, Lackschewitz 1994), the Tetons (Spence and Shaw 1981), the Madison, Gallatin, and Tobacco Root Mountains (Cooper et al. 1997, Pemble 1965), and the Absarokas (Thilenius and Smith 1985). Furthermore, while North American volcanic-alpine vegetation has been described for coastal (Douglas and Bliss 1977, Hunter and Johnson 1983) and Southern Rocky Mountain regions (Baker 1983, Seagrist and Taylor 1998, Taye 1985, Rottman and Harman 1985), there are no comparable descriptions for northern Rocky Mountain volcanic peaks.

The Washburn alpine is also of interest because of its “island” characteristics (i.e. small size and isolation). Application of island biogeography (MacArthur and Wilson 1963, 1967) to alpine ecosystems emphasizes the particular vulnerability of small, remote alpine summits like Mt. Washburn to subalpine encroachment as a result of climate change (Hadley 1987, Bruun and Moen 2003, Halloy and Mark 2003).

The lack of data concerning alpine vegetation on Mt Washburn, its popularity, and its potential vulnerability prompted us to: 1) identify and characterize its plant communities, 2) correlate the presence of these communities with presumptive environmental factors, and 3) quantitatively compare its flora to neighboring alpine areas in the Beartooths and Northern Absaroka Mountains.

Study Area

General Description

Mount Washburn (3124m) is located at the southeast edge of the Washburn Range in north-central Yellowstone National Park (44º 48'N, 110º 26'W; Fig. 3.1). Its planar area above treeline is approximately 0.76 km^2. At its lower altitudes Washburn is populated by forests of whitebark pine (*Pinus albicaulis*), lodgepole pine (*Pinus contorta*), and engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) intermixed with sub-alpine meadows (Weaver and Dale 1974). The transition from sub-alpine to alpine cannot be ascertained simply by change in altitude. However, as one approaches summit ridges (>3000m elev.) one generally passes through a krummholz zone into typical alpine meadows dominated by cushion plants, forbs, and perennial deep rooted graminoids (cf. Billings 2000). Alpine herbivory is due primarily to bighorn sheep (*Ovis canadensis*), marmots (*Marmota flaviscens*), pikas (*Ochotona princeps*) and insects (cf. Blumer and Diemer 1996).

Geology

Two large volcanic eruptions, occurring 2 million and six hudred thousand years ago, resulted in the formation of the Yellowstone Caldera in central YNP (Keefer 1987). The later eruption caused terrain south of the Washburn Range to drop by approximately 600 meters resulting in the present-day appearance of Mt. Washburn as a series of isolated alpine summits which run west to east from Dunraven Pass to the Grand Canyon of the Yellowstone (Parsons 1978).

Surficial rock of the Washburn Range is from the Langford Formation of the Thorofare Creek Group, a unit of the Absaroka Volcanic Supergroup (Smedes and Protska 1972; Fig. 3.1c). On Mount Washburn itself the Langford Formation unconformably overlies strata of the Washburn Group, the oldest member of the Absaroka Volcanic Supergroup. The Langford Formation consists of both light colored lava flows and alluvial facies composed of hornblende and pyroxene andesite fragments deposited between 47-49 million years ago (Smedes and Prostka 1972). While south-facing cliff areas exist on Mount Washburn, summits tend to be well rounded, and north-facing slopes are gradual (<35º). These gentle slopes contrast the large sheer north-faces of peaks from the Lamar River Formation of the Absaroka-Volcanics in northeast Yellowstone National Park (see Chapters 4-6).

Climate

The climate of the Washburn Range appears to be drier than alpine areas in the adjacent Beartooths and Northern Absarokas (Chs. 4, 5). At the nearby (< 9 km) sub-alpine (2489m) Canyon Village weather station precipitation is consistent but relatively low throughout the year (≅ 20mm month^{-1}, 278 mm year^{-1}; Figs. 3.1a, 3.2a). Average temperatures in July (max/min) are 22.3°/3.1°C while those in December are -4.7°/-16.6°C (Fig. 3.2a). In the summer months (July-Sept.) evaporation exceeds precipitation (Fig. 3.2a). At alpine altitudes (2867m) on Parker Peak, 50 km to the east, precipitation totals are much higher (784 mm year^{-1}; Figs. 3.1a, 3.2a) though the climate is still drier than high altitude areas in the N. Absarokas (≅ 1300 mm year^{-1}) or Beartooths (≅ 840 mm year^{-1}). The climate of the Washburn alpine is probably intermediate between Canyon and Parker Peak, i.e. wetter than Canyon Village (because of altitude discrepancies), but drier than the Parker Peak alpine (because of drier conditions in central YNP). Both weather stations predict four months of frost free temperatures compared to three months predicted by weather stations in the Northern Absarokas and Beartooths (Chs. 4, 5).

Summer weather data is available for the Washburn alpine. Warmest temperatures (≅ 17.5°C) on the Washburn summit occur around Julian day 210, i.e. July 29 (Fig. 3.2c), and winds are usually from the southwest, (Fig. 3.2b). Average daily summit summer precipitation is low at approximately 0.75 mm day^{-1} (Fig. 3.2c).

Methods

Field Methods

Mt. Washburn has four minor summits (Elev. 3124m – 3032m) on its east-west ridgeline. Four sites were established, one at each summit, each consisting of five environments: north-facing, south-facing, late snowmelt, ridgetop, and talus (Fig. 3.1). Two additional plots were established at site one to represent ledge associations below cliffs. Within each site, vegetation of each of the five environments was sampled with two replicates. Each sample consisted of ten 20 x 50cm frames placed at one meter intervals along a ten meter sampling tape. Replicate locations were established using a stratified random process. The vegetation of each frame was characterized by listing the plant species present and visually estimating the cover of each (Daubenmire 1959). Vegetation data was gathered in the first week of July 2000 and 2001. Nomenclature follows Dorn (1992). Voucher specimens are deposited in the Yellowstone National Park herbarium (YELLO) in Gardiner MT. An annotated checklist of all species encountered in the Washburn alpine is included as Appendix B.1.

Environmental data were recorded at each plot. Elevations were determined using Trimble™ GeoExplorer 3, and Trimble™ Pro XR receivers. Readings were differentially corrected against the Montana State University, and Idaho National Engineering and Environmental Laboratory (INEEL) GPS base stations. Magnetic aspect (later corrected for declination) and slope were measured with a Brunton compass. Potential annual direct incident radiation was calculated using an algorithm recommended by McCune and Keon (2002). Surface rock cover was measured as a percentage using eighty points located in the plot. This was done by recording rock hits for eight points (nails) on a meter stick placed at 1 meter intervals along the 10m plot line. Soil surface cover was recorded as 1 – rock surface cover. Soil samples were taken at all plot locations to measure organic matter (C and N) phosphorous, pH, soil salinity (conductivity), and soil texture (i.e. % sand, % clay, % silt). Carbon was measured using both LECO (Nelson and Sommers 1996) and Lawson ignition (Storer 1984). Soil nitrogen was determined using both LECO ignition (Nelson and Sommers 1996) and Kjeldahl nitrogen (Bremner 1996). Soil phosphorous was determined using the Bray method (Olsen 1982). Conductivity and pH were measured on 1:1 water slurries with appropriate meters (Thomas 1996). Soil texture was measured with the Boyoucous hydrometer method (Gee and Bauder 1986).

Soil moisture and temperature sensors were installed in each plot at a depth of 15 cm. Sensors were read periodically during the alpine growing season (i.e. late June-early October) over a 5 year period (2000-2004). Sensors were installed at all five environments (and the two ledge plots in site 1) of all four sites (i.e. sites 1-4). Thus 22 sensors were installed. Moisture sensors were Bouyoucos plaster blocks (Beckman Instruments, PO Box 3100, 2500 Harbor Boulevard, Fullerton, CA.), and were read with a Delmhorst KS-D1 soil moisture (electrical resistance) meter. Resistance readings were converted to water potentials with appropriate calibration curves (see Chapter 9). Temperatures were measured with thermocouples manufactured using standard methods (Taylor and Jackson 1986), and read by an Omega HH-25TC thermocouple thermometer (www.Omega.com).

Soil Water and Temperature Modeling

To describe the pattern of early spring (wet) to late summer (dry) soil water availability we curve-fit, for each plot, soil water potential against date (Julian day 175-235; i.e. June 24-August 23) using sigmoidal equations (Eq. 3.1). Weibull, pulse cumulative and other models which create sigmoidal/logistic curves provided poorer fits. Moisture curves for each plot are included as Appendix B.2.

$$f(x) = \frac{a}{1+\exp\left(-\frac{x-b}{-c}\right)} \qquad (3.1)$$

To describe seasonal change in site temperature we curve-fit soil temperature against date (Julian day 180 to 280; i.e. June 29 to October 7). We used unimodal quadratic equations (Eq. 3.2) because temperatures gradually rise from spring to mid-summer and fall back in the autumn. Temperature curves for each plot are included as Appendix B.3.

$$f(x) = c_1x + c_2x^2 + b \qquad (3.2)$$

We used these models to estimate ecologically important parameters for soil water [number of days at particular water potentials (-0.12, -1.5 Mpa etc.), driest day, wettest day], and soil temperature [number of days when soil temperature was above 10º C, maximum predicted temperature, and heatsum]. Heatsum is the area under the predicted temperature curve (i.e. the integral) which lies above 10 degrees C. Soil water and temperature conditions were indexed also by the presence of indicator species as described in Chapter 2.

Community Analysis

Ordination Vegetation samples were ordinated with Non-Metric Multidimensional Scaling (NMDS; Kruskal 1964). Although random starting points were also tried, the best (lowest stress) solutions resulted from using PCoA (Principal Coordinates Analysis) scores as initial starting points (cf. Venebles and Ripley 2005). A tolerance of $1 \cdot 10^{-7}$ was used with 200 iterations to create the scatterplot projection. To improve interpretability of NMDS axes, ordination configurations were rotated with

PCoA so that the variance of points was maximized on the first dimension (Minchin 1987). A dissimilarity matrix created with Bray-Curtis dissimilarity (Bray and Curtis 1957, Faith et al. 1987) was used for both ordinations and classifications (described below).

Classification Hierarchical agglomerative clustering was used to segment the vegetation continuum. Linkage between samples was established with the flexible beta method (Lance and Williams 1967). The value $\beta = -0.25$ was used since it is highly effective for cluster recovery in vegetation datasets (Aho 2006). Wishart's objective function (Wishart 1969) was used to scale the cluster dendrogram. The optimal classification solution was found by pruning the dendrogram to create the nineteen simplest classification solutions (2-20 clusters), then evaluating these results with seven classification evaluators (Appendix B.4). For further detail on these procedures see Chapter 7 and Aho (2006).

Environmental Vectors and Environmental Correlations with NMDS Axes The relationship between vegetation distributions and continuous environmental variables was described by finding the direction of maximum correlation between individual environmental variables and ordination dimensions (Oksanen 2005). Environmental vectors were scaled within ordinations by the strength of their correlation to the NMDS projection of points. The relationship of categorical variables to ordination solutions was quantified with Equation 3.3 (Oksanen 2005). The strength of association for both continuous and categorical variables was tested for significance by permutating response vectors using a Monte Carlo methodology; 1000 permutations were used for this procedure.

$$r^2 = 1 - SSW / SSTO \tag{3.3}$$

where SSW = within-group sums of squares [scatter with respect to treatment (community) centroids for two dimensions of interest] and $SSTO$ = total sums of squares (overall scatter with respect to the scatterplot centroid for the same two dimensions of interest).

Comparison of Floras (Testing Island Biogeography Predictions)

To estimate the effects of size and isolation on the Washburn alpine we compared the Washburn Range (40 plots used in this paper), to the Northern Absarokas (82 plots; 9 andesite peaks), and the Beartooth Plateau (60 plots; 3 granite and 3 limestone peaks). At all three areas vegetation was sampled using the same methods (see methods above), at the same environments (N. face, S. face, ridgetop, talus, and late-melt), in the same proportions (each environment made up approximately 20% of total number of samples).

To compare richness of floras we constructed species area curves. Species richness estimates for area were made by taking random samples from three datasets using jackknife procedures (Palmer 1990, 1991).

To compare the importance of rare species we created Rank Abundance Dominance (RAD) plots. We plotted species cover as an index of abundance (cf. Harpole and Tilman 2006) against species rank with respect to cover. Curves were fit with Preston log-normal models (Preston 1948) since these generally describe local community rank/dominance patterns (Hubbell 2001).

Software Classifications and species area curves were created using PC-ORD (McCune and Mefford 1999). Algorithms for classification evaluators were coded in R

(R Development Core Team 2006). Ordinations, environmental vector analyses, and RAD plots were created in R using MASS (Venables and Ripley 2005), labdsv (Roberts 2005), and vegan (Oksanen 2005) libraries.

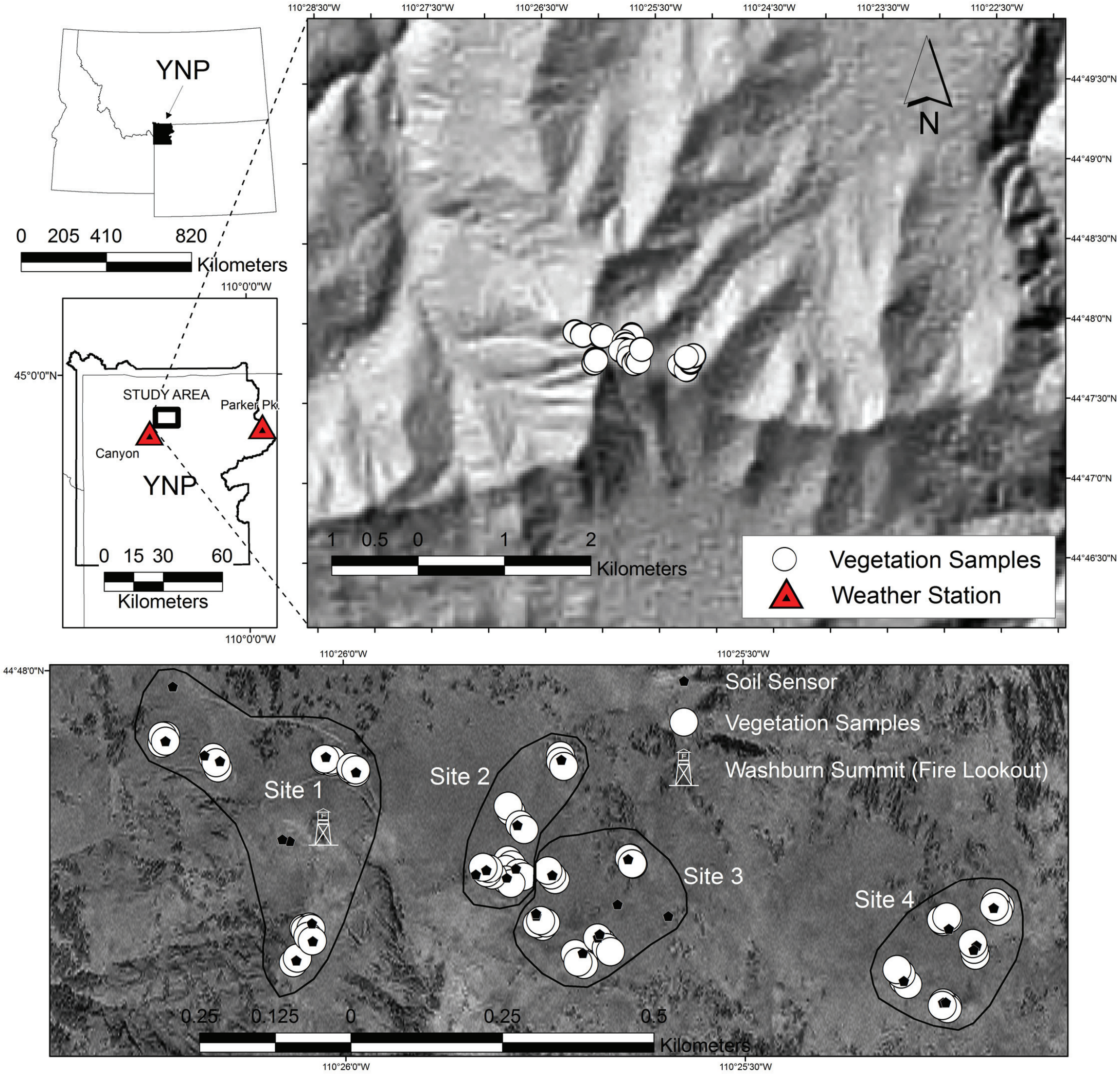


Figure. 3.1. Maps of study area: showing orientation maps, sites 1-4, the main (highest) Washburn summit, and transect and soil sensors locations.

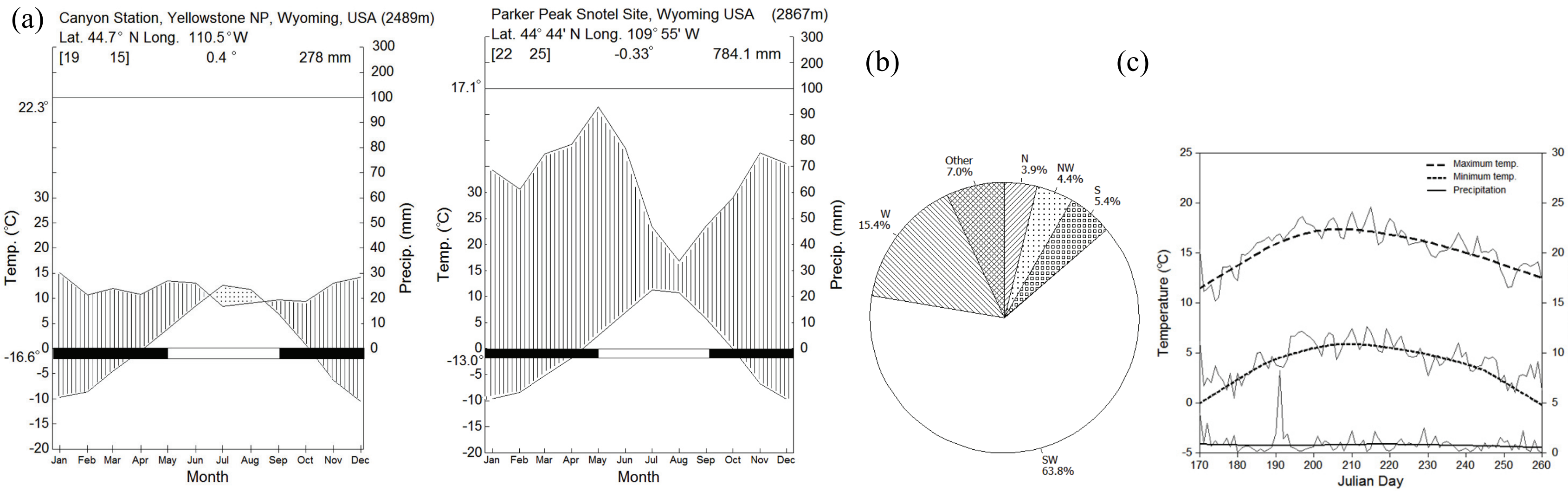


Figure 3.2. Climate of Mount Washburn. **(a)** Climate diagram (cf. Walter and Leith 1967) for the Canyon Village weather station adjacent to (< 11km), and 600m below the Washburn summit and the Parker Peak snotel station, near alpine elevation (2867m) and 50 km to the east (see Fig. 3.1). Raw climate data was provided by the Western Regional Climate Center (WRCC 2006). The upper plotted line indicates average monthly precipitation; the lower humped line indicates average mean monthly temperature. The vertically hatched area indicates the months that precipitation exceeds evaporation. The dotted area (Fig. 3.2a only) indicates months when evaporation exceeds precipitation. Text at the top of the climate diagrams gives general information about the site: the length of records in years for temperature and precipitation data respectively (in brackets), the latitude and longitude, the name of the station, the elevation, and the average yearly precipitation and overall mean temperature. Average daily maximum temperature of the warmest month and average daily minimum temperature of the coldest month are also indicated on the temperature axis. The blackened area of the long rectangle near the bottom of the figure indicates the frost period (i.e. the months when average minimum temperature was < 0ºC). **(b)** Wind direction, at the Washburn summit, for 1965-1997 and 2001-2004 (N = north, S = south, W = west). **(c)** Summer weather data at the Washburn summit (1965-2004) showing mean maximum temperature, mean minimum temperature, and mean precipitation. Localized weighted scatterplot smoother (LOWESS) lines are superimposed. Washburn summit weather data was provided by the National Park Service. For additional regional climate information see Figs. 4.2, 5.1c, and 5.2.

Identification of Communities

The NMDS ordination required only two dimensions to adequately represent the data. Low stress (12.9) in the 2D solution indicated an effective ordination with little possibility of drawing false inference (McCune and Grace 2002).

A consensus of classification evaluators found that six clusters was an optimum pruning solution for the agglomerative classification (Appendix B.4). The six clusters (communities), identified by diagnostic species and environment, were: 1 = *Elymus scribneri* (ELSC), a talus type; 2 = *Senecio canus-Astragalus kentrophyta* (SECA-ASKE) a clumped type on rocky sites; 3 = *Erigeron rydbergii-Oxytropis lagopus* (ERRY-OXLA), a rocky turf and ridgetop type; 4 = *Carex elynoides-Astragalus alpina* (CAEL-ASAL), dense dry turf with moderate snow accumulation; 5 = *Carex paysonis-Artemisia scopulorum* (CAPA-ARSC), on snowbank sites; and 6 = *Arnica rydbergii* (ARRY) a ledge seep community (Table 3.1).

The six cluster classification solution agreed strongly with the ordination configuration. Note the lack of overlap in confidence intervals around cluster centroids (Fig. 3.3a). When treated as a categorical variable, the six clusters explained 91% of the variability in the two dimensional NMDS solution (Table 3.2).

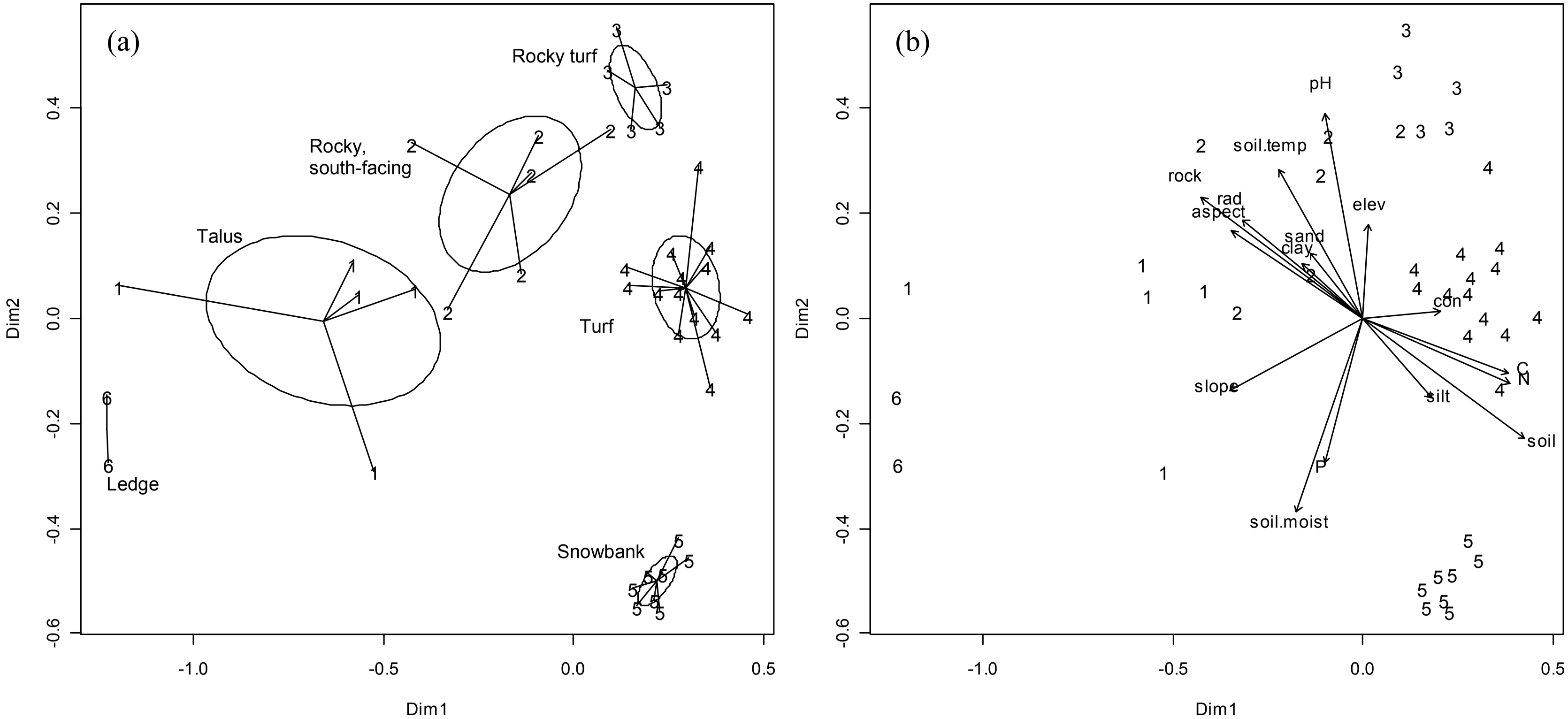


Figure. 3.3. NMDS ordination and vector analysis of Washburn data. **(a)** Communities indicated with spider diagrams. Ellipses indicate 95% confidence intervals around cluster centroids. Community 1 = *Elymus scribneri* talus (ELSC), community 2 = *Senecio canus-Astragalus kentrophyta* (SECA-ASKE), community 3 = *Erigeron rydbergii-Oxytropis lagopus* (ERRY-OXLA), community 4 = *Carex elynoides-Astragalus alpina* (CAEL-ASAL), community 5 = *Carex paysonis-Artemisia scopulorum* (CAPA-ARSC), community 6 = *Arnica rydbergii* (ARRY). **(b)** Vector analysis. Environmental variables are: P = Phosphorous (mg kg^{-1}), C = % soil carbon, N = % soil nitrogen, elev = elevation (m), slope = slope(degrees), aspect = degrees from N, rad = solar radiation (MJ · cm^2/yr.), soil = % cover of surface soil, con = soil conductivity (mmhos cm^{-1}), sand = % sand content of soil, clay = % clay content of soil, silt = % silt content of soil, soil.temp. = soil temp (number of summer days > 10˚C), soil moist = soil moisture (number of summer days wetter than -0.12Mpa). Note that **(b)** is an identical ordination to **(a)**. Final stress for 2D NMDS solution = 12.9.

Table 3.1. Summary relevé table for the six community types. The two character cipher[1] included in each cell indicates constancy (% of sites that contain the species), and cover. Bolded cells indicate constancy ≥ 30%.

	Talus	Rocky/SF	Dry turf		Late melt	Ledge
Species[2]	1. ELSC	2. SECA-ASKE	3. ERRY-OXLA	4. CAEL-ASAL	5. CAPA-ARSC	6. ARRY
Elymus scribneri	**9B**	1A	**3A**	+A	..	**9C**
Draba incerta	..	**3A**	1+	..	..	..
Smelowskia calycina	..	**6B**	**9B**	2A	..	..
Astragalus kentrophyta	..	**9C**	**7C**	1A	..	..
Senecio canus	..	**9C**	1A	++	..	..
Eriogonum ovalifolium	..	1+	**5A**	1A	1A	..
Erigeron rydbergii	..	**3A**	**9D**	**4A**	..	..
Oxytropis lagopus	..	**3A**	**9C**	2A	..	..
Selaginella densa	..	**4B**	**9E**	**7D**	..	..
Potentilla ovina	..	1A	**5B**	**4B**	1A	..
Poa rupicola	..	**4B**	**9C**	**9D**	2A	..
Achillea millefolium	**3A**	**4A**	..	**4B**	**8C**	..
Poa pattersonii	**5B**	**6C**	**7A**	1A	1A	..
Phlox pulvinata	**3A**	**9C**	**9D**	**7D**	..	..
Sedum lanceolatum	**5A**	**9C**	**9B**	**9B**	**7A**	..
Cerastium arvense	**7B**	**9C**	**7A**	**9D**	**9C**	..
Erigeron compositus	**7A**	**8B**	**3A**	2A	..	**4A**
Arenaria obtusiloba	**3B**	**9C**	**9C**	**9C**	**8A**	..
Lomatium cous	**5A**	**9B**	..	**7B**	1A	..
Polemonium viscosum	**5A**	1A	..	**6C**	1+	..
Trisetum spicatum	**3A**	**6B**	..	**3A**	**3A**	..
Festuca brachyphylla	..	**9B**	**7B**	**4A**	**8B**	..
Poa cusickii	1A	**4C**	**5A**	**4A**	2A	..
All mosses	..	1A	**9B**	**7C**	**6C**	**4A**
Carex obtusata	..	1B	**5C**	**6C**	..	..
Carex elynoides	..	1A	**3A**	**7D**	..	..
Poa alpina	1A	..	..	**3A**	**4A**	..
Myosotis alpestris	1A	..	..	**3B**	1A	..
Luzula spicata	..	**3A**	..	**8C**	**9B**	..
Phlox multiflora	..	**3A**	..	**4B**	**4A**	..
Lupinus argenteus	..	..	**5B**	**4C**	**8C**	..
Potentilla diversifolia	..	..	**3A**	**9D**	**9D**	..
Mertensia alpina	..	..	1A	**6C**	**3A**	..
Polygonum bistortoides	..	..	1A	2A	**9C**	..
Besseya wyomingensis	1A	..	..	**7B**	2A	..
Saxifraga rhomboidea	..	..	..	**4A**	**3A**	..
Oxytropis borealis	..	..	..	2B	..	..
Carex paysonis	..	1A	1A	+A	**9E**	..
Astragalus alpinus	..	..	..	**9C**	**3A**	..
Agoseris glauca	..	..	..	2A	**7B**	..
Penstemon procerus	..	..	..	2A	**7A**	..
Arenaria congesta	..	..	..	2A	2A	..
Stellaria monantha	..	..	..	1A	**8A**	..
Androsace septentrionalis	..	..	..	1A	**4A**	..
Artemisia scopulorum	..	..	..	+A	**6C**	..
Carex phaeocephala	..	..	..	+A	**8B**	..
Erigeron simplex	..	..	..	..	**9B**	..
Sibbaldia procumbens	..	..	..	..	**6C**	..
Epilobium anagallidifolium	..	..	..	..	**4A**	..
Aster alpigenus	..	..	..	..	**4A**	..
Lewisia pygmaea	..	..	..	..	**4A**	..
Antennaria media	..	..	..	..	**4A**	..
Draba crassifolia	..	..	..	..	**4A**	..
Aster foliaceus v. apricus	..	..	..	..	**4C**	..
Salix arctica	..	..	..	..	**3A**	..
Pedicularis cystopteridifolia	..	..	..	..	**3A**	..
Veronica wormskjoldii	..	..	..	..	**3A**	..
Poa reflexa	..	..	..	..	2A	..
Senecio integerrimus	..	..	..	..	2A	..
Arnica rydbergii	..	..	..	..	..	**9D**
Cirsium eatonii	..	..	..	..	..	**4B**

Table 1. cont.

[1] For each cell, constancy is indicated by the first symbol, while cover is indicated by the second symbol. For constancy: 0% = ".", 0-10% = +, 10-20% = 1, 20-30% = 2, 30-40% = 3, 40-50% = 4, 50-60% = 5, 60-70% = 6, 70-80% = 7, 80-90% 8, 90-100% = 9. For cover: 0% = ".", 0-01% = +, .01-1% = A, 1-2% = B, 2-5% = C, 5-25% = D, >25% = E. Cells > 30% constancy are bolded. [2] Lower constancy species left out of the table were: *Juncus drummondii, Poa interior, Poa arctica, Poa secunda, Antennaria microphylla, Antennaria umbrinella, Claytonia lanceolata, Dodecatheon pulchellum, Draba cana, Draba densifolia, Epilobium halleanum, Lychnis apetala, Oxytropis parryi, Pinus albicaulis, Ranunculus eschscholtzii, Stellaria umbellata, Taraxacum ceratophorum,* and *Vaccinium scoparium.*

Table 3.2. Correlation of environmental variables to the two dimensional NMDS ordination solution (i.e. Fig. 3.3b). Variables are ranked from strongest to weakest.

	r^2	$P\ r(>r)$
Continuous variables		
% Cover of surface soil (1-rock cover)	0.773	<0.001
% Cover of surface rock (1-soil cover)	0.773	<0.001
Soil moist (days > -0.12 MPa at 15 cm)[1]	0.552	<0.001
%N in soil (LECO)	0.542	<0.001
pH	0.534	<0.001
%C in soil (LECO)	0.522	<0.001
Aspect (degrees from N)	0.485	<0.001
Slope (degree)	0.466	<0.001
Solar radiation (MJ cm^{-2} yr^{-1})	0.449	<0.001
Soil temp (days > 10°C at 15 cm)[2]	0.426	<0.001
P (mg kg^{-1})	0.284	0.004
% Silt	0.184	0.034
Conductivity (mmhos cm^{-1})	0.137	0.056
% Clay	0.119	0.100
% Sand	0.114	0.131
Elev. (m)	0.107	0.141
Categorical variable		
Categories from 6 cluster classification analysis[3]	0.907	< 0.001

[1] Julian days 180-280, [2] Julian days 175-235, [3] Factor fitting of classification solution, see methods.

Environmental Controls

Communities were distributed along several important environmental gradients (Fig. 3.3b). Energy related responses (aspect, radiation, and soil temperature) tend to increase from the lower right (snowbanks) to the upper left (south-facing samples) portions of the ordination (Fig. 3.3b). Soil texture is distributed along the same gradient;

with rock, sand and clay increasing toward south slopes and soil cover and silt increasing toward snowbanks (Fig. 3.3b). Organic matter (carbon and nitrogen) also increases from south slopes to snowbanks. The soil water gradient runs perpendicular to the energy/soil-texture gradient, i.e. from the upper right (dry ridge) to the lower left (talus, snowbank, and ledge) portions of the diagram (Fig. 3.3b). The pH trend is opposite the water trend, with acidity increasing with water flow/leaching. Steepness of slope lies on a vector between energy and water, from ridges to talus-ledges-snowbanks. The environmental variables most strongly associated with the NMDS projection were soil cover ($r^2 = 0.77$, $p < 0.001$), and soil water ($r^2 = 0.55$, $p < 0.001$; Table 3.2). Other well correlated variables were soil nitrogen and carbon, pH, aspect, slope, and solar radiation (Fig. 3.3a, Table 3.2).

Community Descriptions

The six identified communities are described below in paragraphs which identify their major species, describe environments, and place them into context with the ecological literature. Quantitative descriptions/comparisons of vegetation and environment are provided in Tables 3.1 and 3.3 respectively.

Community 1. *Elymus scribneri* (ELSC); 5 plots

This community occupied south facing talus slopes on Mount Washburn (Tables 3.1, 3.3). It had particularly low cover (9.7%) and richness (8.6 spp. per plot). *Elymus scribneri,* the best indicator for this type was also present in other rocky communities (e.g. ERRY and SECA-ASKE; Table 3.1). Common associates include: *Erigeron compositus* and *Cerastium arvense.*

Steep (30°) south-facing slopes yielded high solar radiation (0.94 MJ cm^{-2} yr^{-1}) and warm soils for this community (Table 3.3). Soils were especially moist (in five years of sensor readings, one plot in this type was never drier than -1.5 Mpa; Table 3.3). Soils were also rocky (only 2% surface soil cover), sandy (66% sand), rich in phosphorous (45 mg kg^{-1}) and poor in organic matter ($C \cong 1$ %, $N \cong 0.1\%$).

This community is similar to andesitic talus communities in the northern and southeastern Absarokas dominated by *E. scribneri* and *E. compositus* (Chapter 4**,** Thilenius and Smith 1985), and non-volcanic rocky areas in southwestern Montana dominated by *Elymus scribneri, Festuca brachyphylla, Trisetum spicatum, Achillea millefolium*, and *Lomatium cous* (Cooper et al. 1997). It is also similar to rocky grassland communities of the Copper Basin in Idaho which are dominated by *E. scribneri, Poa rupicola*, and *E. compositus* (Caicco 1983).

Community 2. *Senecio canus-Astragalus kentrophyta* (SECA-ASKE); 6 plots

This community occupied steep, rocky, south facing slopes and ridgetops on Mt. Washburn (Tables 3.1, 3.3). It had relatively low cover (41%) and richness (16.3 spp. $plot^{-1}$) and was indicated by *Senecio canus* and *Astragalus kentrophyta* (Table 3.1). Common associates included *Arenaria obtusiloba, Cerastium arvense, Erigeron compositus, Lomatium cous, Phlox pulvinata,* and *Sedum lanceolatum.*

Like community 1 steep south facing slopes resulted in high levels of solar radiation (0.93 MJ cm^{-2} yr^{-1}) and warm soils [64.5 of 110 spring-fall days (June 29-

October 7) were > 10˚ C]. Soils were dry [only 9 of 60 spring-summer days (June 24-August 23) were > -1.5 MPa; Table 3.3] Soils were also relatively sandy (64% sand), nutrient poor (N ≅ 0.2%) and rocky (only 33% soil cover).

This community is similar to an *Erigeron compositus-Astragalus kentrophyta* cushion plant community identified from the andesitic northern Absarokas (Chapter 4). It is also similar to windswept dry non-prostrate communities in the Tendoy and Tobacco Root Mountains in Southwest Montana dominated by *Lomatium cous, Phlox pulvinata, Sedum lanceolatum* and *Smelowskia calycina* (Cooper et al. 1997).

Community 3. *Erigeron rydbergii-Oxytropis lagopus* (ERRY-OXLA); 5 plots

This type occurred on rocky, moderately-sloped turf sites. Vegetation cover (64.5%) and richness (17.8 spp. plot^{-1}) were intermediate for communities on Mt. Washburn (Table 3.1). Primary indicators were *Erigeron rydbergii* and *Oxytropis lagopus* (Table 3.1). Important associates included *Poa pattersonii, Poa rupicola, Arenaria obtusiloba, Phlox pulvinata Selaginella densa*, *Smelowskia calycina* and mosses (Table 3.1). Community 3 was located on relatively flat (12.3˚ slope), east-west facing (86˚ from N) slopes. Solar radiation inputs were intermediate (0.84 MJ $\text{cm}^{-2}\,\text{yr}^{-1}$) though soils were warm (59/110 days > 10º C) and dry (only 12 of 60 days were wetter than -1.5 MPa; Table 3.3). Soils were also moderately rocky (49% rock surface cover), and had intermediate organic matter (C ≅ 5%, N ≈ 0.4%).

While *Erigeron rydbergii* and *Oxytropis lagopus* often dominated dry turf plots in the Washburn Range, these species rarely occurred in alpine plots from the nearby N. Absarokas and the Beartooths (Chapters 4, 5). *Erigeron rydbergii* is endemic to the

Greater Yellowstone Ecosystem region (Fig. 1.1), and is limited to southern Montana and northwestern Wyoming and parts of Idaho (Pemble 1965, Lackschewitz 1994, Hitchcock and Cronquist 1973). Because of endemism and scarcity of its dominant species, ERRY-OXLA is probably a globally rare alpine type and should be noted by resource managers in Yellowstone National Park.

Community 4. *Carex elynoides-Astragalus alpinus* (CAEL-ASAL); 14 plots

This turf community dominated dry wind sheltered sites. It had particularly high cover (97%) and richness (22 spp. plot^{-1}). Primary indicators were *Carex elynoides* and *Astragalus alpinus* (Table 3.1). Common associates included *Luzula spicata, Poa rupicola*, *Arenaria obtusiloba, Cerastium arvense, Potentilla diversifolia* and *Sedum lanceolatum* (Table 3.1).

Community 4 was located on moderate (17.6˚ slope) northeast facing (64˚) sites. Because of its northern aspect solar radiation inputs were low (0.79 MJ cm^{-2} yr^{-1}; Table 3.3), and soils were cool (only 39/110 days were warmer than 10º C). Soils were also extremely dry (only 11.5/60 days were wetter than -1.5 MPa; Table 3.3). Soils contained little rock (14% cover), were silty (39.8% silt), and contained much more organic matter than other communities (C ≅ 10%, N ≅ 0.7%; Table 3.3). In contrast to its north-facing habitat on Mt. Washburn *C. elynoides* turf occurred only on south-facing sites in the nearby N. Absarokas, and Beartooths (Chapter 5). This distinction demonstrates the generally xeric character of the Washburn Range.

Carex elynoides turf ranges from Montana (Bamberg and Major 1968, Cooper et al. 1997, Damm 2001) through Idaho (Urbanczyk and Henderson 1994), Utah (Lewis

1970), Wyoming (Billings and Bliss 1959), Colorado (Komárková and Weber 1978, Komárková 1979, Willard 1979, Hartman and Rottman 1988, Rottman and Hartman 1985), to New Mexico (Baker 1983). Locally, turf communities dominated by *C. elynoides, Potentilla diversifolia,* and *Arenaria obtusiloba* have been reported in the White Clouds and Copper Basin in Idaho (Richardson and Henderson 1998, Caicco 1983), and the Northern Absarokas and Beartooths (Chapters 4, 5). In the southern Absarokas *C. elynoides-P. multiflora* communities also contain *Trifolium dasyphyllum* (Thilenius and Smith 1985). The genus *Trifolium* does not occur in the alpine of the Northern Absarokas or Mt. Washburn (Chapters 4, 5).

Community 5. *Carex paysonis-Artemisia scopulorum* (CAPA-ARSC); 8 plots

This community occupied snowbank sites on Mount Washburn. It had high cover (87.9%) and particularly high levels of richness (26.1 spp. plot^{-1}). Primary indicators were *Carex paysonis* and *Artemisia scopulorum* (Table 3.1). Associates included *Carex phaeocephala, Luzula spicata, Achillea millefolium, Arenaria obtusiloba, Cerastium arvense, Erigeron simplex, Festuca brachyphylla, Polygonum bistortoides*, and *Stellaria monantha* (Table 3.1).

This community occupied north-facing sites (40^{o} from north), with low solar radiation inputs (0.73 MJ cm^{-2} yr^{-1}; Table 3.3), and resulting cold soils (only 19.2 summer days were warmer than 10˚C; Table 3.3). Soils were very moist (30.1/60 days wetter than -1.5 MPa; Table 3.3), and rich in organic matter (C ≅ 6% to 10%, N ≅ 0.5%), and acidic (pH = 5.7).

Community 5 is similar to andestic *Carex paysonis-Artemisia scopulorum* late-melt communities in the andesitic Northern Absarokas (Chapter 4), and to a number of *C. paysonis* snowmelt communities of the Beaverhead National Forest in Southwestern Montana (Cooper et al. 1997). Community 5 is also somewhat similar to andesitic moist and wet meadow communities in the southern Rockies. In the San Juan Mountains of southern Colorado, dominant snowmelt species include *Artemisia scopulorum*, *Sibbaldia procumbens*, *Erigeron simplex* and *Sedum integrifolium* (Rottman and Hartman 1985). The Sangre de Cristo Mountains in northern New Mexico have late melt communities with *Artemisia scopulorum, Lloydia serotina,* and *Salix arctica* as dominants (Baker 1983). At both of these locations, *Carex nova* replaces *C. paysonis* as the dominant late melt sedge (Rottman and Hartman 1985, Baker 1983).

Community 6. *Arnica rydbergii* (ARRY); 2 plots

This distinctive tall-herb community occurred frequently in drainages, along cliff bases, and on unstable, rocky slopes. It had particularly low vegetation ground cover (15.2%) and richness (3.5 spp. plot^{-1}). While small sample size prevents confident synecological description, its dominant species were *Arnica rydbergii* and *Elymus scribneri*.

This community inhabited steep (32°) south-facing slopes (171° from N) with high radiation inputs (1 MJ $\cdot$ cm^{-2} yr^{-1}) and warm soils (69.7/110 days > 10°C; Table 3.3). Soils were also moist (20.4/60 days wetter than -1.5 MPa), rocky (79% rock cover), sandy (65% sand), and poor in organic matter (C ≅ 1.5%, N ≅ 0.7%; Table 3.3).

This community is essentially identical to an *A. rydbergii-Epilobium clavatum* community from the andesitic N. Absarokas (Chapter 4). A similar community pioneers wet, rocky, recently deglaciated substrates in Glacier National Park, and is dominated by *Arnica diversifolia, Epilobium alpinum, Poa alpina* and *Poa cusickii* (Damm 2001).

Table 3.3. Comparison of environments for the six communities identified on Mt. Washburn. Standard errors are included with mean estimates.

	Talus	Rocky/SF	Dry turf		Late melt	Ledge
	1. ELSC	2. SECA-ASKE	3. ERRY-OXLA	4. CAEL-ASAL	5. CAPA-ARSC	6. ARRY
Site summary						
Number of plots	5	6	5	14	8	2
Mean cover (%)	9.7 ± 3	40.9 ± 7.9	64.5 ± 8.3	96.6 ± 4.8	87.9 ± 6.3	15.2 ± 4.7
Total richness per type	21	32	27	51	55	5
Mean richness per site	8.6 ± 1.7	16.3 ± 0.7	17.8 ± 0.9	21.8 ± 0.9	26.1 ± 1.7	3.5 ± 0.5
Simpson diversity [1]	0.89	0.94	0.80	0.94	0.80	0.47
Shannon-Weiner diversity [2]	2.5	3	2.3	3.2	2.5	0.9
Beta diversity [3]	0.6	0.5	0.3	0.6	0.5	0.3
Topography & solar radiation						
Elevation (m)	3039 ± 19	3056 ± 8	3070 ± 6	3037 ± 9	3038 ± 9	3054 ± 6
Slope (degrees)	30 ± 0.82	22.3 ± 3.95	12.6 ± 2.27	17.64 ±	18.88 ± 1.09	31.75 ± 0.25
Aspect (deg. From N)	137.2 ± 2.04	126.5 ± 0.9	86.6 ±	64 ± 10.81	40 ± 8.6	170.5 ± 7.5
Solar radiation (MJ cm^{-2} yr^{-1})	0.94 ± 0	0.93 ± 0.01	0.84 ± 0.05	0.79 ± 0.02	0.73 ± 0.01	1.0 ± 0.01
Heat load index[4]	0.78 ± 0.01	0.8 ± 0.02	0.81 ± 0.05	0.72 ± 0.03	0.69 ± 0.01	0.9 ± 0.03
Soil temperature, 15 cm						
Temp index (0=cold, 1=hot) [5]	0.75 ± 0.25	0.59 ± 0.1	0.58 ± 0.09	0.3 ± 0.07	0.07 ± 0.03	NA
Observed max temp.(˚C) [6]	15.02 ± 0.79	17.87 ± 1.25	14.9 ± 0.91	14.07 ± 0.5	11.6 ± 0.52	17.5 ± 0.1
Predicted max temp.(˚C) [6]	11.49 ± 0.35	13.85 ± 1.08	12.42 ± 0.5	11.65 ± 0.53	10.09 ± 0.4	17.15 ± 0.32
Pred. day of max. temp [6]	215.38 ± 0.85	217 ± 1.56	208.2 ± 1.67	213.2 ± 0.88	217.7 ± 0.28	215.8 ± 1.65
Heatsum [6, 7]	59.3 ± 16.77	183.5 ± 0.8	97.7 ± 29.75	64.8 ± 24.02	13.65 ± 6.41	321.4 ± 7.04
Days above 10˚C [6]	56.88 ± 4.01	62.95 ± 6.74	56.86 ± 3.57	37.97 ± 5.78	18.9 ± 7.38	68.15 ± 1.25
Soil water, 15 cm						
Moist. index (0=dry, 1=wet) [5]	0.38 ± 0.24	0.25 ± 0.09	0.14 ± 0.08	0.21 ± 0.09	0.88 ± 0.08	NA
Days wetter than -0.12Mpa [8]	23.25 ± 5.9	8.22 ± 0.82	7.32 ± 0.64	8.06 ± 0.41	20.57 ± 0.87	14.94 ± 4.98
Days wetter than -0.25Mpa [8]	16.81 ± 2.16*	9.44 ± 0.75	8.4 ± 0.63	9.07 ± 0.69	23.6 ± 1.02	16.71 ± 3.61
Days wetter than -1.5Mpa [8]	21.97 ± 2.75*	11.61 ± 0.76	11.27 ± 0.74	10.92 ± 1.18	29.26 ± 1.59	20.46 ± 0.42
Days wetter than -2.5Mpa [8]	23.51 ± 3*	12.18 ± 0.81	12.11 ± 0.8	11.38 ± 1.3	30.73 ± 1.77	21.41 ± 0.4
Soil cover and texture						
Cover of surface soil (%)	0.02 ± 0.01	0.33 ± 0.06	0.51 ± 0.06	0.86 ± 0.02	0.86 ± 0.04	0.21 ± 0.13
Cover of surface rock (%)	0.98 ± 0.01	0.67 ± 0.06	0.49 ± 0.06	0.14 ± 0.02	0.14 ± 0.04	0.79 ± 0.13
Sand (%)	66 ± 2.82	62.9 ± 1.84	64.1 ± 3.39	58.25 ±	59.13 ± 3.12	65.0 ± 0.0
Clay (%)	4.0 ± 0.63	4.8 ± 0.83	3.4 ± 0.93	1.96 ± 0.37	2.38 ± 0.53	3.5 ± 2.5
Silt (%)	30.0 ± 2.3	32.3 ± 1.28	32.5 ± 2.51	39.79 ±	38.5 ± 2.96	31.5 ± 2.5
Soil pH and conductivity						
pH	6.5 ± 0.09	6.73 ± 0.07	6.95 ± 0.18	6.54 ± 0.11	5.65 ± 0.13	7.02 ± 0.13
Conductivity (mmhos cm^{-1})	0.09 ± 0.02	0.15 ± 0.03	0.15 ± 0.04	0.26 ± 0.01	0.17 ± 0.01	0.21 ± 0.17
Soil elemental characteristics						
P (mg kg^{-1}), Bray	45 ± 10.69	23.3 ± 2.75	20.6 ± 2.54	29.07 ±	36.25 ± 2.79	27.5 ± 3.5
C (%), Lawson	2.16 ± 0.53	2.96 ± 0.36	4.91 ± 1.48	13.32 ±	10.01 ± 1.28	1.9 ± 0.0
N (%), Kjeldahl	0.11 ± 0.03	0.16 ± 0.02	0.31 ± 0.05	0.62 ± 0.05	0.43 ± 0.03	0.07 ± 0.01
C (%), LECO	1.14 ± 0.31	1.64 ± 0.25	5.15 ± 1.67	8.76 ± 0.45	6.05 ± 0.65	0.99 ± 0.23
N (%), LECO	0.12 ± 0.03	0.16 ± 0.02	0.41 ± 0.11	0.72 ± 0.04	0.51 ± 0.05	0.08 ± 0.01

Table 3.3. cont.

[1](Simpson 1949); [2](MacArthur and MacArthur 1961); [3](Whittaker 1960); [4]Heat load index is a calculation of solar radiation with respect to a southwest/northeast aspect axis (see McCune and Keon 2002); [5]For details on temperature and water indices see Chapter 2; calculated using species with ≥ 60% constancy within groups; [6]For Julian days 180-280; [7]For heatsum description see methods; [8]For Julian days 175-235. *One ELSC site was unused in drier soil water calculations since it never dried to below -0.12 MPa.

Arnica communities line steep seasonally wet swales in the Bridger and Gallatin Mountains of south-central Montana (personal observation). A community dominated by *Arnica longifolia* that co-occurs with *Poa reflexa*, and *Ranunculus eschscholtzii* has been reported from sub-alpine ledges and draws in Grand Teton National Park (Gregory 1983).

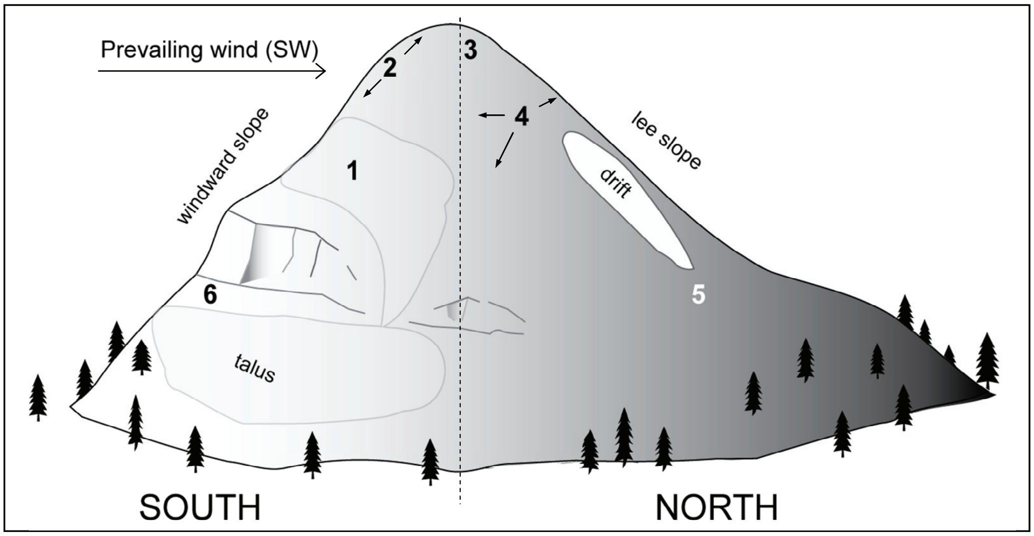
Ecosystem Comparisons

Vegetation

Overview We identified six Washburn communities: ELSC, SECA-ASKE, ERRY-OXLA, CAEL-ASAL, CAPA-ARSC, and ARRY occurring on south facing talus, southern rocky slopes, east/west slopes near ridges, northern lee slopes, snowmelt meadows, and south facing ledges respectively (Fig. 3.4). Three deserve special attention. Talus communities (e.g. ELSC) are common but are poorly described in the North-Central Rockies. The ridge community (i.e. ERRY-OXLA) is noteworthy because it is dominated by GYE endemics (*Erigeron rydbergii, Oxytropis lagopus*). Finally, although Arnica ledge communities (e.g. ARRY) range at least from the Tetons in Wyoming (Gregory 1983), to northern Montana (Damm 2001), this information is unpublished.

Structure and Physiognomy Vegetation cover, height, and clumping are determinants of physiognomy. Mean cover, an index of photosynthetic capacity, was highest in dry dense turf CAEL-ASAL (97%) and snowdrift CAPA-ARSC (88%) communities, lower on rocky sites (41%-65%), and lowest on talus (9%) and ledges (15%) (Table 3.3). Vegetation on ridgetops was clumped, especially short/prostrate (5-10 cm), and often dominated by cushion plants (*Astragalus kentrophyta, Sedum lanceolatum, Draba incerta*) (Table 3.1, Fig. 3.4). Rocky communities (ELSC, SECA-ASKE) were the most physiognomically heterogeneous, with taller (*Senecio canus, Elymus scribneri,* robust *Poas*) or shorter (*Arenaria obtusiloba, Sedum lanceolatum*) plants appearing with suitable microenvironments. Snowbank sites had taller plants (20-35 cm), mostly multi-spike sedges (i.e. *C. paysonis, C. phaeocephala*), which tended to appear in clumps with bare soil between them (Fig. 3.4). Ledge sites were dominated by still taller plants (30-60cm), especially the rhizomatous *Arnica rydbergii*, which in relatively stable subsites was uniformly distributed and, due to lack of either litter or understory plants, were underlain by bare soil (Fig. 3.4).

<u>Composition</u> On Washburn species richness (mean/total) was highest in dry turf (22/51) and snowbanks (26/55). Richness was lower on vegetated rocky sites (16/27 and 17/32), still lower on talus (9/21) and lowest on ledges (4/5). This trend indicates that richness generally increases with resource availability (soil availability/nutrients) regardless of competition (indicated by high vegetation cover). The exception may be the ledge community where, despite low cover, *Arnica rydbergii* may shade out potential competitors. Simpson and Shannon diversity parallel richness with lower diversity in ledge (0.47/0.09) than in other communities (0.8-0.94 / 2.3-3.2) (Table 3.3).



	COMMUNITY NAME	SITE DESCRIPTION	PHYSIOGNOMY	ENVIRONMENT			
				TEMP	H2O	ROCK	OM
1	ELSC	Talus	Clumped, variable	HI	HI	HI	LO
2	SECA-ASKE	Rocky S. facing	Clumped short veg.	HI	MED	MED	MED
3	ERRY-OXLA	Rocky and ridgetop	Clumped short veg.	MED	LOW	MED	MED
4	CAEL-ASAL	Dry dense turf	Dense short turf	MED	LO	LO	HI
5	CAPA-ARSC	Snowbank	Fairly dense tall turf	LO	HI	LO	HI
6	ARRY	Ledge	Open tall herb	HI	HI	HI	LO

Figure 3.4. Sketch of the general distribution, physiognomy, and environmental characteristics of the six identified communities. OM = Soil organic matter.

Productivity We use soil organic matter (Lawson and LECO Carbon) as a long term index of production (Table 3.3). High cover turf (13%) and snowmelt (10%) communities have highest levels of organic matter (OM), rocky communities have lower OM (3-5%), while ledge and talus communities have the lowest OM levels (2%). Similarly total N (Kjeldahl and LECO), falls from turf (0.6-0.4%) to rocky types (0.4-0.2%) to ledge/talus (0.11-0.07%). Given these trends annual productivity of turf sites may be five times that of rocky and talus sites.

Our 'fossil record of production' has three assumptions. (1) The time available for biologically driven carbon accumulation is similar among vegetation types. (2) The belowground fraction of biomass (root/shoot ratios) varies little among vegetation types. This assumption is supported by the fact that a large fraction of alpine biomass is stored belowground (Billings1999). Note that roots may be more concentrated in upper layers of graminoid communities resulting in higher depositions of OM into surface soils. This may cause ‘production’ estimates for graminoid communities to be overestimated. (3) Decomposition of organic matter is similar across vegetation types. Since decomposition is more rapid in warmer soils, local productivity (accumulation of OM) on south slopes may be underestimated.

Environment

Our analyses indicate that soil water, temperature, and soil characteristics (including soil availability), are the primary determinants of plant distributions on Mt. Washburn. These topics are briefly discussed below.

Water We modeled the seasonal drying of soils with sigmoidally declining curves [$\overline{r^2} = 0.96$, $\overline{p} < 0.001$ (points added/deleted to 9 models); $\overline{r^2} = 0.89$, $\overline{p} = 0.014$ (no points added/deleted); Appendix B.2]. While soils at all six communities became dry in the late summer, two communities (ELSC talus and CAPA-ARSC snowbanks) reach dehydration much later than other types (Fig. 3.5a). Soils were wetter than -1.5 MPa, the permanent wilt point of plants (Lambers et al. 1998), for approximately 20 days longer at snowbank sites than dry turf communities i.e. CAEL-AROB, SECA-ASKE, and ERRY-OXLA (Fig. 3.5a). Wet talus soils (demonstrated by ELSC) are common in the alpine (Körner 2003) though they are mechanically limiting to plants due to slope instability and lack of nutrient availability.

Although soil moisture was important in determining community composition (Table 3.2, Fig. 3.3), it was unassociated with either vegetation cover or richness (Table

3.4). Low moisture in dense *Carex elynoides* meadows may be a function of the plants themselves depleting soil water since these sites are generally well watered by wind deposited snow in the spring (cf. Körner 2003, pg. 132). In contrast, barren talus areas were often wet, although as noted above, they lacked other necessary components for plant survival (e.g. stable and productive substrates).

<u>Temperature</u> We modeled the seasonal rise and fall of soil temperature with quadratic equations ($\overline{r^2} = 0.66$, $\overline{p} = 0.002$, Appendix B.3). Soil temperature (heat sum/maximum temperature) fell from ledge (340/18º) through south (186/18º), to ridge (101/15º), to dry turf (56/14º) to snowbank (14/12º; Table 3.3). Temperatures on south facing talus soils were lower than expected, due perhaps to the insulating properties of rock over the soils, or evaporative cooling. Our soil models agree with long term air temperature data that warmest temperatures occur around Julian day 210, i.e. July 29 (Figs. 3.2c, 3.5b).

We used the number of days with soil temperatures above 10º C as an index of growing season length. Growing season is much shorter at snowdrift sites than at other communities (Table 3.3, Fig. 3.5b). Indeed, the brevity of the moist/warm soil season of north-facing turf communities (i.e. CAEL-ASAL, CAPA-ARSC) along with their high productivity indicates that plants in these communities are active well before soils reach 10ºC.

Soil temperature was negatively associated with both vegetation cover and richness (Table 3.4). Higher cover frequently occurred on colder north facing slopes since these areas were less exposed to high winds which blow continually from the southwest and prevent soil accumulation and non-prostrate growth (Figs. 3.2b, 3.4).

Soil Characteristics Bareground (soil surface cover) declined from snowbank and dense turf (86%), to rocky turf (51%), rocky south faces and ledges (31%, 21%) and talus (2%) (Table 3.3). It was well correlated with both vegetation cover and community richness ($r = 0.93$ and $r = 0.79$ respectively; $p < 0.001$; Table 3.4). The correlation is probably due to a cycle including deposition of soil with snow on lee sites, storage of melt water in captured soil, and growth of plants which capture more soil/water. That the soil of lee sites is wind deposited is demonstrated by its silt enrichment relative to that of more wind scoured sites (39% vs. 32%; Table 3.3)

Carbon and nitrogen (%) fall from lee sites on dense turf (≅ 10, 0.6) and under snowbanks (≅ 10, 0.5), to windswept sites including ridges (≅ 5, 0.3), rocky turf (≅ 2, 0.2), talus (≅ 2, 0.1), and ledges (≅ 2, 0.01)(Table 3.3). The decline is well correlated with cover and richness due to processes of biologically driven soil formation ($r \cong 0.8$, 0.6, $p < 0.001$; Table 3.4). In accordance with other alpine studies, soil nitrogen on Washburn appears to be a function of soil organic matter which in turn is a function of soil acidity (Fig. 3.3a; Rehder 1970).

Phosphorus availability (mg kg^{-1}) declines from talus (45) and snowbank (36) through dry dense turf (29) and ledges and rocky turf types (28, 23, 21) (Table 3.3). Except for enrichment of talus sites (source not hypothesized), locally high levels of phosphorous are probably due to both capture of the nutrients by plants and deposition (with silt) on lee slopes.

Conductivity and pH reflect salinity and water movement but probably have little direct effect on plant performance (Lambers et al. 1998). Acid soils under snowbanks (pH = 5.6) are due to leaching of bases by melt water (cf. Bridges 1978). The relatively high pH (7.02) and conductivity (21 mmhos cm^{-1}) of ledge sites is likely due to delivery of water containing calcium and magnesium from cliff areas located above (Table 3.3, Fig. 3.4).

Regional Floristic Comparisons and Application of Island Biogeography

We found that richness per unit area increases from Mt. Washburn through the N. Absarokas and Beartooth Plateau (Fig. 3.6). The paucity of species on Washburn might be attributed to major environmental factors distinguishing the ranges, i.e. precipitation and substrate. Precipitation across the three ranges loosely parallels species richness (cf. Michalet et al. 2002), i.e. it is lowest on the driest range, Washburn (278 mm yr^{-1} at Canyon Village; 760 mm yr^{-1} on Parker Peak; Fig. 3.2), and higher on the wetter Absaroka ($\cong$ 1300 mm yr^{-1}) and Beartooth ($\cong$ 840 mm yr^{-1}) ranges. Substrate is a less likely explanation since the N. Absaroka and Washburn have very similar andesitic substrates (T. Feeley personal comm. 2005) but drastically different levels of predicted richness per unit area (Fig. 3.6).

Lower richness on Washburn may also be due to its small size and isolation relative to the N. Absarokas and Beartooths (i.e. island characteristics; MacArthur and Wilson 1963, 1967). Washburn's planar area above treeline is approximately 0.76 km^2, and its alpine is isolated; >50 km away from nearest neighboring alpine areas. In contrast, the Absarokas and the Beartooths have planar areas above treeline of 2384 km^2

and 768 km^2 respectively (Hadley 1987), and are not isolated; the Absaroka and Beartooth Ranges are directly adjacent to each other (< 5km) and to other alpine areas (e.g. the Gros Ventre, Gallatin Range and Madison Range).

Table 3.4. Pearson product moment correlations of vegetation cover and richness to environmental variables.

	Vegetation cover		Richness	
	r	*p*-value	*r*	*p*-value
Topography and solar radiation				
Elev. (m)	-0.023	0.890	-0.074	0.649
Slope (degrees)	-0.554	<0.001	-0.407	0.009
Aspect (deg. from N)	-0.659	<0.001	-0.645	<0.001
Solar radiation (MJ cm^{-2} yr^{-1})	-0.631	<0.001	-0.699	<0.001
Heat load index	-0.343	0.030	-0.489	0.001
Soil temperature at 15 cm				
Observed max temp.(˚C)	-0.520	0.001	-0.492	0.001
Predicted max temp.(˚C)	-0.466	0.002	-0.452	0.003
Pred. day of max. temp [1]	-0.222	0.168	-0.049	0.764
Heatsum [2]	-0.446	0.004	-0.428	0.006
Days above 10˚C [1]	-0.658	<0.001	-0.570	<0.001
Soil moisture at 15 cm				
Days wetter than -0.12Mpa [3]	-0.330	0.038	-0.172	0.289
Days wetter than -0.25Mpa [3]	-0.066	0.696	0.209	0.208
Days wetter than -1.5Mpa [3]	-0.062	0.711	0.219	0.188
Days wetter than -2.5Mpa [3]	-0.066	0.696	0.215	0.194
Soil texture				
% Cover of surface soil	0.930	<0.001	0.787	<0.001
% Cover of surface rock	-0.930	<0.001	-0.787	<0.001
% Sand	-0.352	0.026	-0.264	0.100
% Clay	-0.355	0.025	-0.299	0.061
% Silt	0.445	0.004	0.341	0.031
Soil pH and conductivity				
pH	-0.288	0.072	-0.477	0.002
Conductivity (mmhos cm^{-1})	0.525	0.001	0.236	0.142
Soil Nutrients				
P (Bray, mg kg^{-1})	-0.227	0.158	-0.201	0.215
%C in soil (Lawson)	0.740	<0.001	0.563	<0.001
%N in soil (Kjeldahl)	0.802	<0.001	0.576	<0.001
%C in soil (LECO)	0.815	<0.001	0.614	<0.001
%N in soil (LECO)	0.822	<0.001	0.629	<0.001

[1] Julian days 180-280, [2] For heatsum description see methods, [3] Julian days 175-235.

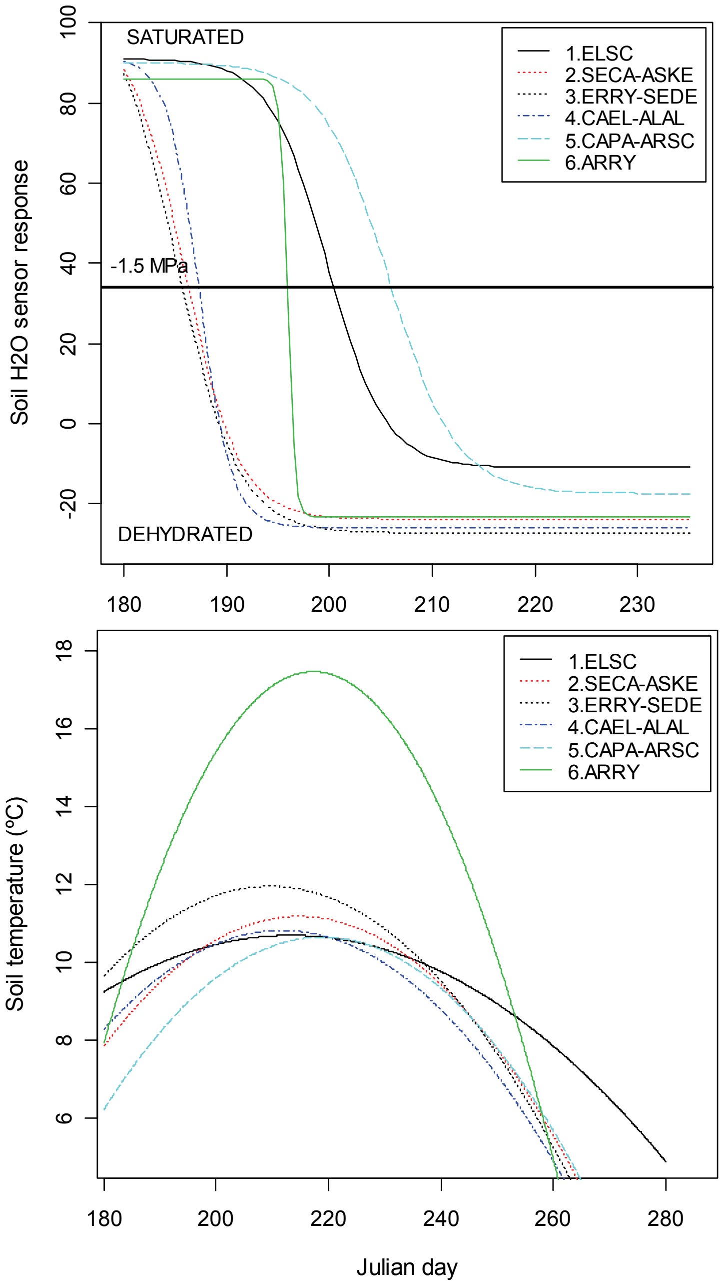


Figure 3.5. Seasonal variation in soil water and temperature at identified communities. (a) Soil moisture at 15 cm depth. Models are sigmoidal (logistic) regressions. Horizontal line indicates the 'wilting point' of vegetation (-1.5 MPa) along the response axis. (b) Soil temperature at 15 cm depth.

Lower richness on small remote islands is due to low rates of immigration and high rates of extinction. Such rates can be inferred by steep tails at the rare end of Rank

Abundance Dominance (RAD) plots (Wilson et al. 1996, Hubbell 2001). This is true since the number of rare species will decease markedly as migration decreases and extinction increases (Hubbell 2001). Notice that the tail of Washburn species abundance curve falls off more rapidly than curves from the Beartooth Plateau or Northern Absarokas (Fig. 3.7). Our results (that smaller alpine islands have lower levels of richness per unit area) agrees with a study of thirteen alpine islands in the southern and central Rocky Mountains (Hadley 1987), and with other theoretical applications of island biogeography to isolated mountain systems (e.g. Bruun and Moen 2003, Halloy and Mark 2003).

Conclusions/Management Implications

Our documentation of the Washburn alpine should be of interest for three reasons. First we describe alpine communities and the alpine ecology of a substrate (andesitic-volcanic) essentially unstudied in the Northern Rockies. Second, we recognize several poorly documented vegetation types, and a globally rare community (i.e. ERRY-OXLA) relevant to YNP land managers. Finally we propose that Washburn has low levels of richness consistent with a small isolated island ecosystem, and may therefore be highly vulnerable to habitat fragmentation.

Three threats to the Washburn alpine ecosystem should be considered: 1) human physical disturbance (trampling/trail road building), 2) exotic plant invasion, and 3) climate change.

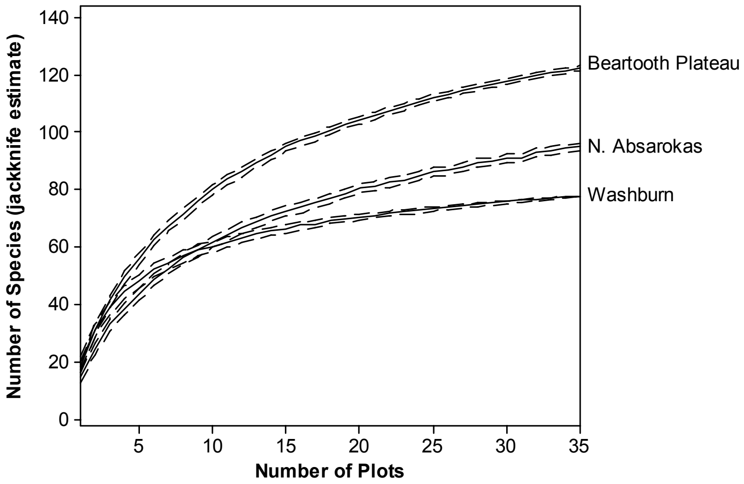


Figure 3.6. Species area curves from jackknife procedure for the Washburn Range, nine mountains in the N. Absaroka-Volcanics, and six mountains on the Beartooth Plateau. Dashed lines are 95% confidence intervals.

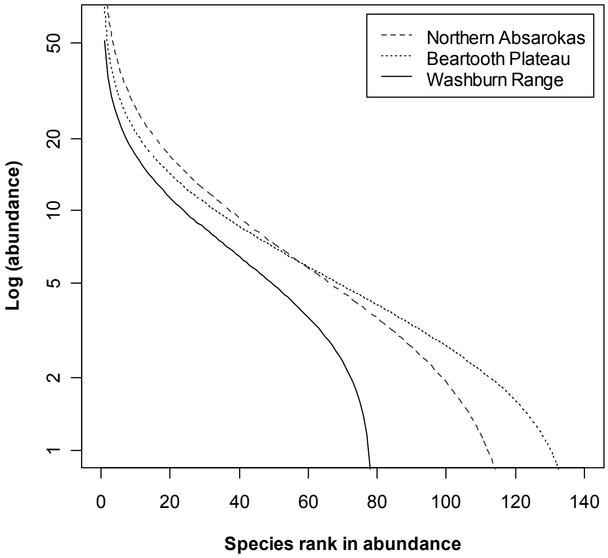


Figure 3.7. Rank Abundance Dominance (RAD) curves for the Beartooth, N. Absaroka and Washburn Ranges. Abundance responses were fit to a log-Normal distribution (Preston 1948).

1) As a result of its easily attained summit and open fire-lookout, anthropogenic impacts in the form of roads, structures, and trails (both marked and unmarked), are obvious throughout the mountain. Physical trampling decreases alpine vegetation density and diversity, and increases erosion (Grabherr 1982). Thus hiker impacts should be

restricted to existing trails and roads. Similarly, additional road building and anthropogenic structures will decrease the already small size of the Washburn alpine.

2) Despite the general resistance of alpine areas to weed invasion (cf. Weaver et al. 2001), invasion vectors along with continual disturbance particularly within and along roadsides has resulted in an unusually high number of invasive species within the Washburn alpine. These include rhizomatous grasses (*Bromus inermis*), rhizomatous forbs (*Polygonum aviculare*) and annual/biennial forbs (*Chenopodium rubrum, Descurainia sophia,* and *Lepidium* sp.). Weed invaders might be managed by minimizing disturbance, and judicious use of herbicides on roadsides.

3) Alpine areas are likely to be greatly affected by global warming (Billings 2000, Halloy and Mark 2003). In the Greater Yellowstone Ecosystem, treelines are expected to move up in elevation, decreasing alpine area, and reducing alpine diversity (Romme and Turner 1990). While it is essentially impossible to manage for global climate change, it should be recognized that small, remote alpine islands like Mt. Washburn may be particularly vulnerable to this process.

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Literature Cited

Aho, K. 2006. Multivariate clustering for objective classification of vegetation data. *In* 2006 Billings Land Reclamation Symposium, June 5-8, 2006, Billings MT . Jointly published by BLRS and ASMR 3134 Montavista Rd., Lexington KY 40502.

Baker, W. L. 1983. Alpine vegetation of Wheeler Peak, New Mexico U.S.A: gradient analysis, classification and biogeography. Arctic and Alpine research. 15(2) 223-240.

Bamberg, S. A., and J. Major. 1968. Ecology of the vegetation and soils associated with calcareous parent materials in three alpine areas in Montana. Ecological Monographs. 38: 127-167.

Billings, W. D. 2000. Alpine Vegetation of North America. pp. 537- 572. *In* North American Terrestrial Vegetation 2nd edition, Barbour, M. D. and Billings, W. D. eds. Cambridge Univ. Press, Cambridge.

Billings, W. D., and L. C. Bliss. 1959. A snowbank alpine environment and its effects on vegetation, plant development, and productivity. Ecology 40(3): 388-397.

Blumer, and Diemer 1996. The occurrence and consequences of grasshopper herbivory in an alpine grassland, Swiss central Alps. Arctic, Antarctic and Alpine research. 28; 435-440.

Bray J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities in southern Wisconsin. Ecological Monographs. 27: 325-349.

Bremner, J. 1996. Total nitrogen, pgs. 1085-1133, *in* Klute, A. (ed.) 1996. Methods of soil analysis I: physical and mineralogical methods. Soil Science Society of America. American Society of Agronomy, Madison WI

Bridges, E. M. 1978. World soils. Cambridge University Press. London, UK.

Brogden, H. E. 1949. A new coefficient: application to biserial correlation and to estimation of selective efficiency. Psychometrika. 14: 169-182.

Bruun, H. H., and J. Moen. 2003. Nested communities of alpine plants on isolated mountains: relative importance of colonization and extinction. Journal of Biogeography. 30: 297-303.

Caicco, S. L. 1983. Alpine vegetation of the Copper Basin area, South-Central Idaho. Master's Thesis, University of Idaho. 99 pages.

Cooper, S. V., Lessica, P., and D. Page-Dumroese. 1997. Plant community classification for alpine vegetation on the Beaverhead National Forest, Montana. Gen. Tech. Rep. INT-GTR -362. Ogden UT: U.S. Department of Agriculture, Forest Service Intermountain Research Station. 61 pgs.

Damm, C. 2001. A phytosociological study of Glacier National Park, Montana, USA, with notes on syntaxonomy of alpine vegetation in the western United States. Doctoral dissertation. University of Göttingen. Göttingen, Germany. 305 pgs.

Daubenmire, R. 1959. A canopy coverage method of vegetation analysis. Northwest Science. 33: 43-64.

Dorn, R. D. 1992. Vascular Plants of Wyoming. Mountain West Publishing. Cheyenne WY.

Douglas, G. W., and L. C. Bliss. 1977. Alpine and high subalpine plant communities of the North Cascades range, Washington and British Columbia. Ecological Monographs. 47: 113-150.

Dufrêne M. & Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetric approach. Ecological Monographs. 67(3): 345-367.

Faith, D. P., Minchin, P. R. & Belbin L. 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio. 69: 57-68.

Feeley, T. 2005. Vulcanologist/geologist, Montana State University.

Gee, G., and J. Bauder. 1986. Particle size analysis, pgs. 383-412, *in*: Klute, A. (ed.) 1996. Methods of soil analysis I: physical and mineralogical methods. Soil Sci. Soc. America. Madison, WI. 1188 pgs.

Goodman, L., and W. Kruskal. 1954. Measures of association for cross-validations. Journal of the American Statistical Association. 732-764.

Grabherr, G. 1982. The impact of trampling by tourists on a high altitudinal gradient in the Tyrolean Alps. Vegetatio. 48: 209-217.

Gregory, S. 1983. Subalpine forb community types of the Bridger-Teton National Forest, Wyoming. Master's thesis, Montana State University, Bozeman, MT.

Hadley, K. S. 1987. Vascular alpine distributions within the central and southern Rocky Mountains, U.S.A. Arctic and Alpine research. 19(3): 242-251.

Halloy, S. R. P., and A. Mark. 2003. Climate change effects on alpine plant biodiversity: a New Zealand perspective on quantifying the threat. Arctic, Antarctic, and Alpine Research. 35(2): 248-254.

Harpole, W. S., and D. Tilman. 2006. Non-neutral patterns of species abundance in grassland communities. Ecology letters. 9: 15-23.

Hartman, E. L., and M. L. Rottman. 1988. The vegetation and alpine vascular flora of the Sawatch Range, Colorado. Madrono. 35(3): 202-225.

Hitchcock, C. L., and A. Cromquist. 1973. Flora of the Pacific Northwest. The University of Washington Press, Seattle, WA.

Hubert, L. J. and J. R. Levin. 1976. A general framework for assessing categorical clustering in free recall. Psychol. Bull. 83: 1072-1080.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton and Oxford, UK.

Hunter, K. B., and R. E. Johnson. 1983. Alpine flora of the Sweetwater Mountains, Mono County, California. Madrono. 30: 89-105.

Jacobs, J. 1974. Quantitative measurement of food selection. Oecologia. 14: 412-417.

Johnson, P. L., and W. D. Billings. 1962. The alpine vegetation of the Beartooth Plateau in relation to cryptogenic processes and patterns. Ecological Monographs. 32: 105-135.

Keefer, W. 1987. The geologic story of Yellowstone National Park. Yellowstone Library and Museum Assoc.

Komárková, V. 1979. Alpine vegetation of the Indian Peaks area, Front Range Colorado Rocky Mountains. PhD dissertation University of Colorado, Boulder. 591 pgs.

Komárková, V., and P. J. Weber. 1978. An alpine vegetation map of Niwot Ridge, Colorado. Alpine and Arctic Research. 10(1): 1-29.

Körner, C. 2003. Alpine plant life: Functional plant ecology of high mountain ecosystems, 2nd edition. Springer-Verlag, Berlin. 338 pgs.

Kruskal, J. B. 1964. Nonmetric Multidimensional Scaling: a numerical method. Psychometrika. 29: 115-129

Lackschewitz, K. H. 1994. Beartooth alpine flora, pgs. 105-113. *In*: Anderson, B. (ed.) Beartooth Country: Montana's Absaroka and Beartooth Mountains. Unicorn Publishing, Helena MT.

Lambers, H., F. S. Chapin III & T. L. Pons. 1998. Plant Physiological Ecology. Springer-Verlag, New York, U.S.A.

Lance, G. N., and W. T. Williams. 1967. A general theory of classification sorting strategies II clustering systems. Computer Journal 10: 271-277.

Lewis, M. E. 1970. Alpine rangelands of the Uinta Mountains: Ashley and Wasatch National Forests. USDA U. S. Forest Service Publication. 75 pgs.

MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. Ecology. 42: 594-598.

MacArthur, R. H., and E. O. Wilson. 1963. An insular theory of insular zoogeography. Evolution. 17: 373-387.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton NJ, USA.

McCune B., and J. B. Grace. 2002. Analysis of ecological communities. MJM software design, Glendale Beach, Oregon.

McCune, B., and D. Keon. 2002. Equations for potential annual direct radiation and heat load. Journal of Vegetation Science. 13: 603-606.

McCune B., and M. S. Mefford. 1999. PC-ORD: Multivariate analysis of ecological data, ver. 4. Mjm software design, Glendale Beach, Oregon.

Michalet, R., Gandoy, C., Joud, D., Pages, J. P., and P. Choler. 2002. Plant community composition and biomass on calcareous and siliceous substrates in the northern French Alps: comparative effects of soil chemistry and water status. Arctic, Antarctic and Alpine research. 34(1): 102-113.

Minchin, P.R. 1987. An evaluation of relative robustness of techniques for ecological ordinations. Vegetatio. 71: 145-156.

Nelson, D. W., and L. E. Sommers. 1996. Total carbon, organic carbon, and organic matter, pgs 961-1010, *in* D. L. Sparks (ed.). Methods of soil analysis, Part 3. Chemical methods. Soil Science Society of America book series number 5. American Society of Agronomy, Madison WI

Oksanen, J. 2005. Community ecology package, vegan ver. 1.6-6. http://www.cran.r-project.org

Olsen, S. R., and L. E. Sommers. 1982. Phosphorous, pgs 416-418, *in* Page, A. L. et al. (eds.). Methods of soil analysis Part 2. Agron Mongr. 9. 2nd ed. ASA and SSSA. Madison, WI.

Palmer, M. W. 1990. The estimate of species richness by extrapolation. Ecology. 71: 1195-1198.

Palmer, M. W. 1991. Estimating species richness: the second order jackknife reconsidered. Ecology. 72:1512-1513.

Parsons, W. H, 1978. K/H geology field guide series: Middle Rockies and Yellowstone. Kendall/Hunt publishing company. 233 pgs.

Pemble, R. H. 1965. A survey of distribution patterns in the Montana alpine flora. Masters Thesis, University of Montana, Missoula. 146 pages.

Preston, F.W. 1948. The commonness and rarity of species. Ecology 29, 254-283.

R Development Core Team. 2006. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Rehder, H. 1970. Zur Ökologie insbesendore Sticekstoffversorgung subalpiner und alpiner Pflanzengsellchschaften im Natrschutzgebiet Scahchen (Wettersteingebirge). DissBot. 6.

Richardson, C. A., Henderson, D. M. 1999. Classification and ordination of the alpine plant communities of Railroad Ridge, White Cloud Peaks, Idaho. Great Basin Naturalist. 59(1): 63-78.

Richmond, G., Mullenders, W., Coremans, M. 1978. Climatic implications of two pollen analyses from newly recognized rocks of latest Pliocene age in the Washburn Range, Yellowstone National Park, Wyoming. Dept. of the Interior, US Geological Survey Geological Survey bulletin 1455.

Roberts, D. W. 2005. Laboratory for Dynamic Synthetic Vegephenomenology, labdsv ver. 1.2-1, http://www.cran.r-project.org

Romme, W. H., and M. G. Turner. 1990. Implications of Global Climate Change for Biogeographic patterns in the Greater Yellowstone Ecosystem. Conservation Biology. 5(3): 573-585.

Rottman, M. L., Hartman E. L. 1985. Tundra vegetation of three cirque basins in the Northern San Juan Mountains, Colorado. Great Basin Naturalist. 45: 87-93.

Rousseeuw, P. J. 1987. Silhouettes: A graphical aid to the interpretation and validation of cluster analysis. J. Comput. Appl. Math. 20: 53-65.

Seagrist, R. V., and K. J. Taylor. 1998. Alpine vascular flora of Buffalo Peaks, Mosquito Range, Colorado USA. Madrono. 45(4) 319-325.

Shultz, C. 1969. Mount Washburn volcano, a major eocene volcanic vent (abs.). Special Paper - Geological Society of America (1969).

Simpson, E. H. 1949. Measurement of diversity. Nature. 163: 688.

Smedes, H. W., and Protska, H. J. 1972. Stratigraphic framework of the Absaroka Volcanic Supergroup in the Yellowstone National Park region: U.S.G.S. Prof. Pap. 720-C, US Gov. Print. Office, Wash. DC, 33 pgs.

Spence, J. R., and R. J. Shaw. 1981. A checklist of the alpine vascular flora of the Teton Range, Wyoming, with notes on biology and habitat preferences. Great Basin Naturalist. 41(2): 232-241

Storer, D. A. 1984. A simple high sample volume ashing procedure for determing soil organic matter. Comm. Soil. Sci. Plant Anal. 15: 759-772.

Taye, A. C. 1995. Alpine Vascular flora of the Tushar Mountains, Utah. Great Basin Naturalist. 55(3): 225-236.

Taylor, S. T., and R. D. Jackson. 1986. Temperature. *In*, pp. 927-941. A. Klute ed. Methods of soil analysis, part 1, physical and mineralogical methods, 2nd edition. Soil Science Society of America Inc. Madison, WI.

Thilenius, K. F., and D. R. Smith. 1985. Vegetation and Soils of an Alpine Range In the Absaroka Mountains, Wyoming. USDA Forest Service General Technical Report RM-121, 18 pgs. Rocky Mountain Forest and Range Experiment Station, Fort Collins Colo.

Thomas, G. 1996. Soil pH and acidity. Pgs 475-490. *In* Methods of soil analysis I: Physical and minerogical methods. Klute, A. (ed.). 1996. Soil Sci. Soc. America. Madison WI. 1188 pgs.

Tomback, D., Anderies, A., Carsey, K., Powell, M., Mellmann-Brown, S. 2001. Delayed seed germination in whitebark pine and regeneration patterns following the Yellowstone fires. Ecology. 82 (9): 2587-2600.

Urbanczyk, S. A., and D. A. Henderson. 1994. Classification and ordination of alpine plant communities, Sheep Mountain, Lemhi County, Idaho. Madrono. 41(3): 205-223.

USGS. 1972. Geologic Map of Yellowstone National Park. Miscellaneous Geologic Investigations Map 1-711. USGS, Department of Interior Reston, VA, USA.

Venables S., and B. Ripley. 2005. MASS ver. 7.2-20. http://cran.r-project.org

Walter, H.,and H. Leith. 1967. Klimadiargramm-Weltaltas. Gustav Fisher, Jena.

Weaver, T. and D. Dale. 1974. Pinus albicaulis in central Montana: environment, vegetation and production. American Midland Naturalist 92: 222-230.

Weaver, T., Gustafson, D., and J. Lichthardt. 2001. Exotic plants in early and late seral vegetation of fifteen northern Rocky Mountain environments (HTs). Western North American Naturalist. 61(4): 417-427.

Western Regional Climate Center (WRCC). 2006. Reno NV. 89512.

Whittaker, R. H. 1960. Vegetation of the Sisikyou Mountains, Oregon and California. Ecological Monographs. 30: 279-338.

Willard, B. E. 1979. Plant Sociology of alpine tundra, Trail Ridge, Rocky Mountain National Park, Colorado. Quarterly of the Colorado school of mines. 74: 4.

Wilson, J. B., Wells, T. C. E., Trueman, I. C., Jones, G., Atkinson, M. D., Crawley, M. J., Dodd, M. E., J. Silvertown. 1996. Are there assembly rules for plant species abundance? An investigation in relation to soil resources and successional trends. The Journal of Ecology. 84 (4): 527-538.

Wishart, D. 1969. An algorithm for hierarchical classifications. Biometrics 25: 165-170.

CHAPTER 4

ALPINE COMMUNITIES OF THE ABSAROKA VOLCANICS

Introduction

North American alpine vegetation occurs on the Mountains of Labrador and Appalachians in the east, and along the length of the Rocky Mountain and Coastal Cordilleras in the west (Billings 2000). Within the Rockies, most studies of alpine vegetation have been conducted on granitic, limestone, or sandstone/shale substrates. Studies on granite sites extend from the Brooks Range in Alaska (Cooper 1989), through Montana (Johnson and Billings 1962), Idaho (Urbanczyk and Henderson 1994), Wyoming (Billings and Bliss 1959), Utah (Briggs and MacMahon 1983), and Colorado (Komárková 1979, many others). Studies have been conducted on limestone substrates from Alaska (Cooper 1989), through the Canadian Rockies (Knapik et al. 1973), Montana (Bamberg and Major 1968), Idaho (Richardson and Henderson 1999), Utah (Bockheim 1997), and Colorado (Hartman and Rottman 1988). Alpine vegetation of sandstone/shale substrates has been studied in Alberta (Hrapko and LaRoi 1978) and Colorado (Langenheim 1962).

Although volcanic substrates (e.g. andesites) are common within alpine environments of North American, their vegetation remains largely unstudied, particularly in the Northern Rocky Mountains. Previous phytosociological work exists for the volcanic regions in the North Cascades (Douglas and Bliss 1977), Sierras (Hunter and Johnson 1983), Great Basin Mountains (Taye 1995), and the Southern Rockies (Rottman and Hartman 1985, Baker 1983). Worldwide, the physical environments of andesitic alpine vegetation have been studied in the Sangre de Cristo range in New Mexico (Baker 1983), and on volcanoes in Asia (Tateno and Hirose 1987), Africa (Young and Peacock 1992), and Central and South America (Islebe and Velázquez 1994).

Our paper describes andesitic-alpine vegetation of the Absaroka Mountains. The Absaroka Volcanic Supergroup which comprises the substrate for most of the Absaroka Range is the largest Eocene volcanic region in the Northern Rockies ($\cong$ 25,000 km^2, Hiza 1999), and contains one of the largest areas of concentrated alpine habitat in North America (Hadley 1987). Except for a small, domestically grazed region in the southern part of the range (Thilenius and Smith 1986), the Absaroka alpine is unstudied.

Goals

Our project focused on three tasks: 1) Establishing an ecosystem-level classification of communities in the Absaroka Volcanics. 2) Comparing vegetation of these communities with each other and with other North American alpine communities on similar and dissimilar substrates. 3) Determining the relationships between alpine communities and their physical environments.

Study Area

Geology

We studied nine volcanic peaks in the Northern Absarokas located in or near the northeast boundary of Yellowstone National Park (Fig. 4.1). The primary surficial substrates are from the Absaroka Volcanic Supergroup, specifically the Lamar River

Formation of the Washburn Group, and the Wapiti Formation from the Sunlight Group (Smedes and Prostka 1972; Figs., 4.1, 4.2a). The Lamar River Formation, deposited between 49 and 47 million years ago, consists of medium-brown andesitic lavas, alluvial volcanoclastics (sedimentary accumulations of newly erupted volcanic products), minor mafic flows, vent facies (rocks produced near the eruptive source), and intrusive rocks (Smedes and Prostka 1972). The younger Wapiti Formation overlies the Lamar River Formation on summits of most Absaroka peaks in the study area. It includes dark brown volcanic breccias, with interfingered vent and alluvial facies (Protska et al. 1975). The mineralogical composition of both formations is mostly andesitic, though flows often contain diverse inclusions.

Climate

The Northern Absaroka climate is similar to other mountainous areas in the Northern and Central Rocky Mountains (cf. Billings 2000, Damm 2001, Weaver 1990; Fig. 4.2 b,c). Precipitation exceeds evaporation all twelve months of the year. At sub-alpine altitudes in the region (NE Entrance; elev. 2241m; Fig 4.2b) highest amounts of precipitation occur during the spring as rainfall. Near alpine elevations (Fisher Creek; elev. ≅ 2800m; Fig. 4.2c) most precipitation occurs as snow during winter months (i.e. Nov.-March). Annual precipitation increases dramatically with altitude (Figs. 4.2 b, c). The Northern Absarokas alpine appears to have a shorter growing season (≅ 3 months of frost free temperatures; Fig. 4.2b, c) than alpine areas in the Niwot Range in Colorado (4 months), or the sunny Sierras (8 months; Billings 2000).

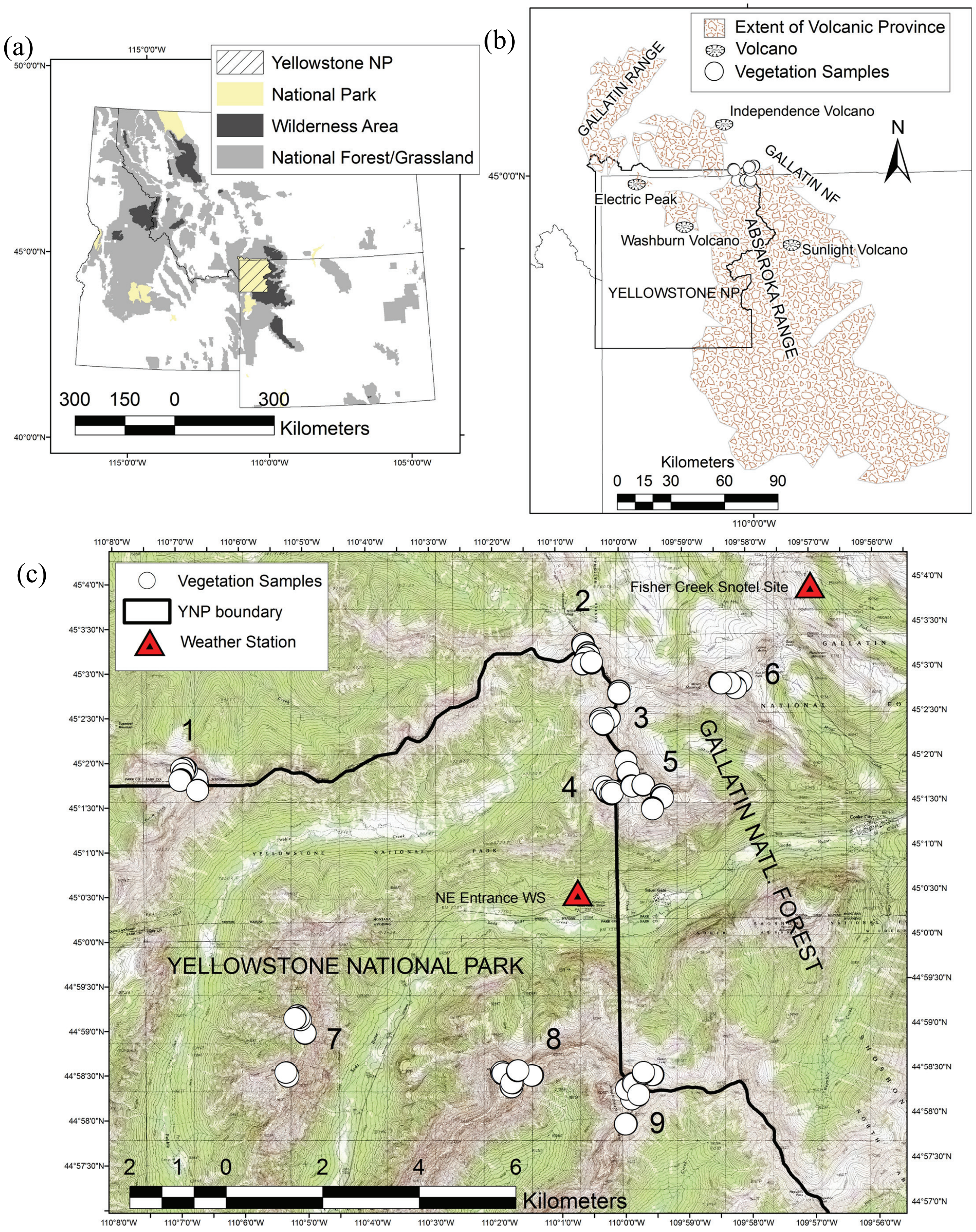

Figure 4.1. N. Absaroka Study Area. (a) Location of YNP and other federal lands. (b) Extent of the Absaroka volcanic province, important eruptive sources, and locations of sampled mountains; volcanic geology based on Feeley (2003). (c) Sampled mountains and locations of weather stations. 1. Cutoff, 2. Wolverine, 3. Sunset, 4. Meridian, 5. Mineral, 6. Miller, 7. Barronette, 8. Abiathar, and 9. Amphitheatre.

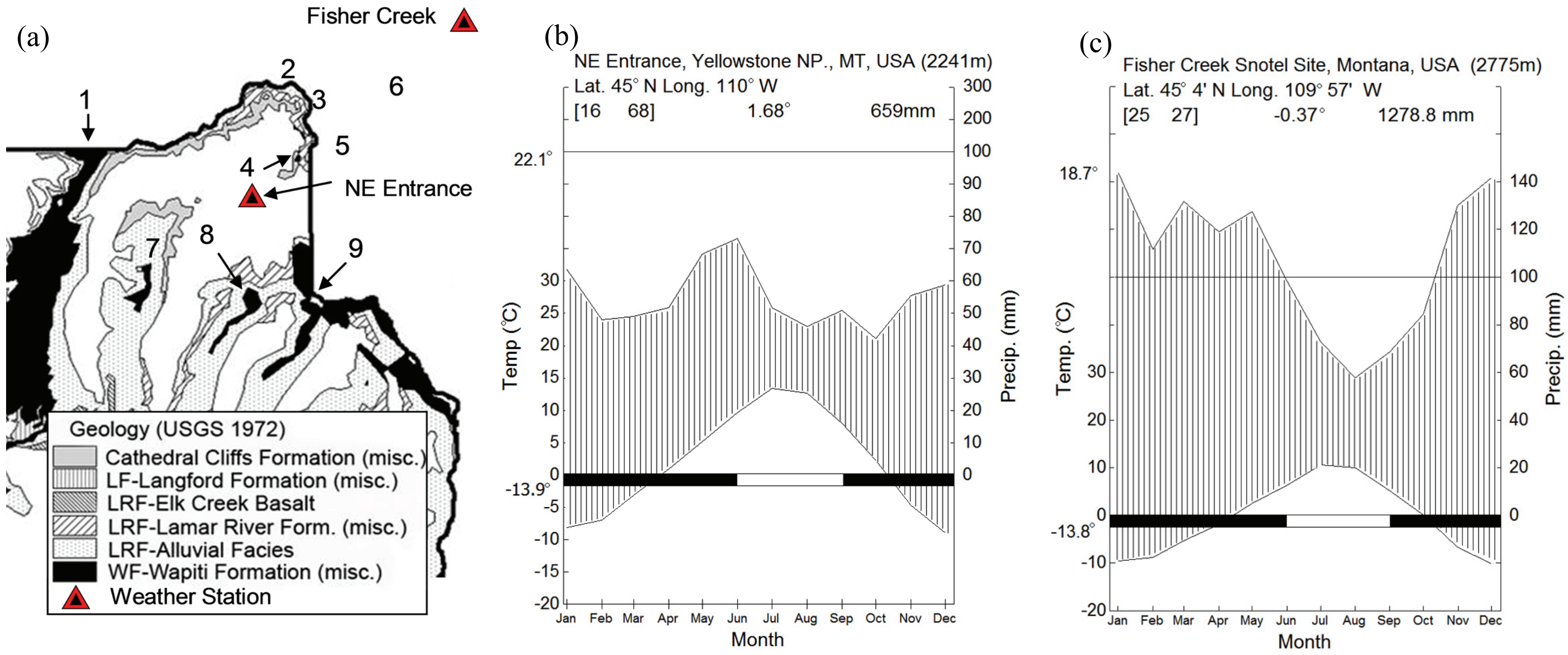

Figure 4.2. Volcanic geology and climatic description of the study area. (a) Locations of Absaroka Volcanic supergroup formations. LF = Langford formation, LRF = Lamar River formation, WF = Wapiti formation, and locations of surveyed peaks: 1. Cutoff, 2. Wolverine, 3. Sunset, 4. Meridian, 5. Mineral, 6. Miller, 7. Barronette, 8. Abiathar, and 9. Amphitheatre. (b, c) Climate diagrams (Walter and Leith 1967) for the Northeast Entrance weather station and the Fisher Creek Snotel site directly adjacent to study area. The upper plotted line indicates average monthly precipitation. The lower plotted line is average mean monthly temperature. The hatched area between the plotted lines indicates the months (in this case all 12 months) that precipitation exceeds evaporation. Text at the top of the figure gives general information about the site, the number of years of temperature and precipitation data were used to create the figure (in brackets), and the overall mean temperature and average yearly precipitation. Along the temperature axis, average daily maximum temperature of the warmest month and average daily minimum temperature of the coldest month are also indicated. The blackened area of the rectangle at the bottom of the figure indicates the frost period (the months where average minimum temperature was below zero degrees). Raw climate data was provided by the Western Regional Climate Center (WRCC 2006).

Anthropogenic Impacts

Due to their location in Yellowstone National Park (YNP), most peaks in our study site have been protected from mining, domestic grazing, and other large-scale anthropogenic impacts. Many Absaroka peaks, however, have small exotic mountain goat (*Oreomnos americanus*) populations (Lemke 2004). While mountain goats may be harmful to alpine ecosystems (Houston et al. 1994), this paper does not attempt to quantify their impact on the Absaroka Volcanics.

Methods

Field Methods

Nine high altitude mountains (>3000m) were sampled to study alpine vegetation of the Absaroka Volcanics. These were Abiathar, Amphitheatre, Barronette, Cutoff, Meridian, Miller, Mineral, Sunset, and Wolverine peaks (Fig. 4.1). While the planar area above treeline for the Absaroka Mountains is 2384 km^2 (Hadley 1987), the nine sampled mountains have broken areas of alpine vegetation encompassing only about 1.2 km^2. Primary alpine environments were sampled on each mountain. These were: ledges at cliff bases, talus slopes, south facing slopes, ridgetops, north facing slopes, and late-melting snowbank sites. East and west facing slopes, the other common units, were omitted because their environments are intermediate between north and south facing environments (Geiger et al. 2003), and their vegetation is expected to be intermediate as well (Aayd and Dix 1964). Two plots were selected from each environmental zone on each mountain.

Random samples were taken in each plot. Plots were sited by placing a 50 meter tape perpendicular to the contour within a homogeneous environmental zone. A ten meter line was staked parallel to the contour starting at a random point on the 50 meter tape. Along the ten meter line, ten 20 x 50cm frames were placed (one at each meter) and sampled for percent cover of all plant species present. The ten frames summed to a $1m^2$ sampling unit.

Within 110 established transects, more than 125 vascular plant species were positively identified. Additional species occurring in the 2 x 10 meter area surrounding the transect line were also recorded. All other encountered species (those occurring in neither the $1m^2$, nor the 2 x 10 meter sampling areas) were also identified and recorded to establish a floral checklist for the region. Voucher specimens for all reported species were placed in the Yellowstone National Park herbarium (YELLO) in Gardiner, MT. Nomenclature follows Dorn (1992).

Environmental data were recorded in each of the 110 vegetation plots. Elevations were determined using Trimble™ GeoExplorer 3, and Trimble™ Pro XR receivers. Readings were differentially corrected at the Montana State University, and Idaho National Engineering and Environmental Laboratory (INEEL) GPS base stations. Magnetic aspect (later corrected with respect to declination) and slope were measured with a Brunton compass. Potential annual direct incident radiation was calculated using an algorithm recommended by McCune and Keon (2002). Soil moisture and temperature indices were determined for communities using indicator species as described in Chapter 2. Surface rock cover was measured by placing a meter stick perforated with eight nails at 1 meter intervals along the 10m vegetation transect line, and calculating the percentage of rock/nail hits. Soil surface cover was calculated as 1 – rock surface cover. Soil samples were taken at all plots to measure elemental constituents (i.e. N, C, P), pH, soil salinity (conductivity), and soil texture (i.e. % sand, % clay, % silt). Carbon and nitrogen were determined using LECO ignition methods (Nelson and Sommers 1996, Bremner 1996). The Bray method was used to determine soil phosphorous (Olsen and Sommers 1982). Conductivity and pH were measured on 1:1 water slurries with appropriate meters (Thomas 1996). Soil texture was measured with the Boyoucous hydrometer method (Gee and Bauder 1986).

Data Analysis

Classification Hierarchical agglomerative clustering was used to segment the vegetation continuum (Goodall 1973). Linkage between samples was established with the flexible beta method (Lance and Williams 1967). The value $\beta = -0.25$ was used since it is highly effective for cluster recovery in vegetation datasets (Aho 2006). Wishart's objective function (Wishart 1969) was used to scale the cluster dendrogram. The optimal classification solution was found by pruning the dendrogram to create the twenty-four simplest classification solutions (2-25 clusters), then evaluating these results with six separate classification evaluators (Appendix C.1). A dissimilarity matrix created with Bray-Curtis dissimilarity (Bray and Curtis 1957, Faith et al. 1987) was used for both classifications and ordinations (described below). For further detail on these procedures see Chapter 7 and Aho (2006).

Ordination Vegetation samples were ordinated with Non-Metric Multidimensional Scaling (NMDS; Kruskal 1964). Although random starting points were also tried, the best (lowest stress) solutions resulted from using PCoA (Principal Coordinates Analysis) scores as initial starting points (cf. Roberts 2005). A tolerance of $1 \cdot 10^{-7}$ was used with 200 iterations to create the scatterplot projection. To improve interpretability of NMDS axes, ordination configurations were rotated with PCoA so that the variance of points was maximized on the first dimension (Minchin 1987).

Environmental Vectors and Environmental Correlations with NMDS Axes The relationship between vegetation distributions and continuous environmental variables was described by finding the direction of maximum correlation between environmental variables and ordination dimensions (Oksanen 2005). These environmental vectors were scaled within ordinations by the strength of their correlation to the NMDS projection of points. The relationship of categorical variables to ordination solutions was quantified with Eq. 4.1 (Oksanen 2005). The strength of association for both continuous and categorical variables was tested for significance by permutating response vectors using a Monte Carlo methodology; 1000 permutations were used for this procedure.

$$r^2 = 1 - SSW / SSTO \tag{4.1}$$

where SSW = within-group sums of squares [scatter with respect to treatment (community) centroids for two dimensions of interest] and $SSTO$ = total sums of squares (overall scatter with respect to the scatterplot centroid for the same two dimensions of interest).

Indicator Species Analysis Indicator species analysis was used to quantitatively establish association between particular species and vegetation types identified with flexible-β clustering. To calculate *p*-values for the test of no association between indicator values and assigned classes, groups were randomly assigned to sample units with a Monte Carlo procedure using 1000 permutations (Dufrêne and Legendre 1997).

<u>Diversity measures</u> Diversity of communities identified with cluster analysis was described with three indices: gamma, beta and alpha diversity. Gamma-diversity is simply total richness, beta-diversity describes sample heterogeneity, and alpha-diversity measures species richness and heterogeneity (McCune and Grace 2002). We used two methods to calculate β-diversity. The first (Eq. 4.2) utilized the equation suggested by Whittaker (1960).

$$\beta_W = S/\alpha - 1 \tag{4.2}$$

Where β_W = Whittaker (1960) beta-diversity measure, S = total number of species for all samples recorded in a dataset (i.e. gamma diversity), α = the average sample diversity where each sample is a standard size and diversity is measured as species richness (Macgurren 1988).

The second measure was simply average dissimilarity (Bray-Curtis) of plots within in a particular community type (Porembski et al. 1996, Harrison 1997). Average dissimilarity is a good measure of the unstructured heterogeneity of data although it cannot describe rates of species turnover (Velland 2001). We also used two different measures to calculate α- diversity; the Shannon-Wiener (Eq. 4.3) and Simpson (Eq. 4.4) indices.

$$p_i = \frac{x_i}{\sum_{i=1}^{S} x_i}$$

$$H' = -\sum_{i=1}^{S} p_i \ln p_i \tag{4.3}$$

$$D = 1 - \sum_{i=1}^{S} p_i^2 \tag{4.4}$$

Where *pi* = the proportion of cover at a site of interest belonging to species *i*, x_i = cover of species *i*, *S* = total number of species, *H'* = Shannon Wiener index (MacArthur and MacArthur 1961), *D* = Simpson's index (Simpson 1949).

Software Classifications were created using PC-ORD (McCune and Mefford 1999). Algorithms for classification evaluators were coded in R (R Development Core Team 2006). NMDS Ordinations, environmental vector analyses, and indicator species analyses were run in R using MASS (Venables and Ripley 2005), labdsv (Roberts 2005), and vegan (Oksanen 2005) libraries.

Identification of Communities

Classification

Our classification divided the vegetation continuum into four "super" groups, each with component communities. The super-groups represented four major environmental/vegetation types (1. ledge/cliff-base, 2. talus, 3. ridgetops/turf, and 4. late-snowmelt). Low β-diversity in the ledge/cliff-base type (average Bray-Curtis dissimilarity = 0.38) indicated low heterogeneity, and that no further subdivision was needed. In contrast, uniformly high β diversity in the other three super groups (0.83, 0.73, and 0.75, for talus, turf and snowbank respectively) mandated subdivision (B. McCune per. comm.). These three groups were each separately reclassified revealing an optimum of four talus subclasses, five turf subclasses, and five snowbank subclasses. Thus our cluster-analyses yielded a nested classification with two perspectives: a general interpretation with four super groups (Fig. 4.3, Table 4.1), and a high resolution interpretation with 15 communities (Fig. 4.3, Table 4.2). Final classes were: ledge/cliff drainage (community 1) talus types (communities 2a, 2b, 2c, and 2d), ridge and turf types (communities 3a, 3b, 3c, 3d, and 3e), and snowbank types (communities 4a, 4b, 4c, 4d, and 4e). Pruning analysis results which show the validity of 4 and 15 cluster perspectives are included in Appendix C.1.

Ordination

Variation in community data was best explained with a three dimensional NMDS ordination (final stress = 15.54; cf. Kruskal 1964, McCune and Grace 2002). Along the first axis, major communities were distributed as a continuum from talus (types 2a, 2b, 2c, and 2d) to ridge (3a), north slopes (3b), to turf (3c, 3d, and 3e), to snowbank (4a-4e; Figs. 4.4 and 4.5). The continuum structure allowed the first dimension to serve as a guide in ordering summarized relevé table columns which we use to describe the composition and environments of the communities (Tables 4.1, 4.2).

Environmental Vectors and Environmental Correlations with NMDS Axes

The strength of association between points in the ordination scatterplots and environmental variables is demonstrated by the direction and length of the environmental vector arrows (Fig. 4.4). Their relative importance is quantified in Table 4.3. The first axis is strongly associated with rock cover and soil cover, soil organic matter (%C and %N), phosphorous, soil texture (sand and silt), pH, and conductivity (Fig. 4.4). The second axis separates talus and snowmelt subtypes and is strongly associated with elevation and clay (Fig. 4.4). The third axis is strongly associated with slope, aspect, and solar radiation (Figs. 4.4, 4.5). The environmental variables most strongly associated with the 3 dimensional NMDS projection were soil/rock cover, pH, and soil organic matter (Table 4.3).

To test validity of the classification and to check agreement between classification and ordination solutions, the 4 and 15 cluster flexible-β solutions were evaluated as categorical variables (Table 4.3). Both were significant ($p < 0.001$) explanatory variables for the ordination configurations (Table 4.3). The fifteen cluster solution explained 82% of variation for a projection of dimensions 1 and 3, and 87% of variation for a projection of dimensions 1 and 2 (Table 4.3). Both clustering solutions explained variability far better than the six topographic assignments made in the field i.e. north face, south face, ridge, ledge, talus and snowmelt (Table 4.3).

Application

The remainder of this chapter describes and compares the community/ecosystems identified, i.e. the 4 major vegetation super groups and the 15 communities they include. First communities are named, described, and compared to previously identified North America alpine communities. Second, Absaroka Volcanic community vegetation and environments are compared to each other. In this comparison we consider higher taxa, specifically functional groups, and plant families. Finally compositional differences between the Absaroka Volcanics and vegetation of other North American alpine areas are described.

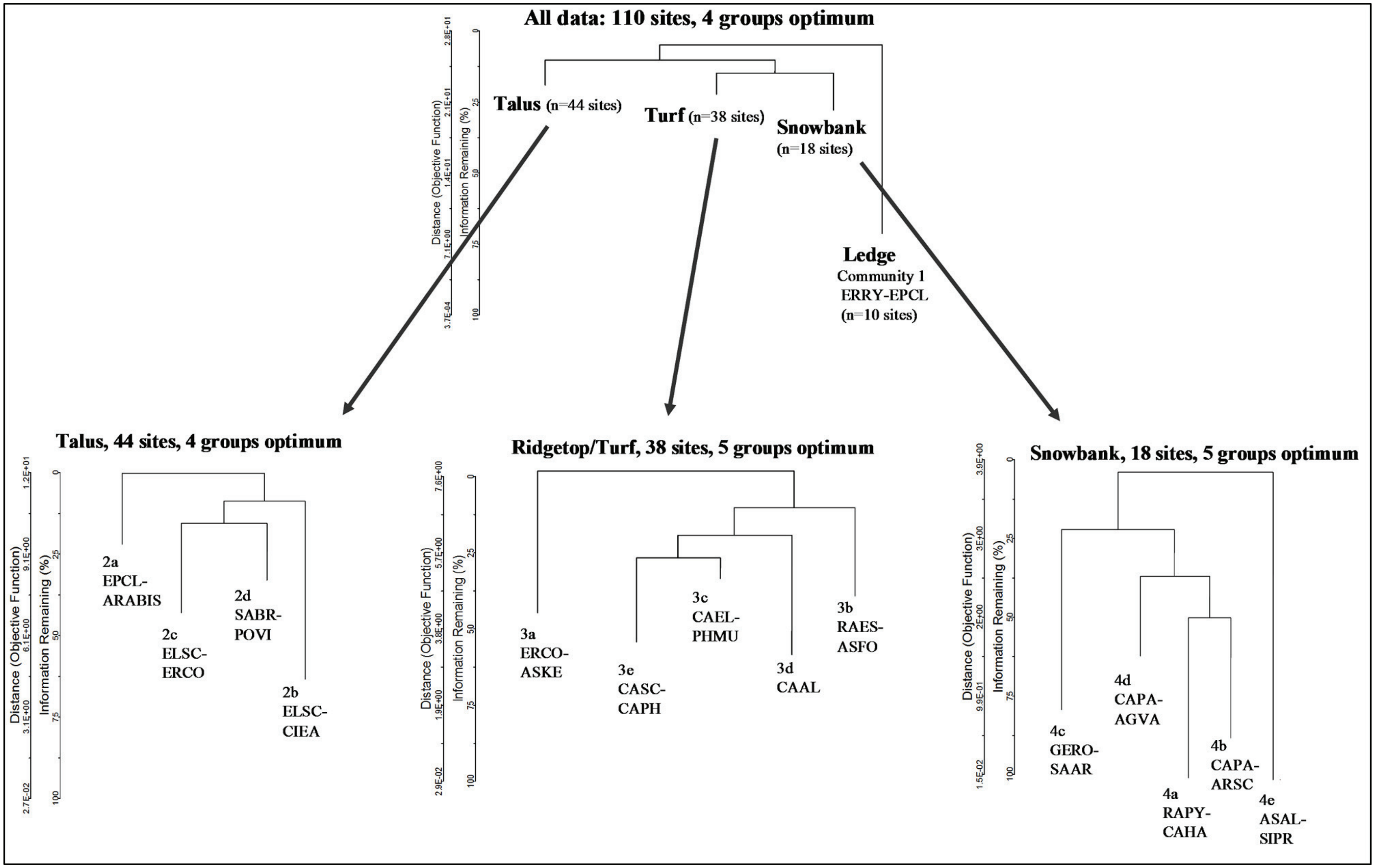

Figure 4.3. Dendrograms showing the division of the entire data set into four super-types (ledge, talus, turf, and snowbank) and subdivision of those types into fifteen communities. Flexible-β agglomerative classification was used to identify types.

Table 4.1a. Summary relevé table for four vegetation super-groups in the Absaroka Volcanics. This table lists all species that occur with >30% constancy in at least one super-group. The two character cipher[1] in each cell indicates constancy (percentage of sites that contain the species) and cover of the species in that community. Shaded cells indicate constancy > 30% .

	LEDGE	TALUS	TURF	SNOWBANK
Arnica rydbergii	9E	1A	..	1A
Epilobium clavatum	8A	2A	..	1A
Cirsium eatonii	5A	1A	+A	+A
Poa cusickii	3A	..	+A	2A
Achillea millefolium	3B	2A	5B	..
Poa alpina	3A	2A	5B	..
Elymus scribneri	8B	8C	5B	1A
Arabis spp. (all)	3A	4A	2A	4A
Lomatium cous	2A	3A	3A	+A
Erigeron compositus	..	4A	5B	..
Festuca brachyphylla	..	4A	9C	8C
Poa pattersonii	2A	5A	6B	3A
Trisetum spicatum	3A	3A	8C	5A
Astragalus kentrophyta	..	3A	8D	..
Arenaria congesta	..	+A	2A	+A
Antennaria umbrinella	..	1A	3B	2A
Selaginella densa	..	+A	3C	2A
Cerastium arvense	..	2A	6A	++
Mertensia alpina	..	+A	5B	1A
Poa secunda	..	2A	3B	..
Smelowskia calycina	..	1A	3A	..
Carex phaeocephala	2A	+A	3C	2A
Silene acaulis	..	..	4B	2A
Arenaria obtusiloba	..	+A	6B	4A
Erigeron simplex	1A	1A	6B	7B
All mosses	..	2A	5C	8D
Luzula spicata	..	1A	5B	7B
Deschampsia cespitosa	1A	+A	1A	3D
Carex paysonis	2A	+A	+A	7D
Sedum lanceolatum	1A	2A	8B	4A
Androsace septentrionalis	2A	2A	6A	3A
Sibbaldia procumbens	1A	+A	1A	7D
Veronica wormskjoldii	1A	..	+A	3B
Antennaria media	1A	1A	1A	5B
Carex haydeniana	1A	+A	+A	5C
Potentilla diversifolia	..	+A	2A	3B
Artemisia scopulorum	..	++	1A	5C
Stellaria monantha	..	++	1A	5A
Salix arctica	..	..	+A	6D
Aster alpigenus	..	..	1A	4C
Agrostis variabilis	..	..	+A	6C

[1] For each cell in the body of the table, constancy is indicated by the first symbol, while cover is indicated by the second symbol. For constancy: 0% = ".", 0-10% = +, 10-20% = 1, 20-30% = 2, 30-40% = 3, 40-50% = 4, 50-60% = 5, 60-70% = 6, 70-80% = 7, 80-90% 8, 90-100% = 9. For cover: 0% = ".", 0-0.01% = +, 0.01-1% = A, 1-2% = B, 2-5% = C, 5-25% = D, >25% = E.

Species not included in table were: *Agoseris aurantiaca, Agoseris glauca, Agoseris glauca* var. *laciniata, Anemone tetonensis, Antennaria lanata, Antennaria microphylla, Arenaria congesta, Arenaria rubella, Arnica latifolia, Aster foliaceus* var. *apricus, Astragalus alpinus, Besseya wyomingensis,*

Table 4.1a (cont.)

Botrychium species, Carex albonigra, Carex atrata, Carex elynoides, Carex pyrenaica, Carex scirpoidea, Castilleja pulchella, Claytonia megarhiza, Cystopteris fragilis, Dodecatheon pulchellum, Draba crassifolia, Draba globosa, Draba incerta, Draba lonchocarpa, Epilobium anagallidifolium, Erigeron humilis, Erigeron ursinus, Eriogonum ovalifolium, Geum rossii, Hieracium gracile, Juncus drummondii, Juncus mertensianus, Juncus parryi, Lepraria cacuminum, Lewisia pygmaea, Lloydia serotina, Lupinus argenteus, Luzula wahlenbergii, Myosotis alpestris, Oxyria digyna, Penstemon montanus, Penstemon procerus, Phacelia hastata, Phacelia sericea, Phleum alpinum, Phlox multiflora, Phlox pulvinata, Phyllodoce glanduliflora, Pinus albicaulis, Poa interior, Poa leptocoma, Poa reflexa, Poa rupicola, Polemonium pulcherrimum, Polemonium viscosum, Polygonum bistortoides, Polygonum douglasii, Polygonum viviparum, Potentilla ovina, Potentilla rubricaulis, Ranunculus eschscholtzii, Ranunculus pygmaeus, Sagina saginoides, Salix reticulata, Saxifraga adscendens, Saxifraga bronchialis, Saxifraga cespitosa, Saxifraga occidentalis, Saxifraga oppositifolia, Saxifraga rhomboidea, Saxifraga rivularis, Sedum integrifolium, Senecio canus, Senecio fremontii, Senecio werneriifolius, Stellaria umbellata, Taraxacum ceratophorum, Taraxacum laevigatum, and *Viola adunca.*

Table 4.1b. General and environmental description of the four super-groups. Standard errors included with mean estimates.

	LEDGE	TALUS	TURF	SNOWBANK
General description				
Number of plots	10	44	38	18
Avg. plot cover (%)	54.6 ± 7.4	12.4 ± 1.3	56.8 ± 4.5	96.7 ± 7.5
Total richness (γ-diversity)	28	71	88	86
Avg. rich. per plot	7.1 ± 1.2	9.3 ± 0.8	19.6 ± 0.9	20.2 ± 1.2
α-diversity Simpson[1]	0.27	0.94	0.96	0.93
α-diversity Shan.-Weiner[2]	0.82	3.41	3.67	3.24
β-diversity[3]	0.75	0.87	0.78	0.77
β-diversity[4]	0.38	0.83	0.73	0.75
Environmental factors				
Water index (0=dry 1=wet)[5]	0.70 ± 0.2	0.25 ± 0.14	0.44 ± 0.11	0.78 ± 0.09
Temp index (0=cold 1=hot)[5]	0.46 ± 0.17	0.75 ± 0.19	0.36 ± 0.09	0.18 ± 0.06
Incid. radiation (MJ cm^{-2} yr^{-1})	0.83 ± 0.04	0.78 ± 0.03	0.85 ± 0.02	0.74 ± 0.03
Heat load index[6]	0.67 ± 0.04	0.68 ± 0.03	0.79 ± 0.02	0.74 ± 0.03
Elevation (m)	2979 ± 25	3102 ± 10.	3181 ± 12	3179 ± 17
Slope (degrees)	29 ± 1.3	28.86 ± 1.33	17 ± 1.45	17.17 ± 1.84
Aspect (degrees from N)	117 ± 9.29	95.36 ± 8.59	103.84 ± 8.99	49.11 ± 13.18
Cover of surface soil (%)	0.31 ± 0.05	0.17 ± 0.02	0.49 ± 0.05	0.75 ± 0.05
Cover of surface rock (%)	0.69 ± 0.05	0.83 ± 0.02	0.51 ± 0.05	0.25 ± 0.05
Sand in soil (%)	66.2 ± 1.95	67.21 ± 0.92	61.74 ± 1.24	58.94 ± 2.08
Clay in soil (%)	4.65 ± 1.02	4.74 ± 0.38	4.93 ± 0.52	3.5 ± 0.64
Silt in soil (%)	29.15 ± 1.54	28.05 ± 0.73	33.32 ± 1.17	37.56 ± 2.33
Soil C (%)	1.33 ± 0.33	0.58 ± 0.09	2.12 ± 0.31	4.65 ± 0.64
Soil N (%)	0.12 ± 0.03	0.06 ± 0.01	0.2 ± 0.03	0.38 ± 0.05
C/N ratio	10.68 ± 0.59	10.23 ± 0.38	10.14 ± 0.2	12.25 ± 0.31
Soil P (mg kg^{-1})	23.7 ± 3.56	13.62 ± 1.55	19.26 ± 1.41	25.35 ± 3.55
pH	6.65 ± 0.12	6.96 ± 0.07	6.68 ± 0.07	5.56 ± 0.08
Cond. (mmhos cm^{-1})	0.12 ± 0.03	0.07 ± 0.01	0.13 ± 0.01	0.17 ± 0.03

[1](Simpson 1949), 2(MacArthur and MacArthur 1961), [3](Whittaker 1960), [4]Average Bray-Curtis dissimilarity within type, [5]See Chapter 2 for explanation of index; 30% used as minimum within-group constancy for indicator species.[6]Heat load index is a calculation of solar radiation with respect to a southwest/northeast aspect axis, as opposed to a north south aspect axis (see McCune and Keon 2002).

Table 4.2a. Summary relevé table for fifteen alpine community types in the Absaroka Volcanics. This table lists all species that occur with >30% constancy in at least one community. The two character cipher[1] in each cell indicates the constancy (percentage of sites that contain the species) and cover of the species in the community. Shaded cells indicate >30% constancy.

	LEDGE	TALUS				TURF					SNOWBANK				
	ARRY EPCL (1)	EPCL ARABIS (2a)	ELSC CIEA (2b)	ELSC ERCO (2c)	SABR POVI (2d)	ERCO ASKE (3a)	RAES ASFO (3b)	CAEL PHMU (3c)	CAAL (3d)	CASC CAPH (3e)	RAPY CAHA (4a)	CAPA ARSC (4b)	GERO SAAR (4c)	CAPA AGVA (4d)	ASAL SIPR (4e)
Arnica rydbergii	9E	3B	5B	+A	..	..	..	..	..	..	4A	..	..	1A	..
Epilobium clavatum	7A	5B	4A	+A	+A	..	..	..	..	..	..	4B	..	..	..
Cirsium eatonii	4A	..	9C	..	..	1A	..	1A	..	..	..	..	..	1A	..
Polemonium viscosum	..	..	2A	1A	3A	..	..	..	..	..	..	..	..	..	..
Elymus scribneri	7B	3A	9C	9C	9C	9C	3A	3A	2A	..	..	..	..	..	..
Arabis spp. (all)	2A	5A	4A	3A	3A	2A	4A	1A	..	3A	..	..	..	..	..
Senecio fremontii	..	3A	..	2A	2A	..	6A	..	..	..	..	2A	..	..	..
Erigeron compositus	..	..	2A	6A	7A	9C	1+	4B	2A	..	..	..	..	..	..
Poa secunda	..	..	2A	2A	2A	7B	4B	2A	..	..	..	..	..	..	..
Lomatium cous	1A	..	..	5A	4A	3A	..	4A	9A	..	..	2A	..	..	..
Achillea millefolium	2B	..	5A	3A	2A	5A	4B	6C	4A	1A	..	..	..	3B	..
Senecio canus	..	..	..	++	+A	4A	..	1A	2A	..	..	..	..	..	..
Saxifraga bronchialis	..	..	1A	..	3B	++	1A	1A	..	..	..	..	2B	..	..
Oxyria digyna	..	2A	..	..	1A	..	3A	..	..	..	9C	..	..	..	..
Aster foliaceus	..	..	..	+A	2A	..	6B	..	..	3A	..	..	..	..	..
Astragalus kentrophyta	..	..	1A	4A	4A	9D	4A	9D	7C	9D	..	..	..	..	..
Astragalus alpinus	..	..	1A	..	2A	1A	..	..	9B	..	..	..	..	..	..
Poa pattersonii	1A	3A	7A	1A	9C	7B	1A	6C	9B	9A	..	7B	4A	3A	..
Antennaria microphylla	++	..	..	+A	2A	++	..	1A	2A	3B	..	..	..	1A	..
Cerastium arvense	..	..	..	1A	6A	7B	6A	3A	9A	6A	..	..	..	1+	..
Poa rupicola	..	..	..	++	..	2A	..	3A	4B	..	..	..	..	..	..
Smelowskia calycina	..	..	..	+A	3A	2A	..	6B	9A	3A	..	..	..	..	..
Androsace septentrion.	1A	..	2A	3A	4A	4A	9A	6A	2A	8A	..	4A	4A	1A	4A
Trisetum spicatum	2A	3A	1A	2A	4A	7B	6C	9D	9B	9C	9B	4A	4A	4A	..
Phlox multiflora	..	..	..	+A	+A	..	1A	7D	4C	..	..	..	..	..	..
Penstemon procerus	..	..	2A	..	..	..	..	3A	..	..	4A	2A	..	..	..
Taraxacum species	..	1+	..	..	..	1+	..	1A	2A	..	9A	..	..	..	..
Poa alpina	2A	2A	..	+A	4A	1A	8C	3A	9C	9C	9B	4A	2A	4A	..
Sedum lanceolatum	+A	1A	2A	2A	2A	7B	6A	9C	7C	9A	..	4A	2A	4A	9A
Draba crassifolia	..	2A	..	..	..	++	3A	..	..	..	..	2A	2A	1A	..
Arenaria congesta	..	..	..	+A	++	1A	1A	4C	..	3A	..	..	..	1A	..

Table 4.2a (cont.)

Community Type	(1)	(2a)	(2b)	(2c)	(2d)	(3a)	(3b)	(3c)	(3d)	(3e)	(4a)	(4b)	(4c)	(4d)	(4e)
Ranunculus eschscholtzii	+A	2A	..	1A	..	..	6A	..	4A	1A	..	4B	2A	3A	..
Carex albonigra	..	..	..	++	..	..	..	..	9E	..	..	..	..	..	..
Carex elynoides	..	..	..	..	..	..	..	4D	..	..	..	..	..	..	..
Saxifraga rhomboidea	..	..	..	..	..	..	..	4A	..	..	..	..	..	..	..
Festuca brachyphylla	..	2A	1A	2A	8B	9C	9C	9C	9C	9C	9D	9D	7B	8B	9A
Poa cusickii	2A	..	..	..	..	+A	..	..	..	..	..	..	4C	..	9A
Mertensia alpina	..	..	..	+A	1A	2A	6A	7C	9C	6A	..	4C	2A	..	..
Antennaria umbrinella	..	..	1A	1A	1A	2A	1A	7C	2A	3C	..	4B	4A	1A	..
Poa reflexa	+A	..	4A	..	..	..	..	..	..	..	..	7A	..	3A	..
Carex phaeocephala	1A	..	..	+A	1A	1B	1A	3B	2A	9D	..	4B	4A	..	4A
Epilobium anagallidifolium	..	2A	..	..	..	..	4A	..	..	..	..	..	..	4B	..
All mosses	..	3A	2A	1A	2A	3B	8B	6C	9D	4C	9D	9E	9D	9D	..
Lloydia serotina	..	..	..	..	2A	..	..	..	4C	..	..	7B	..	..	..
Myosotis alpestris	..	..	..	..	..	++	..	..	4A	..	4A	..	..	..	..
Antennaria media	+A	2A	2A	+A	++	..	6A	1A	2A	1A	4A	4B	..	8C	9A
Erigeron simplex	+A	1+	..	2A	1A	2A	9C	7B	9C	9C	..	9C	9A	6A	4A
Arenaria obtusiloba	..	..	..	2A	+A	2A	4A	9C	7C	9C	..	2A	9A	1+	9A
Draba incerta	..	..	..	1A	..	..	..	2A	2A	6A	..	..	4A	..	..
Potentilla ovina	..	..	..	..	..	..	1A	..	4A	3A	..	..	..	..	..
Castilleja pulchella	..	..	..	..	..	..	..	..	9C	..	..	..	..	..	..
Silene acaulis	..	..	..	..	..	3B	4A	2A	4C	9C	..	2A	7A	1A	..
Agoseris glauca	..	..	1A	..	..	1A	..	..	2A	..	..	2A	..	3A	..
Besseya wyomingensis	..	..	..	..	..	..	1A	2A	..	3A	..	..	2A	..	..
Carex haydeniana	+A	1A	1C	..	+A	..	3A	..	..	..	9D	2A	4A	6C	..
Potentilla species	..	..	..	..	..	..	..	..	7C	3B	..	..	..	..	..
Luzula spicata	..	..	..	+A	2A	1A	6B	7C	9B	9C	9A	7C	9B	3A	9A
Selaginella densa	..	..	..	+A	..	1B	..	4D	..	9C	..	..	4A	..	9C
Potentilla diversifolia	..	..	1A	++	++	++	..	3A	4A	6C	..	4C	..	3A	9B
Erigeron humilis	..	..	..	..	..	..	1A	1A	..	..	9C	2A	..	..	..
Carex scirpoidea	..	..	..	..	..	..	..	..	..	3B	..	..	..	..	..
Polygonum bistortoides	..	..	..	..	++	..	..	3A	..	4B	..	..	2A	..	9B
Stellaria monantha	..	..	..	++	+A	..	..	4A	4B	..	9B	9A	2A	4A	..
Stellaria umbellata	..	1A	..	..	..	..	..	..	..	..	4A	..	..	3A	..
Deschampsia cespitosa	+A	..	..	..	+A	..	3A	..	..	4B	..	..	4C	8D	..
Artemisia scopulorum	..	..	..	++	..	..	1A	1A	4C	3C	9A	9D	7B	1A	..
Carex paysonis	1A	1A	..	..	..	..	1A	..	..	1A	..	9D	4C	8D	9D
Ranunculus pygmaeus	..	..	..	..	..	..	..	..	..	..	9C	..	..	..	..
Saxifraga rivularis	..	..	..	..	..	..	..	..	..	..	9A	..	..	..	..
Saxifraga occidentalis	..	..	..	..	..	..	3A	..	..	1A	..	2B	..	1A	9A

Table 4.2a (cont.)

Community Type	(1)	(2a)	(2b)	(2c)	(2d)	(3a)	(3b)	(3c)	(3d)	(3e)	(4a)	(4b)	(4c)	(4d)	(4e)
Sibbaldia procumbens	+A	..	..	+A	..	..	..	..	..	8C	..	7C	4C	9D	9D
Geum rossii	..	..	..	..	..	..	..	..	2A	..	..	..	4B	..	..
Veronica wormskjoldii	++	..	..	..	..	..	1A	..	..	..	..	..	2A	9C	..
Aster alpigenus	..	..	..	..	..	..	1A	..	..	8B	..	2A	4C	4A	9D
Poa leptocoma	..	..	..	..	..	..	..	..	..	..	9C	..	..	1A	..
Sagina saginoides	..	..	..	..	..	..	..	..	..	..	..	4A	..	..	..
Sedum integrifolium	..	..	..	..	..	..	..	..	..	..	..	4A	..	..	..
Lepraria cacuminum	..	..	..	..	..	..	..	..	..	3C	..	..	..	..	9D
Salix arctica	..	..	..	..	..	..	1B	..	..	..	4A	4A	9E	8C	..
Salix reticulata	..	..	..	..	..	..	..	..	..	3C	..	..	..	1A	9D
Juncus drummondii	..	..	..	..	..	..	..	..	..	1A	..	..	2A	4A	..
Agrostis variabilis	..	..	..	..	..	..	..	..	..	1A	..	4A	4C	9D	9A
Agoseris aurantiaca	..	..	..	..	..	..	..	..	..	..	..	..	..	3A	..
Luzula wahlenbergii	..	..	..	..	..	..	..	..	..	..	..	..	..	3C	..
Phleum alpinum	..	..	..	..	..	..	..	..	..	..	..	..	..	3B	..
Phyllodoce glanduliflora	..	..	..	..	..	..	..	..	..	..	..	..	..	4D	..
Polygonum viviparum	..	..	..	..	..	..	..	..	..	..	..	..	..	3A	..
Carex pyrenaica	..	..	..	..	..	..	..	..	..	..	..	..	..	4C	4A
Lewisia pygmaea	..	..	..	..	..	..	..	..	..	..	..	..	..	4A	4A

[1] For each cell in the body of the table, constancy is indicated by the first symbol, while cover is indicated by the second symbol. For constancy: 0% = ".", 0-10% = +, 10-20% = 1, 20-30% = 2, 30-40% = 3, 40-50% = 4, 50-60% = 5, 60-70% = 6, 70-80% = 7, 80-90% 8, 90-100% = 9. For cover: 0% = ".", 0-0.01% = +, 0.01-1% = A, 1-2% = B, 2-5% = C, 5-25% = D, >25% = E.

Species not included in table were: *Agoseris glauca* var. *laciniata, Anemone tetonensis, Antennaria lanata, Arenaria rubella, Arnica latifolia, Botrychium* sp., *Carex atrata* var. *erecta, Claytonia megarhiza, Cystopteris fragilis, Dodecatheon pulchellum, Draba globosa, Draba lonchocarpa, Erigeron ursinus, Eriogonum ovalifolium, Hieracium gracile, Juncus mertensianus, Juncus parryi, Lupinus argenteus, Penstemon montanus, Phacelia hastata, Phacelia sericea, Phlox pulvinata, Pinus albicaulis, Poa interior, Polemonium pulcherrimum, Polygonum douglasii, Potentilla rubricaulis, Saxifraga adscendens, Saxifraga cespitosa, Saxifraga oppositifolia, Senecio werneriifolius* v. *alpina, Taraxacum ceratophorum, Taraxacum laevigatum*, and *Viola adunca* .

Order of species in relevé table was sorted with respect to fidelity of species to communities using R-code SORTID (see Chapter 2; Appendix A.1).

Table 4.2b. General and environmental description for the fifteen community types. For explanation of footnotes see Table 4.1b

	LEDGE	TALUS				TURF					SNOWBANK				
	ARRY EPCL (1)	EPCL ARABIS (2a)	ELSC CIEA (2b)	ELSC ERCO (2c)	SABR POVI (2d)	ERCO ASKE (3a)	RAES ASFO (3b)	CAEL PHMU (3c)	CAAL (3d)	CASC CAPH (3e)	RAPY CAHA (4a)	CAPA ARSC (4b)	GERO SAAR (4c)	CAPA AGVA (4d)	ASAL SIPR (4e)
General description															
Mountains	5	5	4	6	4	6	3	3	1	3	1	2	1	3	1
Number of plots	10	9	7	14	14	14	6	8	4	6	2	4	4	6	2
Avg. plot cover (%)	55	7	19	10	15	37	31	75	93	80	58	118	90	108	73
Total richness (γ-div.)	28	23	31	46	45	48	44	47	43	42	20	41	36	58	21
Avg. rich. per plot	7.1	5.6	9.7	8.5	12.4	15.1	19	21.1	26	24.2	17	21	18	22.7	18.5
α-diversity Simpson[1]	0.29	0.9	0.87	0.9	0.92	0.92	0.93	0.94	0.89	0.95	0.83	0.81	0.74	0.93	0.82
α-diversity Shan.-Weiner[2]	0.8	2.6	2.5	2.9	2.9	2.9	3.1	3.1	2.9	3.2	2.1	2.4	2.1	3.1	2
β-diversity[3]	0.7	0.8	0.7	0.8	0.7	0.7	0.6	0.6	0.4	0.4	0.2	0.5	0.5	0.6	0.1
β-diversity[4]	0.38	0.93	0.64	0.7	0.67	0.56	0.68	0.59	0.55	0.59	0.22	0.46	0.44	0.64	0.17
Environ. factors (Avg.)															
H_2O ind (0=dry 1=wet)[5]	0.7	0.75	0.6	0.62	0.21	0.39	0.85	0.41	0.4	0.56	0.83	0.79	0.71	0.93	0.62
Temp ind (0=cold 1=hot)[5]	0.46	0.31	0.62	0.6	0.45	0.52	0.21	0.33	0.25	0.24	0.04	0.13	0.21	0.14	0.22
Incid. Rad. (MJ cm^{-2} yr^{-1})	0.83	0.73	0.94	0.91	0.59	0.91	0.61	0.93	0.76	0.93	0.57	0.61	0.74	0.81	0.95
Heat load index[6]	0.67	0.58	0.82	0.8	0.53	0.84	0.6	0.86	0.68	0.86	0.6	0.63	0.76	0.78	0.91
Elevation (m)	2979	3022	3102	3139	3116	3165	3151	3223	3131	3227	3237	3079	3241	3174	3213
Slope (degrees)	29	33.4	26	24.6	31.6	14.2	25.8	13.3	24	15	27	24.5	14	13.8	9
Aspect (degrees from N)	117	71.6	136.7	138.4	47	122.7	24.7	144.5	75.5	103.7	13	12	12.5	75.7	153
Soil cover (%)	31.1	11.7	18.6	17.6	18.5	21.8	27.9	77	78.4	76.3	76.3	64.6	73.1	89	53.8
Rock cover (%)	68.9	88.3	81.5	82.4	81.5	78.2	72.1	23	21.6	23.8	23.5	35.4	26.9	11	46.3
Sand in soil (%)	66.2	66.2	70.8	66.8	66.4	63.8	60	57.8	63.2	63.4	63.5	69	53.1	56.2	59.3
Clay in soil (%)	4.7	3.9	2.9	5.1	5.8	5.8	6.4	3.6	6.3	2.4	8	2.8	1.9	4.4	0.5
Silt in soil (%)	29.2	29.9	26.3	28.1	27.8	30.4	33.6	38.6	30.5	34.2	28.5	28.2	45	39.4	40.3
Soil C (%)	1.3	0.2	0.9	0.5	0.7	1	0.6	3.9	2.8	3.4	2.3	3.5	5.9	5.1	4.8
Soil N (%)	0.1	0	0.1	0	0.1	0.1	0.1	0.3	0.3	0.3	0.2	0.3	0.5	0.4	0.3
C/N ratio	10.7	9.8	10.8	9.9	10.5	9.7	9.1	11.1	9.8	11	12.1	12.8	11.8	11.8	13.8
Soil P (mg kg^{-1})	23.7	11.2	21.6	11.8	13	13.7	15.8	26	24.5	23.2	60	22.3	20	23.8	10.5
pH	6.6	7	6.6	7.1	7	7.1	6.6	6.3	6.6	6.3	5.6	5.3	5.5	5.5	6
Cond. (mmhos cm^{-1})	0.12	0.09	0.06	0.06	0.07	0.09	0.06	0.19	0.23	0.12	0.27	0.15	0.16	0.11	0.29

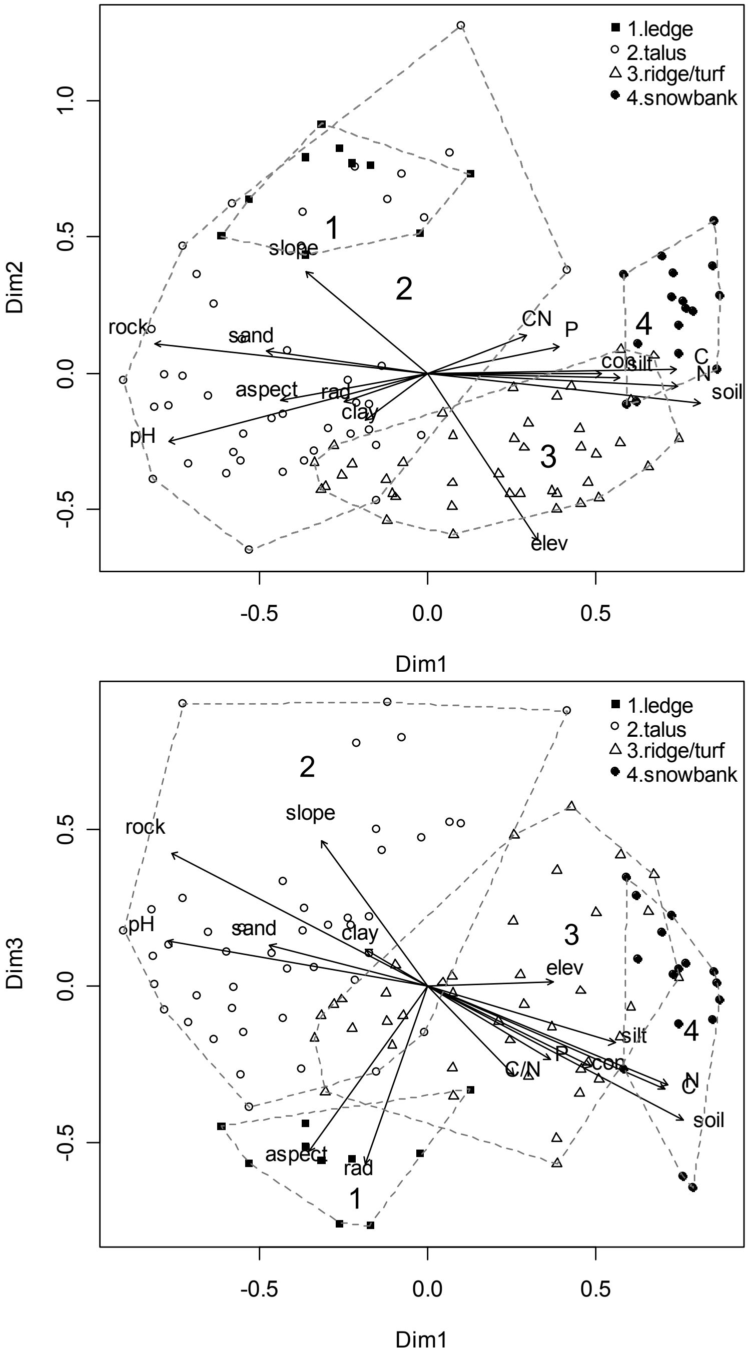

Figure 4.4. Ordination of alpine vegetation data showing the relationship of individual stands within vegetation super-groups to environmental gradients. The four super-groups are indicated by different symbols and dashed lines. Environmental variables are: P = Phosphorous (mg kg^{-1}), C = % soil carbon, N = % soil nitrogen, elev = elevation (m), slope = slope(degrees), aspect = degrees from N, rad = solar radiation (MJ · cm^{2}/yr.), soil = % cover of surface soil, con = soil conductivity (mmhos cm^{-1}), sand = % sand content of soil, clay = % clay content of soil, silt = % silt content of soil, C/N = carbon/nitrogen ratio, pH = pH.

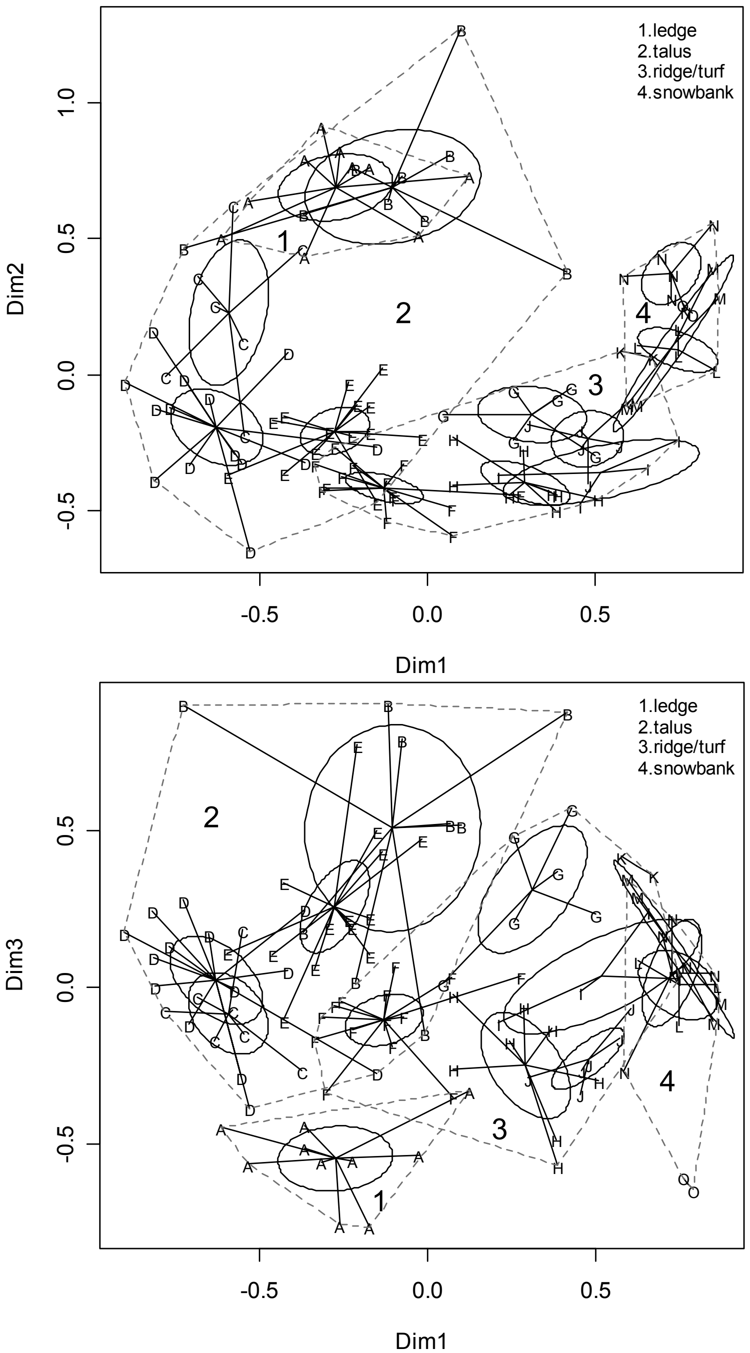

Figure 4.5. Fifteen type community classification (shown with spider diagrams and 95% confidence intervals) overlaid on NMDS ordination. A = 1 ARRY-EPCL, B = 2a EPCL-ARABIS, C = 2b ELSC CIEA, D = 2c ELSC ERCO, E = 2d SABR-POVI, F = 3a ERCO-ASKE, G = 3b RAES-ASFO, H = 3c CAEL-PHMU, I = 3d CAAL, J = 3e CASC-CAPH, K = 4a RAPY-CAHA, L = 4b CAPA-ARSC, M = 4c GERO-SAAR, N = 4d CAPA-AGVA, O = 4e ASAL-SIPR. Vegetation super groups indicated with dashed lines.

Table 4.3. Vector fitting of important environmental variables to NMDS ordination dimensions 1 and 2, and dimensions 1 and 3. Significant variables are noted with asterisks[1].

	Dims 1 and 2		Dims 1 and 3	
	r^2	$Pr(>r)$	r^2	$Pr(>r)$
Continuous variables				
Soil cover	0.557	<0.001***	0.634	<0.001***
Rock cover	0.557	<0.001***	0.634	<0.001***
pH	0.555	<0.001***	0.524	<0.001***
% N in soil	0.453	<0.001***	0.495	<0.001***
%C in soil	0.449	<0.001***	0.498	<0.001***
Elevation	0.398	<0.001***	0.122	<0.001***
%Silt content of soil	0.266	<0.001***	0.28	<0.001***
Slope	0.223	<0.001***	0.262	<0.001***
Conductivity	0.219	<0.001***	0.251	<0.001***
%Sand content of soil	0.194	<0.001***	0.197	<0.001***
Aspect (deg. From n)	0.164	<0.001***	0.332	<0.001***
P (mg kg^{-1})	0.144	<0.001***	0.163	0.001***
C/N	0.087	0.004**	0.121	0.002**
Solar radiation (MJ cm^{-2} yr^{-1})	0.06	0.032*	0.294	<0.001***
%Clay content of soil	0.045	0.069	0.035	0.143
Categorical variables (classification results)				
Topographic types in field	0.505	<0.001***	0.480	<0.001***
Flexible-β super-groups (4 types)	0.630	<0.001***	0.590	<0.001***
Flexible-β (15 types)	0.868	<0.001***	0.815	<0.001***

[1] Signif. codes: "***"≤ 0.001 "**"≤ 0.01 "*"< 0.05. P values based on 1000 permutations.

Community Descriptions

1. Ledge/Cliff Drainage

Community 1. *Arnica rydbergii-Epilobium clavatum* (ARRY-EPCL) This distinctive community type occurs frequently in drainages, along cliff bases, and on unstable, steep, rocky slopes in the Absarokas (5 of 9 mountains, 10 plots). Community 1 is essentially an *A. rydbergii* monoculture (46% cover, 100% constancy, Fig. 4.6, Tables 4.1-4.2), with relatively high cover (55%), but low levels of diversity (Table

4.2b). Species with high (>50%) constancy were: *Elymus scribneri, Arnica rydbergii,* and *Epilobium clavatum*, and *Cirsium eatonii*. Important associates (>30% constancy) were *Poa alpina, Poa cusickii, Trisetum spicatum,* and *Achillea millefolium*.

This community persists on steep (29˚), rocky (only 31% soil cover), sunny (83 MJ cm^{-2} yr^{-1}) slopes with poorly developed sandy soils (66.2 % sand). Soils had relatively low levels of carbon (1.3%) and nitrogen (0.12%), and were acidic/neutral (pH = 6.6), with intermediate levels of conductivity (0.12 mmhos cm^{-1}). This community had higher levels of phosphorous (23.7 mg kg^{-1}) compared to other major environmental types possibly due to deposition of fecal matter from birds and other animals using cliff areas as a refuge (cf. Bazely and Jefferies 1985). Community 1 tends to occur at lower altitudes due to its location under talus slopes and cliffs (Fig 4.6). Multi-year models of soil moisture and soil temperature on Mt. Washburn showed *A. rydbergii* soils were particularly warm and moist (Chapter 3).

This community appears to be identical to an *Arnica rydbergii* community from the Washburn Range in central Yellowstone National Park (Chapter 1). A similar community pioneers wet, rocky, recently deglaciated substrates in Glacier National Park, and is dominated by *Arnica diversifolia, Epilobium alpinum, Poa alpina* and *Poa cusickii* (Damm 2001). Arnica communities line steep seasonally wet swales in the Bridger and Gallatin Mountains of south-central Montana (personal observation). A community dominated by *Arnica longifolia* that co-occurs with *Poa reflexa*, and *Ranunculus eschscholtzii* has been reported from sub-alpine ledges and draws in Grand Teton National Park (Gregory 1983). *A. rydbergii* has low levels of tissue nitrogen (Bowman et al. 1993), that doesn't increase with increasing soil nitrogen (Aho et al. 1998), indicating this species may be highly tolerant of nitrogen poor conditions (cf. Mattson 1980).

Figure 4.6. *Arnica rydbergii-Epilobium clavatum* community (ARRY-EPCL) on Barronette Peak.

2. Talus/Scree

Alpine talus/scree is often erroneously assumed to be too inhospitable for consistent plant germination and growth (Körner 2003). As a result these areas are often ignored in alpine phytosociological studies (e.g. Baker 1983, Hrapko and LaRoi 1983, Richardson and Henderson 1999). Talus sites had lower cover (12.4%) and, due to their high heterogeneity, the highest levels of β-diversity of any major type (cf. Billings and Bliss 1959; Table 4.1b). Predictably Absaroka talus communities were rockier (avg. rock surface cover = 83%), than other major vegetation types (Tables 4.1b, 4.2b). Soils were also sandier (avg. = 67% sand in soil), lower in organic matter (avg. N = 0.06%, avg. C = 0.6%, avg. C/N ratio = 10.2, avg. P = 13.6 mg kg^{-1}; Table 4.1b), and more alkaline (pH = 6.96). Our classification identified four community types on talus/scree.

Community 2a. *Epilobium clavatum-Arabis* spp. (EPCL-ARABIS) This community, occurring on 5 mountains (9 plots) occupied an ecotone between cliff ledge sites (type 1) and drier, less shaded talus sites (Fig. 4.7). Though it had the lowest cover (avg. = 7%) and plot richness (avg. = 5.6 spp. plot^{-1}) of any community type, its shaded areas allowed for the frequent occurrence of mosses (Table 4.2a). Species with high constancy (>50%) included *Epilobium clavatum* and *Arabis* spp.. While *Arabises* could not be keyed consistently to species due to a high degree of variability in development during periods of sampling, Arabis species definitively identified in this type included *A. drummondii, A. lemonii,* and *A. microphylla.* Other important species (>30% constancy) included *Elymus scribneri, Poa pattersonii, Trisetum spicatum*, *Arnica rydbergii, Senecio fremontii*, and mosses (Table 4.2a).

This community occurred on the steepest slopes (33°) of any of the fifteen types (Fig. 4.7, Table 4.2b). Large boulders often provided shade allowing the frequent occurrence of mosses. EPCL-ARABIS had relatively low levels of direct incident radiation (73 MJ · cm^{-2} yr^{-1}), and had the highest surface rock cover of any community type (88%). Soils which did exist were sandy, and poorly developed, with the lowest recorded levels of nitrogen (0.03%), carbon (0.02%), and phosphorous (11.2 mg kg^{-1}) of any of the fifteen types (Table 4.2b).

This community is not well described by existing literature although it appears to be similar to *Epilobium alpinum* talus communities reported from Glacier National Park (Damm 2001), and to stream-bank *Epilobium anagallidifolium* communities in the Colorado Rockies which include *Deschampsia cespitosa* and a number of moss species

(Komárková 1979). Since *E. alpinum*, until recently*,* included *E. clavatum* and *E. anagallidifolium* (Kershaw 1998), little information exists with respect to the specific distribution of *E. clavatum*.

Figure 4.7. *Epilobium clavatum-Arabis* sp. (EPCL-ARABIS) on Meridian peak with particularly high quantities of *Arnica rydbergii*, the large dominant forb seen throughout the photograph.

Community 2b. *Elymus scribneri-Cirsium eatonii* (ELSC-CIEA) This type occurred on four mountains (9 plots) and had the highest cover of any talus community (avg. = 19%). High constancy species (> 50%) included *Elymus scribneri, Poa pattersonii, Achillea millefolium, Arnica rydbergii,* and *Cirsium eatonii*. Other important species (constancy > 30%) included *Poa reflexa, Arabis* spp., and *Epilobium clavatum*. Species which occurred infrequently (<30%), but that were indicative of this site included *Phacelia hastata* (Table 4.2a).

This community occurred on slopes with particularly sandy soils (71% sand), which were the result of weathering of siliceous materials abundant at talus sites. Due to its steep (26°) south-facing (137° from N) environment, ELSC-CIEA received the highest levels of direct incident radiation of any community (94 MJ cm^{-2} yr^{-1}). Soils were neutral (pH = 7), poorly developed: N = 0.08%, C/N ratio = 10.8, and rocky (rock cover = 82%).

Group 2b is very similar to sparse, rocky communities reported for the southeastern Absarokas dominated by *E. scribneri* and *E. compositus* (Thilenius and Smith 1985), and rocky *E. scribneri* communities in central Idaho (Caicco 1983), and southwestern Montana (Cooper et al. 1997).

Elymus scribneri has been reported for rocky sites in the eastern Absarokas (Thilenius and Smith 1985), the Uintas of northern Utah (Hayward 1952, Lewis 1970), and the Sawatch Range of Colorado (Hartman and Rottman 1988). While *E. scribneri* is widespread from Montana to New Mexico (Hitchcock 1950, Pemble 1965), it appears to be only a major alpine community component in the northern and north-central Rocky Mountains (e.g. Cooper et al. 1997, Caicco 1983).

Community 2c. *Elymus scribneri-Erigeron compositus* (ELSC-ERCO) This community occupied drier talus sites on six of the nine mountains (14 plots). Vegetation cover (avg. = 10 %), and species richness (avg. = 8.5 spp. $plot^{-1}$) were relatively low (Table 4.2b, Fig. 4.8). Existing vegetation tended to be patchy and highly heterogeneous; note high β-diversity values (Table 4.2b). Species with >50% constancy included *Elymus scribneri, Astragalus kentrophyta, Erigeron compositus* and *Lomatium cous*. Species with >30% constancy included *Achillea millefolium*, *Androsace septentrionalis*, and

Arabis spp. Species with < 30% constancy that nonetheless appeared to be important to this type included *Claytonia megarhiza*, and *Polemonium pulcherrimum* (Table 4.2a).

The environment of community 2c was hot (91 MJ cm^{-2} yr^{-1}), steep (slope = 28°), and rocky (82% rock cover). The aspect was more southerly than for any other type (135° from north). Soils were neutral (pH = 7.1), and had little organic matter (N = 0.05%, C = 0.5%, P = 11.8 mg kg^{-1}). On the Washburn Range *E. scribneri* talus soils are particularly moist (at 15 cm depth soils at some plots never dry beyond -1.5 MPa at 15 cm depth) (Chapter 3).

ELSC-ERCO is somewhat similar to rocky grassland communities of the Copper Basin in Idaho which are dominated by *E. scribneri, Poa rupicola*, and *E. compositus* (Caicco 1983). This type is also similar to communities in the southeastern Absarokas dominated by *E. scribneri* and *E. compositus* (Thilenius and Smith 1985), talus communities on the Washburn Range characterized by *E. scribneri, E. compositus*, and *Cerastium arvense* (Chapter 3), and non-volcanic rocky areas in southwestern Montana dominated by *E. scribneri, Festuca brachyphylla, Trisetum spicatum, Achillea millefolium*, and *Lomatium cous* (Cooper et al. 1997).

Though often present in this type *Claytonia megarhiza* was previously unreported for YNP. *C. megarhiza* persists on rocky sites from Glacier National Park, and other areas throughout Montana (Pemble 1965, Bamberg and Major 1968), to the mountains of northern, central, and southern Colorado (Komárková 1979, Willard 1979, Rottman and Hartman 1985, Hartman and Rottman 1988, Seagrist and Taylor 1998).

Figure 4.8. Warm talus on Wolverine Peak *Elymus scribneri-Erigeron compositus* (ELSC-ERCO) community.

Community 2d. *Saxifraga bronchialis-Polemonium viscosum* (SABR-POVI) This group occupied steep north-facing talus sites on 4 of 9 mountains (14 plots). Species richness was higher for this community than any other talus type (avg. = 12.4 spp. plot^{-1}). Species with >50% constancy included *Elymus scribneri, Festuca brachyphylla, Poa pattersonii, Trisetum spicatum, Astragalus kentrophyta, Erigeron compositus, Cerastium arvense.* Other important species (>30% constancy) were *Poa alpina, Androsace septentrionalis,* and *Lomatium cous*. Species which occurred primarily or solely in group 2d included *Draba lonchocarpa*, *Saxifraga bronchialis* and *Polemonium viscosum*.

This community had a more north facing aspect (47˚ from N) than other talus types allowing the development of a unique talus flora (Fig. 4.9). Because of its north-facing aspect the community had particularly low potential radiation inputs (57 MJ cm^{-2} yr^{-1}). As with other talus communities soils were neutral (pH = 7), and poorly developed, with low levels of N (0.7%), C (0.7%), and P (13 mg kg^{-1}). Slopes were very steep (32°) and rocky (cover = 82%).

This community type is very similar to S. *bronchialis* north-facing scree slope communities in Glacier National Park. Other shared species include *Poa alpina, Smelowskia calycina, Trisetum spicatum*, and *Potentilla diversifolia.* Group 2d is somewhat similar to talus communities of the Copper Basin in Idaho, which include *E. scribneri* and *P. viscosum* (Caicco 1983), and to *S. bronchialis* talus sites of Niwot Ridge in central Colorado (Komárková 1979). Several species from group 2d frequently appear in andesitic talus of the San Juan Mountains of Colorado including *Claytonia megarhiza* and *Polemonium viscosum* (Rottman and Hartman 1985). This community appears to be transitional between several rocky site communities previously described for southwestern Montana (Cooper et al. 1997).

Figure 4.9. *Saxifraga bronchialis-Polemonium viscosum* (SABR-POVI) communities were found along steep, relatively barren north facing slopes like this one on Wolverine Peak.

3. Ridgetops/Turf

This super group encompasses a wide physiognomic spectrum from exposed cushion plant ridgetops to closed canopy, densely vegetated graminoid-dicot meadows. Measures of α-diversity were highest for this super group reflecting the diversity of species within its sub-types (Table 4.1b). Soils were generally neutral (pH = 6.9), and well developed with intermediate to high levels of nitrogen (avg. = 0.2%), carbon (avg. = 2.1%), and phosphorous (avg. = 19.3 mg kg^{-1}). We recognize five ridgetop/turf community types.

Community 3a. *Erigeron compositus*-*Astragalus kentrophyta* (ERCO-ASKE) This ridgetop community occurred on 6 of 9 mountains (14 plots), and was transitional between talus and densely vegetated turf sites (Fig. 4.10). Community 3a had intermediate levels of richness (15.1 spp. $plot^{-1}$), and cover (37%), and was dominated (constancy > 50%) by cushion plants (e.g. *Astragalus kentrophyta, Sedum lanceolatum, Arenaria obtusiloba*), small forbs (*Erigeron compositus*, *Achillea millefolium*, *Androsace septentrionalis, Cerastium arvense*) and hearty graminoids (*Elymus scribneri*, *Festuca brachyphylla, Poa pattersonii, Poa secunda, Trisetum spicatum*). Rarer species (constancy < 50%) that nonetheless were indicative of this type included several cushion plants (*Phlox pulvinata,* and *Silene acaulis*), and forbs from the genus *Senecio* (*S. werneriifolius* and *S. canus*).

Although some ridgetops in the Absarokas are rounded or flat with relatively high accumulations of soil (see group 3c CAEL-PHMU), others like community 3a, were exposed, and rocky (Fig. 4.10). Community 3a was intermediate between talus and turf communities for most soil characteristics (i.e. N = 1.0%, C = 0.7%, P = 13 mg kg^{-1}, rock cover = 75%). Soil pH (7.1) was more basic than for any other community type. Relatively high pH is probably due to soil dryness since well drained soils have low cation exchange rates. Soils on *Erigeron compositus-Astragalus kentrophyta* ridgetops on Mount Washburn were extremely dry (Chapter 3). Predictably, incident radiation (91 MJ cm^{-2} yr^{-1}) and elevation (3165 m) were both high for this community.

The geographic extent of this community is suggested by the wide distribution of *Erigeron compositus*. *E. compositus* is common on rocky alpine sites from Washington (Douglas and Bliss 1977, Billings 2000), Montana (Cooper et al. 1997), Wyoming (Thilenius and Smith 1985), Colorado (Hartman and Rottman 1988, Seagrist and Taylor 1998), and on andesitic ridgetops in California (Hunter and Johnson 1983).

An *Erigeron compositus* community similar to this type has been described for the eastern Absarokas (Thilenius and Smith 1985). While most of the species in ERCO-ASKE occur in rocky alpine areas in southwestern Montana (Cooper et al. 1997), these areas are often dominated by *Geum rossii, Arenaria obtusiloba, Dryas octopetala*, and *Carex rupestris,* and thus appear more similar to community 4c (GERO-SAAR).

Fig. 4.10. *Erigeron compositus-Astragalus kentrophyta* (ERCO-ASKE) community along the Wolverine Peak summit ridge.

Community 3b. *Ranunculus eschscholtzii-Aster foliaceus* (RAES-ASFO) This lightly vegetated (cover = 31%), but relatively rich (15.3 spp. plot^{-1}) community was found on steep north facing rocky sites on 3 mountains (6 plots). Dominant species (constancy > 50%), included *Festuca brachyphylla, Luzula spicata, Poa secunda, Trisetum spicatum, Achillea millefolium, Androsace septentrionalis, Arabis* spp.*, Arenaria obtusiloba, Aster foliaceus* (var. apricus), *Astragalus kentrophyta, Cerastium arvense, Erigeron simplex, Mertensia alpina, Ranunculus eschscholtzii, Sedum lanceolatum, Senecio fremontii*, *Silene acaulis* and mosses. Other important associates (constancy > 30%) include *Deschampsia cespitosa, Elymus scribneri, Carex haydeniana,* and *Oxyria digyna.* Distinguishing species which occurred solely or primarily in group 3b included *Draba crassifolia, Oxyria digyna,* and *Saxifraga occidentalis.*

North slopes in the Northern Absarokas were heavily sculpted by glacial activity most recently during the Pinedale epoch, 25,000 BP (Keefer 1976). As a result these slopes are generally much steeper, and soils less developed than south facing slopes. Community 3b aspect (25˚ from N) was more northerly and slopes were steeper (26˚) than any other community in the ridgetop/turf type (Fig. 4.11). Radiation inputs for this community were low (61 MJ cm^{-2} yr^{-1}), and soils were rocky (72% rock cover), poorly develpoed (N = 0.07%, C = 0.6%, P = 15.8 mg kg^{-1}), with low levels of conductivity (0.06 mmhos cm^{-1}) and intermediate pH (6.6).

Although not well described by existing literature RAES-ASFO is similar to moist slope communities in southwestern Montana which include *Ranunculus eschscholtzii, Aster foliaceus Carex haydeniana,* and *Deschampsia cespitosa* (Cooper et al. 1997), rocky unstable areas around snowbanks in the Olympic Mountains dominated by *R. eschscholtzii* (Bliss 1969), and north facing scree slopes in the central Rockies that contain *Oxyria digyna*, *Cerastium beeringianum*, and *Androsace septentrionalis* (Komárková 1979). *Oxyria digyna,* a distinguishing species of this type, commonly occupies on, and is well adapted to, north facing short season locations (Komárková 1979, Billings 2000).

Figure 4.11. *Ranunculus eschscholtzii-Aster foliaceus* community (RAES-ASFO) on a north facing, rocky slope on Amphitheatre Peak

Community 3c. *Carex elynoides-Phlox multiflora* (CAEL-PHMU) This dense dry turf community type occurred on 3 mountains (8 plots) on south facing slopes or plateau-like summits with relatively deep soils (Fig. 4.12). Levels of cover (75%) and richness (21 spp. plot^{-1}) were generally high. This community was dominated (constancy > 50%) by graminoids (i.e. *Carex elynoides, Festuca brachyphylla*, *Luzula spicata*, *Poa* *pattersonii, Trisetum spicatum*), and forbs tolerant of dry conditions (*Achillea millefolium, Androsace septentrionalis*, *Antennaria umbrinella, Arenaria congesta, Arenaria obtusiloba, Astragalus kentrophyta, Erigeron compositus, Erigeron simplex, Mertensia alpina, Phlox multiflora, Saxifraga rhomboidea, Sedum lanceolatum, Selaginella densa, Smelowskia calycina, Stellaria monantha,* and mosses, particularly *Polytrichium juniperinum*). Important associates (constancy > 30%) include *Carex phaeocephala, Elymus scribneri, Poa alpina, Aster alpigenus, Cerastium arvense, Potentilla diversifolia, Penstemon procerus, Polygonum bistortoides, Sibbaldia procumbens* and *Silene acaulis. Carex elynoides* occurred only within this type.

This community occurred on dry, gently sloping (13°) slopes on south facing aspects or flat expansive ridgetops (Fig 4.12). CAEL-PHMU had particularly high levels of potential radiation (93 MJ cm^{-2} yr^{-1}). Soils were abundant (77% soil cover), well developed (N = 0.34%, C = 3.9%, P = 26 mg kg^{-1}), and silty (39%). Soil pH and conductivity was intermediate for the study area (pH = 6.3, EC = 0.19 mmhos cm^{-1}). Multi-year moisture models of *C. elynoides* turf on the Washburn Range predict that over a period of period of 60 summer days (late June to early August) soil water potential at 15 cm will be wetter than -1.5 MPa on only 5.5 days (Chapter 3).

Carex elynoides turf ranges from Montana (Bamberg and Major 1968, Cooper et al. 1997, Damm 2001) through Idaho (Urbanczyk and Henderson 1994), Utah (Lewis 1970), Wyoming (Billings and Bliss 1959), Colorado (Komárková and Weber 1978, Komárková 1979, Willard 1979, Hartman and Rottman 1988, Rottman and Hartman 1985), to New Mexico (Baker 1983). Locally, turf communities dominated by *C.*

elynoides, Potentilla diversifolia, and *Arenaria obtusiloba* have been reported in the White Clouds and Copper Basin in Idaho (Richardson and Henderson 1999, Caicco 1983), the Northern Absarokas and Beartooths (Chapters 4, 5), and the andesitic Washburn Range (Chapter 3).

Figure 4.12. A large *Carex elynoides-Phlox multiflora* meadow (CAEL-PHMU) along a high altitude plateau on Mineral Peak.

Community 3d. *Carex albonigra* (CAAL) This community consists of dense (93% cover), extremely rich (26 spp. plot^{-1}) *Carex albonigra* turf on four Wolverine Peak plots (Fig. 4.13). Two of these sites resemble the dry turf of community 3c. The other two are wet, snowmelt sites resembling communities 4b and 4d. Dominant species (constancy > 90%) include *C. albonigra, Festuca brachyphylla, Luzula spicata, Trisetum spicata, Poa alpina, Astragalus alpinus, Castilleja pulchella*, *Cerastium arvense, Lomatium cous*, *Mertensia alpina,* and *Smelowskia calycina.* Important associates (constancy >50%) include *Poa rupicola, Artemisia scopulorum, Geum rossii, Myosotis alpestris, Potentilla ovina,* and *Silene acaulis.*

This community occurred on moderately steep (24°) wet to dry sites on Wolverine Peak. Radiation inputs were relatively low (76 MJ cm^{-2} yr^{-1}), reflecting the north-facing aspect of some of the plots. Soils were abundant (78% soil cover), and well developed (N = 0.29%, C = 2.8%, P = 24.5 mg kg^{-1}). Soil pH and conductivity were intermediate for the study area (pH = 6.6, EC = 0.23 mmhos cm^{-1}).

Wet to dry meadows containing *C. albonigra* have been described for the Olympic Mountains in Washington (Billings 2000), the San Francisco Mountains in northern Arizona (Billings 2000), the major ranges of southwest Montana (Cooper 1997), and the San Juan mountains of southern Colorado (Rottman and Hartman 1985). In southern Colorado *C. albonigra* communities are co-dominated by *Artemisia scopulorum,* and *Geum rossii* (Rottman and Hartman 1985).

Figure 4.13. A moist *Carex albonigra* meadow (CAAL) on the north face of Wolverine.

<u>Community 3e. *Carex scirpoidea-Carex phaeocephala* (CASC-CAPH)</u> This dense (80% cover), rich (24 spp. plot^{-1}) turf community occurs on 3 mountains (6 plots). Group 3e had the highest levels of α-diversity of any of the 15 communities (Table 4.2b). Dominant species (constancy > 90%) include *C. phaeocephala, Festuca brachyphylla, Luzula spicata, Trisetum spicatum, Poa alpina* and *Poa pattersonii, Arenaria obtusiloba, Erigeron simplex, Sedum lanceolatum, Selaginella densa,* and *Silene acaulis.* Secondary species (constancy >50%) include *Deschampsia cespitosa*, *Androsace septentrionalis, Aster alpigenus, Cerastium arvense, Draba incerta, Mertensia alpina, Polygonum bistortoides, Potentilla diversifolia, Sibbaldia procumbens* and mosses.

This community occurred on dry to moist, gradual sloped (15˚), high elevation (3227m) sites (Fig. 4.14). Like group 3c this community had particularly high levels of potential radiation (93 MJ cm^{-2} yr^{-1}). Soils were abundant (76% cover), and well developed (N = 0.31%, C = 3.4%, P = 23.2 mg kg^{-1}). Soil pH and conductivity were intermediate for the study area (pH = 6.3, EC = 0.12 mmhos cm^{-1}).

Community 3e is very similar to moist alpine turf communities in southwest Montana which include *C. scirpoidea, C. phaeocephala, L. spicata, P. alpina, E. simplex*, and *C. arvense* (Cooper et al. 1997), and wet to dry turf communities of the eastern North Cascades which include *C. scirpoidea, C. phaeocephala, P. diversifolia, F. ovina,* and *A. obtusiloba*. Since *C. scirpoidea* is rare south of Montana (Kershaw et al. 1998) this community may be limited to the Northern Rockies and northern coastal ranges. *C. phaeocephala* occurs in dry to moist alpine meadows from Canada (Hrapko 1970), Washington (Bliss 1969), Montana (Johnson and Billings 1962), Wyoming (Scott 1966), and Colorado (Komárková 1979).

Figure 4.14. *Carex scirpoidea – Carex phaeocephala* meadow (CASC-CAPH) along a south facing slope on Amphitheatre Peak.

4. Snowbank

This major group is directly associated with late-melting snowdrifts, and is well documented in the alpine literature (e.g. Billings and Bliss 1959, Galen and Stanton 1995, many others). Since few plants are tolerant of very short growing seasons and the low temperatures of late summer, late melt communities are phytosociologically different from other alpine communities (Billings 2000). Snowbank communities in the Northern Absarokas had higher cover (96.7%), and were richer (20.2 spp. plot^{-1}) than the other three major types (Table 4.1b). Environments were usually north facing (49° from north), with low levels of annual radiation (74 MJ cm^{-2} yr^{-1}), and abundant soils (75% cover) that were well developed (N = 0.4%, C = 4.7%, P = 25.4 mg kg^{-1}, C/N ratio = 12.2) and acidic (pH = 5.6). Our classification subdivided this group into five subtypes.

Community 4a. *Ranunculus pygmaeus*–
Carex haydeniana (RAPY-CAHA) This community type occurred on late melt cliff-ledge sites on Cutoff Peak, and had intermediate levels of cover (58%), and richness (17 spp. plot^{-1}). While limited sample size (*n* = 2 plots) prevents confident synecological description (i.e. constancy is likely exaggerated, and cover variance artificially low), several species (constancy >90%) appeared to be indicative of this type including *C. haydeniana, Festuca brachyphylla Oxyria digyna, Erigeron humilis, Ranunculus pygmaeus*, and hydrophilic mosses.

RAPY-CAHA occurred on steep (27°), wet, north facing (13° from north) ledges perched on top of the enormous north-east face of Cutoff Peak (Fig. 4.15). This type had the lowest potential radiation inputs of any community (57 MJ cm^{-2} yr^{-1}). Soils were abundant (76% soil cover), and well developed (N= 0.19%, C = 2.3%). Group 4a also had much higher phosphorous levels than other Northern Absaroka communities. High P levels may be due to high numbers of exotic mountain goats on Cutoff Peak (Lemke 2004) who use ledges as a passage to refuge terrain on steep north facing slopes. Goat fecal cover was 0.2% within this type. Like most snowbank communities soils were acidic (pH = 5.6), with high levels of conductivity (0.27 mmhos cm^{-1}).

Community 4a is somewhat similar to late melt "nivation hollow" communities in the Canadian Rockies dominated by *Oxyria digyna* and *Ranunculus pygmaeus* (Hrapko and LaRoi 1978), saturated wetland communities in the Tobacco Root, Gravelly and Madison Mountains of Southeast Montana which include *C. haydeniana, Carex scopulorum, Deschampsia cespitosa, Juncus drummondii,* and *Veronica wormskjoldii* (Cooper et al. 1997). RAPY-CAHA is similar to two associations in the Niwot Range; one which includes *R. pygmaeus, O. digyna, Saxifraga rivularis,* and *Besseya alpina*, and another which includes *C. haydeniana* and *Poa grayana* (Komárková 1979). *R. pygmaeus* and *C. haydeniana* are both well documented associates of wet late-snowmelt communities throughout the Rocky Mountains (Komárková 1979).

Figure 4.15. A moist, north facing *R. pygmaeus – C. haydeniana* snowbank community (RAPY-CAHA) on Cutoff Peak.

Community 4b. *Carex paysonis-Artemisia scopulorum* (CAPA-ARSC) This type, occurring on 2 mountains (4 plots) had similar cover levels (118%), but was less diverse (21 spp. plot^{-1}), and encompassed smaller areas than group 4d. Community 4b was dominated (constancy >90%) by Carex *paysonis, Festuca brachyphylla, Artemisia scopulorum, Erigeron simplex, Stellaria monantha,* and hydrophilic mosses. Other constant species (>50%) included *Luzula spicata*, *Poa pattersonii, Poa reflexa, Sibbaldia procumbens, Lloydia serotina,* and *Salix arctica.* Species occurring only in group 4b included *Sagina saginoides* and *Sedum integrifolium.*

The environment for CAPA-ARSC is similar to community 4a, i.e. it occurred on steep (25˚), wet, north facing (12˚ from north) ledges above sheer Absaroka north-faces

(Fig. 4.16). Like most snowbank communities annual radiation inputs were low (61 MJ cm^{-2} yr^{-1}). Soils were somewhat rocky (35% rock cover), though well developed (N= 0.27%, C = 3.5%, P = 22.3 mg kg^{-1}), and were more acidic than any other community type (pH = 5.6). Multi-year models on Mt. Washburn found *C. paysonis-A. scopulorum* community soils were particularly cold and wet (Chapter 3).

Community 4b is very similar to a *Carex paysonis-Artemisia scopulorum* snowbank community from the andesitic Washburn Range in central Yellowstone National Park (Chapter 3). Community 4b is also similar to andestic moist and wet meadow communities in the southern Rockies. In the San Juan Mountains of southern Colorado, dominant snowbank species include *Artemisia scopulorum*, *Sibbaldia procumbens*, *Erigeron simplex* and *Sedum integrifolium* (Rottman and Hartman 1985). The Sangre de Cristo Mountains in northern New Mexico have late melt communities with *Artemisia scopulorum, Lloydia serotina,* and *Salix arctica* as dominants (Baker 1983). At both of these locations, *Carex nova* replaces *C. paysonis* as the dominant sedge (Rottman and Hartman 1985, Baker 1983).

Figure 4.16. *Carex paysonis-Artemisia scopulorum* snowbank community (CAPA-ARSC) on the north face of Miller Peak.

Community 4c. *Geum rossii- Salix arctica* (GERO-SAAR) This community, found on 4 late melt plots on Abiathar Peak, had high levels of cover (90%), and moderately high levels of richness (18 spp. plot^{-1}). Community 4c was dominated (constancy >90%) by *Luzula spicata, Salix arctica, Arenaria obtusiloba*, *Erigeron simplex* and hydrophilic mosses Other constant species (>50%) included *Agrostis variabilis, Carex haydeniana, Carex paysonis, Carex phaeocephala, Deschampsia cespitosa, Festuca brachyphylla, Poa cusickii, Poa pattersonii, Trisetum spicatum, Androsace septentrionalis, Antennaria umbrinella, Artemisia scopulorum, Aster alpigenus, Draba incerta, Erigeron rydbergii, Geum rossii*, *Selaginella densa, Sibbaldia procumbens* and *Silene acaulis.* While *G. rossii* is extremely dominant in the neighboring Beartooths, GERO-SAAR was the only community in the study area where *Geum rossii* occurred to any appreciable extent (Table 4.2a).

This community occurred on gradual (14°), north facing (13° from north) slopes on Abiathar Peak (Fig. 4.17). Soils were abundant (73% cover), and had higher levels of carbon and nitrogen than any other community (N = 0.49%, C = 5.9%, P = 20 mg kg^{-1}). As with most snowbank communities, annual radiation inputs were relatively low (74 MJ cm^{-2} yr^{-1}). Soils, relatively high in silt at most snowbank communities, were particularly silty in group 4c. Soils were acidic (pH = 5.5), and had intermediate levels of conductivity (0.16 mmhos cm^{-1}).

Late melt or otherwise wet communities similar to community 4c, which possess both *Geum rossii* and *Salix arctica* have been reported for the Pintlar and Pioneer Mountains of Montana, where *C. phaeocephala* and *A. alpigenus* were additional dominants (Cooper et al. 1997), the Niwot Range in Colorado (Komárková 1979), Rocky Mountain National Park, where *S. acaulis* and *L. spicata* are also dominants (Willard 1979), the Sangre de Cristo Range in New Mexico where *A. scopulorum* is an additional dominant (Baker 1983), and the San Juan mountains of Colorado (Rottman and Hartman 1985).

Geum rossii may be one of the most ubiquitous alpine plant species in the central Rocky Mountains (Mellman-Brown 2002). Turf/fellfield communities dominated by *G. rossii* have been widely reported from the Beartooths (Lackschewitz 1994, Mellman-Brown 2002), and Pioneer and Tobacco Root Mountains in Montana (Chambers et al. 1990, Cooper et al. 1997), the eastern Absarokas in Wyoming (Thilenius and Smith

1985), Idaho (Richardson and Henderson 1999), Utah (Lewis 1970), the Colorado Rockies (Ehleringer and Miller 1975, Komárková 1979, Willard 1979, Baker 1983), and the Ruby Mountains of northeastern Nevada (Loope 1970).

The infrequent appearance of the unpalatable *Geum rossii* in the Absarokas may be the result of policies preventing domestic grazing in YNP over the last 100 years (c.f. Billings 2000). The eastern Absaroka Range, where domestic grazing has been frequent and continuous, has much higher quantities of *G. rossii* (Thilenius and Smith 1985), as do the grazed peaks of the Beartooths (Johnson and Billings 1962, Mellman-Brown 2002), and the Tobacco Root, Pioneer, and Madison Ranges in Southwestern Montana (Cooper et al. 1997). *G. rossii* has also been associated with grazing and soil disturbance caused by pocket gophers in Rocky Mountain National Park (Willard 1979).

Figure 4.17. *Geum rossii* – *Salix arctica* meadow (GERO-SAAR) near the summit of Abiathar Peak. Dominant graminoids are *Deschampsia cespitosa* and *Carex paysonis*.

Community 4d. *Carex paysonis-Agrostis variabilis* (CAPA-AGVA) This high abundance (cover = 108%), rich (23 spp. plot^{-1}) snowmelt community occurred on four mountains (6 plots). Cover (greater than 100% due to multiple vegetation layers) was higher for this type than for any other community. Constants (>80%) were *Agrostis variabilis*, *Festuca brachyphylla, Carex paysonis, Achillea millefolium*, *Sibbaldia procumbens, Deschampsia cespitosa*, *Veronica wormskjoldii, Salix arctica,* and hydrophilic mosses. Important associates (constancy >40%) included *Carex haydeniana, Juncus drummondii, Poa alpina, Antennaria media, Aster alpigenus, Epilobium anagallidifolium, Erigeron simplex* and *Stellaria monantha*. Many species occurred only in this group including *Carex pyrenaica, Luzula wahlenbergii, Antennaria lanata Erigeron ursinus, Phleum alpinum* and *Phyllodoce glanduliflora.*

This community occurred on gradual (14˚), east-west facing (76˚ from north) slopes (Fig. 4.18). As a result of its aspect potential radiation inputs were relatively high for a snowmelt community (81 MJ cm^{-1} yr^{-1}). Soil cover was higher for this type than for any other community (89%). Soils were well developed (N= 0.42%, C = 5.13%, P = 23.8 mg kg^{-1}), and acidic (pH = 5.5), with low levels of conductivity (0.11 mmhos cm^{-1}).

This type is very similar to a number of *C. paysonis* snowmelt communities of the Beaverhead National Forest in Southwestern Montana (Cooper et al. 1997). Several species specific to group 4d were also dominant in Southwest Montana sites including *Carex pyrenaica, Phleum alpinum, Antennaria lanata, Erigeron ursinus,* and *Phyllodoce* sp. Communities dominated by *C. paysonis, Aster alpigenus,* and *Achillea millefolium* have also been reported on Mount Hood in Oregon (Titus and Tsuyuzaki 1999).

Snowmelt communities dominated by *C. pyrenaica*, *J. drummondii,* and *S. procumbens* occur in the eastern Rocky Mountains of Colorado (Komárková and Weber 1978, Willard 1979, Hartman and Rottman 1988). In the andesitic San Juan Mountains of southern Colorado, snowmelt communities are often dominated by *D. cespitosa, J. drummondii, Erigeron simplex, S. procumbens,* and several sedges including *Carex nova, C. albonigra,* and *C. nigricans* (Rottman and Hartman 1985).

Figure 4.18. *Carex paysonis-Agrostis variabilis* community (CAPA-AGVA) near the summit of Amphitheatre Peak.

Community 4e. *Aster alpigenus-Sibbaldia procumbens* (ASAL-SIPR) This well drained late snowmelt community occurred at two sites on Amphitheatre Peak, and was relatively barren (cover = 49%), and species poor (18 spp. plot^{-1}). Like community 4a limited sample size (*n* = 2 plots) prevents confident description, although dominant species (>90% constancy) were *Carex paysonis, Aster alpigenus, Sibbaldia procumbens*, *Salix reticulata,* and the lichen *Lepraria cacuminum*. This community had much lower cover and richness than other late melt sites (Table 4.2b).

This community occurred on relatively flat (9˚), south-facing (153˚ from N) slopes (Fig. 4.19). The ASAL-SIPR environment is a simultaneous snow and solar radiation sink. High accumulations of snow were topographically driven by steep slopes downwind of the community. High loess content of soils (40% silt) confirms the area as a wind deposition zone. The community had the highest radiation input of any community (94 MJ $cm^{-2} yr^{-1}$). Soils were relatively rocky (46% soil cover), and well developed (N= 0.35%, C = 4.8%), except for phosphorous (10.5 mg kg^{-1}) which was the lowest for any of the fifteen communities. C/N ratio was higher for this group than for any of the fifteen communities (13.8). Alpine soils with high C/N ratios (≈ 14), have been found to be only moderately productive (Körner 2003). Soils in group 4e were acidic (pH = 6), with particularly high levels of conductivity (0.29 mmhos cm^{-1}).

This community is highly similar to a late melt association in Glacier National Park dominated by *Sibbaldia procumbens, Lepraria cacuminum, Carex paysonis,* and *Salix arctica* (Damm 2001). The Glacier community was described as very simple, with shallow soils overlaying bedrock, and high winds (Damm 2001).

Aster alpigenus has been associated with late melt sites in the Olympic Mountains (Billings 2000), the Sierras (Hunter and Johnson 1983), and on Mount Hood in Oregon (Titus and Tsuyuzaki 1999). *Sibbaldia procumbens* is a late melt indicator from the Canadian Rockies (Hrapko and LaRoi 1978), to Montana (Damm 2001, Cooper et al. 1997), and Colorado (Komárková 1979, Hartman and Rottman 1988).

Figure 4.19. *Aster alpigenus-Sibbaldia procumbens* community (ASAL-SIPR) near the summit of Amphitheatre Peak.

Comparison of Communities--Vegetation

Physiognomy

Visual differences among alpine communities depend largely on differences in plant cover and bare ground, and on the heights of dominant species. Tall communities (>3 dm) appear in warm moist ledge and wet, warm talus sites, i.e. ARRY-EPCL, and ELCSC-EPCL respectively. In the other shorter stature communities cover increases from talus (13%), to ridgetop (48%) to dry turf (75%) to snowbank sites (102%). Due to the morphology of large multispike sedges (e.g. *C. paysonis, C. phaeocephala, C. haydeniana*) snowbank sites demonstrate a clumped appearance not present in dry turf types. Vegetation on ridgetops was also clumped, especially short/prostrate (5-10 cm), and often dominated by cushion plants (e.g. *Astragalus kentrophyta, Sedum lanceolatum, Silene acaulis*) (Table 4.2a). Talus communities were clumped and physiognomically heterogeneous, with taller or shorter plants occurring with suitable microenvironments (Table 4.2a).

Species Constancy

In the Absaroka Volcanics, a few species occurred commonly (>50% constancy) across all vegetation types. These included. *Festuca brachyphylla, Elymus scribneri, Trisetum spicatum, Poa pattersonii,* and *Sedum lanceolatum*. However most species occurred infrequently (only 20 species occurred in more than 20% of the plots) and in particular gradient portions illustrated by our relevé tables (Tables 4.1a, 4.2a).

The species most characteristic of a community (constants) are usually present within that community. A novel way of demonstrating this is by calculating changes in community abundance and richness as a constancy threshold is applied (Tables 4.4 and 4.5). As noted above species constancies greater than 50% were relatively uncommon within communities. The number of species with > 50% constancy was particularly low in ledge (community 1 = 3 spp., Table 5.5), and talus communities (community 2a = 2 spp., 2b = 5 spp., 2c = 3 spp., 2d = 5 spp.), higher in snowbank communities (community 4a = 14 spp., 4b = 11 spp., 4c = 8 spp., 4d = 11 spp., 4e = 16 spp.), and highest in turf communities (community 3a = 10 spp., 3b = 14 spp., 3c = 15 spp., 3d = 18 spp., 3e = 19 spp. Table 4.6). Species with low constancy may represent rare species, or accidentals that will be unlikely to persist since alpine communities are resistant to colonization (Norton and Burrows 1979, Weaver et al. 2001).

Species Fidelity and Indicator Species Analysis

A species with high fidelity occurs in only one or two community types, though not necessarily with high constancy. High fidelity species are easily identifiable in Tables 4.1a and 4.2a, where they appear either in only one community (one column) or several similar communities (2-3 adjacent columns). High fidelity species with high constancy and abundance are the best indicator species. Indicator species analysis (ISA; Dufrêne and Legendre 1997) which is based on fidelity and abundance reinforces patterns evident from a qualitative examination of relevé tables. ISA indicator species for the fifteen communities are highly similar to the relevé-derived diagnostic species listed in the previous community descriptions section (Table 4.6, Appendix C.2).

Distribution of Functional Groups

Just as certain species have a higher fidelity for one environment than another, we expect certain life forms to favor particular environments. We demonstrate this by examining the distribution of functional groups (e.g. cushion plants, ferns, mosses, and shrubs) and taxonomic families across the ledge to talus to turf to snowbank gradient.

Graminoids

This functional group was the largest cover component in nine of the fifteen communities. Grasses (Poaceae) were more dominant in talus and ridge vegetation, while sedges and rushes (Cyperaceae, Juncaceae) were more dominant in turf and snow bank sites (Tables 4.7, 4.8). Species within Poaceae exhibited relatively high constancy across most of the 15 communities (Table 4.5), and would constitute a large fraction of community cover if low constancy species were removed (Table 4.4).

Forbs Communities with forbs as the largest component included several rocky community types including ledges (ARRY-EPCL relative cover (*RC*) = 91 %) and talus communities EPCL-ARABIS and ELSC-CIEA (Table 4.7). The importance of Asteraceae in ARRY-EPCL (Tables 4.4, 4.5, 4.7, 4.8) is due to the monodominance of *Arnica rydbergii*. Note that while the relative cover of graminoids and forbs varied widely across the fifteen communities (Table 4.7) richness of these functional groups varied little (Table 4.8). Regardless of widely differing environmental conditions, roughly 50%-60% of the species in each community were erect forbs, while 25-30% of species were graminoids (Table 4.8).

Cushion Plants Cushion plants were most prevalent along dry exposed ridgetops i.e. ERCO-ASKE (cover = 13%, richness = 6 spp., *RC* = 36%, relative richness (*RR*) = 13% Tables 4.4, 4.5, 4.7, 4.8). They were also common in dry turf (CAEL-PHMU), and two talus communities ELSC-ERCO and SABR-POVI (RC ≈ 20%, Table 4.8). The cushion plant life form may be an adaptation to these dry, cold, or nutrient poor environments for three reasons. First, cushion plants are well adapted to dryness of ridgetops and *Carex elynoides* turf, since their shape reduces overall evapotranspiration (Körner and De Moraes 1979). Second, in exposed windy ridgetop environments cushion plants function as heat traps which gives them a competitive advantage over less prostrate shrubs (Gauslaa 1984). Finally, cushion plants can be seen as litter/nutrient traps in nutrient poor talus sites since they create favorable micro-environments for decomposers and adventitious roots (Körner 2003).

In the Northern Absarokas the cushion plant *Astragalus kentrophyta*, was particularly dominant along ridgetops and comprised most of the high relative cover of Fabaceae in ERCO-ASKE (*RC* = 22%; Table 4.7). This dominance may be due to the N-poor environment of this community (0.1 total %N; Table 4.2b). All alpine legumes are nodulated giving them an advantage at N-poor sites (Bowman et al. 1996). Note however that if N accumulates locally, N-fixation may be suicidal since nodulated plants will eventually decrease their competitive advantage and exclude themselves from sites they have enriched (Begon et al. 1996). This process may be minimized on ridgetops where poorly bound soil N may be continually washed downhill preventing accumulation.

Mustards and Talus Families Mustards were most dominant in talus communities (Tables 4.7, 4.8). Members of Brassicaceae often thrive in disturbed soils world-wide and talus/scree sites in the Absaroka Volcanics were particularly unstable. Other important talus families were Onagraceae (due to the frequent occurrence of *Epilobium clavatum*) Ranunculaceae (due to the occurrence of *Ranunculus eschscholtzii*), and Polemoniaceae (i.e. *Polemonium viscosum, P. pulcherrimum*) (Tables 4.7, 4.8).

Shrubs and Snowbank Families Shrubs had the highest cover in late snowmelt communities. High shrub cover was due to alpine dwarf willows, *Salix arctica*, and *S. reticulata*. Along with Salicaceae a number of families preferred snowbank communities including Juncaceae, Cyperaceae, and Violaceae (Tables 4.4, 4.5, 4.7, 4.8).

Annuals Shallow rooted annual plants are rare, and their contribution to total cover is insignificant in most alpine communities (Reynolds 1984, Billings 2000), including the Absarokas (Tables 4.4, 4.5, 4.7, 4.8). While they provided little cover, annuals appeared in all of our communities. They included *Draba crassifolia* and *Draba praelta* (those these species can also be biennial, or short-lived perennials), *Androsace septentrionalis*, *Polygonum douglasii*, and *Sagina saginoides*.

Mosses, Lichens, Ferns, and Fern Allies Mosses were the dominant cover type in the snowbank community CAPA-ARSC (*RC* = 38%), and other north-facing snowmelt communities (i.e. RAPY-CAHA, GERO-SAAR, CAPA-AGVA). Although mosses were grouped for analysis, individual species included *Aulacomnium palustre, Barbilophozia hatchery, Brachythecium albicans, Bryum* sp., *Desmatadon latifolius, Dicranum* spp. *Dicranoweisia crispula, Drepanocladus* spp., *Hypnum* spp., *Hypnum revolutum, Philonotis fontana, Pohlia cruda, Polytrichium juniperinum,* and *Tortula ruralis.*

In the south facing snowbank community ASAL-SIPR lichens were a particularly large cover component due to the dominance of *Lepraria cacuminum* (Table 4.8). Ferns (i.e. *Cystopteris fragilis*) occurred only on talus and ledges, while fern allies (i.e. *Selaginella densa*) occurred in well drained communities across the ledge, talus, turf, snowmelt gradient (Table 4.7, 4.8)

Table 4.4. Percent cover of families and functional groups of the 15 identified community types. The first number in each cell is simply percent cover, the second number indicates the percent cover only using species that occur with >50% constancy within a category. “+” indicates cover between 0.1% and 1%, “tr” indicates cover < 0.1%.

	LEDGE		TALUS			TURF						LATE-SNOWMELT			
	ARRY EPCL (1)	EPCL ARABIS (2a)	ELSC CIEA (2b)	ELSC ERCO (2c)	SABR POVI (2d)	ERCO ASKE (3a)	RAES ASFO (3b)	CAEL PHMU (3c)	CAAL (3d)	CASC CAPH (3e)	RAPY CAHA (4a)	CAPA ARSC (4b)	GERO SAAR (4c)	CAPA AGVA (4d)	ASAL SIPR (4e)
Number of plots	10	9	7	14	14	14	6	8	4	6	2	4	4	6	2
Total cover	55\49	7\1	19\11	10\3	15\7	37\25	31\21	75\49	93\74	80\54	58\57	118\98	90\63	108\73	73\72
Functional Group															
All Anthophyta	55\49	7\1	19\11	9\3	15\7	34\25	29\19	68\46	82\63	65\50	47\46	73\53	77\50	95\61	45\43
Annuals	tr\0	+\0	tr\0	+\0	+\0	+\0	+\+	+\+	tr\0	+\+	0\0	+\0	+\0	+\0	tr\0
Cushion plants	0\0	0\0	1\0	2\+	3\+	13\11	1\0	14\12	10\4	11\11	0\0	+\0	2\1	6\0	0\0
Fern allies	0\0	0\0	0\0	+\0	0\0	1\0	0\0	5\0	0\0	5\5	0\0	0\0	+\0	0\0	5\5
Ferns	tr\0	0\0	0\0	tr\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0
Forbs	50\47	5\1	9\7	3\+	4\+	9\4	11\7	26\18	34\22	27\17	11\10	37\22	14\3	28\17	19\19
Graminoids	5\1	2\0	9\5	4\2	7\6	12\11	15\11	27\15	38\37	26\22	36\36	34\31	18\3	56\39	11\9
Grasses	3\1	1\0	6\5	4\2	7\6	11\11	13\10	14\13	12\10	11\10	19\19	11\9	13\2	30\26	2\2
Lichens	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	5\0	0\0	0\0	0\0	0\0	24\24
Mosses	0\0	+\0	tr\0	tr\0	+\0	1\0	2\2	3\3	11\11	5\0	10\10	45\45	13\13	13\13	0\0
Rushes	tr\0	0\0	tr\0	tr\0	+\0	tr\0	1\1	3\3	1\1	2\2	1\1	4\4	1\1	6\0	+\+
Sedges	1\0	+\0	3\0	+\0	+\0	1\0	1\0	11\0	26\26	12\10	16\16	20\18	4\0	20\13	8\7
Trees/shrubs	0\0	0\0	0\0	0\0	tr\0	0\0	2\0	0\0	0\0	3\0	+\0	1\0	43\43	5\5	15\15
Families															
Apiaceae	tr\0	0\0	0\0	+\+	+\0	+\0	0\0	+\0	+\+	0\0	0\0	+\0	0\0	0\0	0\0
Aspleniaceae	tr\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0
Asteraceae	49\47	2\0	8\7	2\+	1\+	6\5	7\5	10\8	8\4	11\5	4\3	18\15	7\2	9\4	10\10
Boraginaceae	0\0	0\0	0\0	tr\0	+\0	+\0	+\+	4\4	4\3	+\+	+\0	3\0	tr\0	0\0	0\0
Brassicaceae	tr\0	+\+	+\0	+\0	+\0	+\0	+\0	2\2	+\+	1\+	0\0	+\0	+\0	tr\0	0\0

Table 4.4 cont.

	ARRY EPCL (1)	EPCL ARABIS (2a)	ELSC CIEA (2b)	ELSC ERCO (2c)	SABR POVI (2d)	ERCO ASKE (3a)	RAES ASFO (3b)	CAEL PHMU (3c)	CAAL (3d)	CASC CAPH (3e)	RAPY CAHA (4a)	CAPA ARSC (4b)	GERO SAAR (4c)	CAPA AGVA (4d)	ASAL SIPR (4e)
Bryophyta	0\0	+\0	tr\0	tr\0	+\0	1\0	2\2	3\3	11\11	5\0	10\10	45\45	13\13	13\13	0\0
Caryophyllaceae	0\0	+\0	0\0	+\0	1\+	4\2	1\+	7\2	8\4	9\9	1\1	2\+	2\2	1\0	+\+
Crassulaceae	tr\0	tr\0	+\0	+\0	tr\0	1\1	+\+	2\2	3\3	+\+	0\0	+\0	tr\0	tr\0	tr\tr
Cyperaceae	1\0	+\0	3\0	+\0	+\0	1\0	1\0	11\0	26\26	12\10	16\16	20\18	4\0	20\13	8\7
Ericaceae	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	6\0	0\0
Fabaceae	0\0	0\0	+\0	+\0	+\0	8\7	+\0	6\6	6\6	5\5	0\0	0\0	0\0	+\0	0\0
Hydrophyllaceae	0\0	0\0	+\0	+\0	0\0	+\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0
Juncaceae	tr\0	0\0	tr\0	tr\0	+\0	tr\0	1\1	3\3	1\1	2\2	1\1	4\4	1\1	6\0	+\+
Liliaceae	0\0	0\0	0\0	0\0	+\0	0\0	0\0	0\0	4\0	0\0	0\0	2\2	0\0	0\0	0\0
Onagraceae	+\+	1\1	+\0	tr\0	tr\0	0\0	+\0	0\0	0\0	0\0	0\0	1\0	0\0	1\0	0\0
Ophioglossaceae	0\0	0\0	0\0	tr\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0
Pinaceae	0\0	0\0	0\0	0\0	tr\0	0\0	+\0	0\0	0\0	0\0	0\0	+\0	0\0	0\0	0\0
Poaceae	3\1	1\0	6\5	4\2	7\6	11\11	13\10	14\13	12\10	11\10	19\19	11\9	13\2	30\26	2\2
Polemoniaceae	0\0	0\0	tr\0	+\0	+\0	+\0	tr\0	6\6	3\0	0\0	0\0	0\0	0\0	0\0	0\0
Polygonaceae	0\0	+\0	0\0	0\0	tr\0	tr\0	+\0	+\0	0\0	1\0	2\2	0\0	tr\0	+\0	1\1
Portulacaceae	0\0	tr\0	0\0	tr\0	tr\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	+\0	tr\0
Primulaceae	tr\0	0\0	tr\0	+\0	+\0	+\0	+\+	+\+	tr\0	+\+	0\0	+\0	+\0	tr\0	tr\0
Ranunculaceae	tr\0	+\0	tr\0	+\0	0\0	0\0	+\+	0\0	+\0	tr\0	3\3	1\0	+\0	+\0	0\0
Rosaceae	tr\0	0\0	tr\0	tr\0	tr\0	tr\0	tr\0	1\0	3\2	8\6	0\0	7\4	5\0	11\10	7\7
Salicaceae	0\0	0\0	0\0	0\0	0\0	0\0	2\0	0\0	0\0	3\0	+\0	+\0	43\43	5\5	15\15
Saxifragaceae	0\0	0\0	+\0	0\0	2\0	tr\0	+\0	+\0	+\0	tr\0	+\+	1\0	1\0	+\0	+\+
Scrophulariaceae	tr\0	0\0	+\0	0\0	0\0	0\0	+\0	+\0	2\2	+\0	tr\0	+\0	+\0	3\3	0\0
Selaginellaceae	0\0	0\0	0\0	+\0	0\0	1\0	0\0	5\0	0\0	5\5	0\0	0\0	+\0	0\0	5\5
Violaceae	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	+\0	0\0

Table 4.5. Species richness of families and functional groups of the 15 community types. The first number in each cell simply represents the total number of species present, the second number indicates the number of species with >50% constancy.

	LEDGE		TALUS			TURF						LATE-SNOWMELT			
	ARRY EPCL (1)	EPCL ARABIS (2a)	ELSC CIEA (2b)	ELSC ERCO (2c)	SABR POVI (2d)	ERCO ASKE (3a)	CAAL (3b)	CAEL PHMU (3c)	CASC CAPH (3d)	RAES ASFO (3e)	RAPY CAHA (4a)	CAPA ARSC (4b)	GERO SAAR (4c)	CAPA AGVA (4d)	ASAL SIPR (4e)
Number of plots	10	9	7	14	14	14	6	8	4	6	2	4	4	6	2
Total richness	28\3	23\2	31\5	46\3	45\5	48\10	44\14	47\15	43\18	42\19	20\14	41\11	36\8	58\11	21\16
Functional group															
All Anthophyta	27\3	22\2	30\5	43\3	43\5	46\10	42\13	45\14	42\17	39\18	19\13	39\10	34\7	57\10	19\14
Annuals	1\0	1\0	1\0	1\0	1\0	3\0	2\1	1\1	1\0	1\1	0\0	3\0	2\0	2\0	1\0
Cushion plants	0\0	0\0	3\0	4\1	5\1	6\2	5\0	6\2	5\1	3\3	0\0	1\0	3\1	2\0	0\0
Fern allies	0\0	0\0	0\0	1\0	0\0	1\0	0\0	1\0	0\0	1\1	0\0	0\0	1\0	0\0	1\1
Ferns	1\0	0\0	0\0	1\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0
Forbs	16\2	14\2	18\3	29\1	28\1	30\3	25\9	28\8	28\10	24\9	12\7	27\5	18\3	35\4	11\8
Graminoids	11\1	8\0	9\2	10\1	10\3	10\5	11\4	11\4	9\6	11\6	6\6	10\5	12\2	18\5	7\5
Grasses	7\1	6\0	7\2	7\1	7\3	8\5	7\3	8\3	6\4	6\4	4\4	6\3	7\1	9\3	3\3
Lichens	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	1\0	0\0	0\0	0\0	0\0	1\1
Moss (+/-)	0\0	1\0	1\0	1\0	1\0	1\0	1\1	1\1	1\1	1\0	1\1	1\1	1\1	1\1	0\0
Rushes	1\0	0\0	1\0	1\0	1\0	1\0	1\1	1\1	1\1	2\1	1\1	1\1	2\1	5\0	1\1
Sedges	3\0	2\0	1\0	2\0	2\0	1\0	3\0	2\0	2\1	3\1	1\1	3\1	3\0	4\2	3\1
Trees/shrubs	0\0	0\0	0\0	0\0	1\0	0\0	2\0	0\0	0\0	1\0	1\0	2\0	1\1	2\1	1\1
Family															
Apiaceae	1\0	0\0	0\0	1\1	1\0	1\0	0\0	1\0	1\1	0\0	0\0	1\0	0\0	0\0	0\0
Aspleniaceae	1\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0
Asteraceae	8\1	5\0	9\3	11\1	10\1	12\2	11\4	12\3	10\1	8\2	5\3	9\2	5\2	15\2	3\2
Boraginaceae	0\0	0\0	0\0	1\0	1\0	2\0	1\1	1\1	2\1	1\1	1\0	1\0	1\0	0\0	0\0
Brassicaceae	1\0	2\1	1\0	3\0	3\0	4\0	2\0	4\1	2\1	3\1	0\0	1\0	2\0	1\0	0\0
Bryophyta	0\0	1\0	1\0	1\0	1\0	1\0	1\1	1\1	1\1	1\0	1\1	1\1	1\1	1\1	0\0
Caryophyllaceae	0\0	1\0	0\0	4\0	5\1	5\1	4\1	5\1	4\2	4\3	2\1	4\1	3\2	6\0	1\1

Table 4.5. cont.

	ARRY EPCL (1)	EPCL ARABIS (2a)	ELSC CIEA (2b)	ELSC ERCO (2c)	SABR POVI (2d)	ERCO ASKE (3a)	CAAL (3b)	CAEL PHMU (3c)	CASC CAPH (3d)	RAES ASFO (3e)	RAPY CAHA (4a)	CAPA ARSC (4b)	GERO SAAR (4c)	CAPA AGVA (4d)	ASAL SIPR (4e)
Crassulaceae	1\0	1\0	1\0	1\0	1\0	1\1	1\1	1\1	1\1	1\1	0\0	2\0	1\0	1\0	1\1
Cyperaceae	3\0	2\0	1\0	2\0	2\0	1\0	3\0	2\0	2\1	3\1	1\1	3\1	3\0	4\2	3\1
Ericaceae	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	1\0	0\0
Fabaceae	0\0	0\0	2\0	2\0	2\0	3\1	1\0	1\1	2\2	1\1	0\0	0\0	0\0	1\0	0\0
Hydrophyllaceae	0\0	0\0	1\0	1\0	0\0	2\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0
Juncaceae	1\0	0\0	1\0	1\0	1\0	1\0	1\1	1\1	1\1	2\1	1\1	1\1	2\1	5\0	1\1
Liliaceae	0\0	0\0	0\0	0\0	1\0	0\0	0\0	0\0	1\0	0\0	0\0	1\1	0\0	0\0	0\0
Onagraceae	1\1	2\1	1\0	1\0	1\0	0\0	1\0	0\0	0\0	0\0	0\0	1\0	0\0	1\0	0\0
Ophioglossaceae	0\0	0\0	0\0	1\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0
Pinaceae	0\0	0\0	0\0	0\0	1\0	0\0	1\0	0\0	0\0	0\0	0\0	1\0	0\0	0\0	0\0
Poaceae	7\1	6\0	7\2	7\1	7\3	8\5	7\3	8\3	6\4	6\4	4\4	6\3	7\1	9\3	3\3
Polemoniaceae	0\0	0\0	1\0	3\0	2\0	1\0	1\0	1\1	1\0	0\0	0\0	0\0	0\0	0\0	0\0
Polygonaceae	0\0	1\0	0\0	0\0	2\0	2\0	1\0	1\0	0\0	1\0	1\1	0\0	1\0	1\0	1\1
Portulacaceae	0\0	1\0	0\0	1\0	1\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	1\0	1\0
Primulaceae	1\0	0\0	1\0	1\0	1\0	1\0	1\1	1\1	1\0	1\1	0\0	2\0	2\0	1\0	1\0
Ranunculaceae	1\0	1\0	1\0	1\0	0\0	0\0	1\1	0\0	1\0	1\0	1\1	1\0	1\0	1\0	0\0
Rosaceae	1\0	0\0	1\0	2\0	1\0	1\0	1\0	2\0	4\1	4\2	0\0	2\1	2\0	2\1	2\2
Salicaceae	0\0	0\0	0\0	0\0	0\0	0\0	1\0	0\0	0\0	1\0	1\0	1\0	1\1	2\1	1\1
Saxifragaceae	0\0	0\0	1\0	0\0	1\0	1\0	2\0	2\0	2\0	1\0	1\1	2\0	1\0	1\0	1\1
Scrophulariaceae	1\0	0\0	1\0	0\0	0\0	0\0	2\0	2\0	1\1	1\0	1\0	1\0	2\0	2\1	0\0
Selaginellaceae	0\0	0\0	0\0	1\0	0\0	1\0	0\0	1\0	0\0	1\1	0\0	0\0	1\0	0\0	1\1
Violaceae	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	0\0	2\0	0\0

Table 4.6. Significant indicators[1] for the fifteen groups identified in this study as determined by indicator species analysis (Dufrêne and Legendre 1997). Underlined species in the table were not significant at α = 0.05, but are included since they were statistically the best indicators for their respective types. *P*-values are the result of tests of the hypothesis of no association between indicator value for a particular and its "maximum group".

Max group	Species	indicator value (*IV*)	*p* – value	Max group	species	indicator value (*IV*)	*p* - value
1 ARRY_EPCL	*Arnica rydbergii*	93.4	<0.001***	4a RAPY_CAHA	*Carex haydeniana*	63.8	0.005**
2a EPCL_ARABIS	*Arabis* spp. (all)	13.9	0.28	4a RAPY_CAHA	*Erigeron humilis*	87.9	<0.001***
2a EPCL_ARABIS	*Draba crassifolia*	8.2	0.631	4a RAPY_CAHA	*Festuca brachyphylla*	33.1	0.002**
2b ELSC_CIEA	*Cirsium eatonii*	82.1	<0.001***	4a RAPY_CAHA	*Oxyria digyna*	81.1	<0.001***
2b ELSC_CIEA	*Elymus scribneri*	27.2	0.004**	4a RAPY_CAHA	*Poa leptocoma*	91.2	<0.001***
2c ELSC_ERCO	*Claytonia megarhiza*	9.9	0.523	4a RAPY_CAHA	*Ranunculus pygmaeus*	100	<0.001***
2d SABR_POVI	*Polemonium viscosum*	15.8	0.306	4a RAPY_CAHA	*Saxifraga rivularis*	100	<0.001***
2d SABR_POVI	*Saxifraga bronchialis*	16.4	0.284	4a RAPY_CAHA	*Stellaria monantha*	27.9	0.052*
3a ERCO_ASKE	*Astragalus kentrophyta*	29.8	0.004**	4a RAPY_CAHA	*Taraxacum* spp.	78.9	0.002**
3a ERCO_ASKE	*Erigeron compositus*	52.7	<0.001***	4b CAPA_ARSC	*All mosses*	43.5	0.008**
3a ERCO_ASKE	*Senecio canus*	30.5	0.039*	4b CAPA_ARSC	*Artemisia scopulorum*	57.8	0.007**
3b RAES_ASFO	*Androsace septentrionalis*	34.1	0.016*	4b CAPA_ARSC	*Carex paysonis*	47.9	0.014*
3b RAES_ASFO	*Aster foliaceus* v. *apricus*	49.9	0.009**	4b CAPA_ARSC	*Poa reflexa*	36	0.019*
3c CAEL_PHMU	*Arenaria congesta*	34.7	0.03*	4b CAPA_ARSC	*Sagina saginoides*	50	0.008**
3c CAEL_PHMU	*Carex elynoides*	50	0.002**	4b CAPA_ARSC	*Sedum integrifolium*	50	0.007**
3c CAEL_PHMU	*Phlox multiflora*	49.6	0.009**	4c GERO_SAAR	*Geum rossii*	39.8	0.019*
3c CAEL_PHMU	*Saxifraga rhomboidea*	50	0.002**	4c GERO_SAAR	*Poa cusickii*	38.9	0.053*
3c CAEL_PHMU	*Sedum lanceolatum*	28.1	0.044*	4c GERO_SAAR	*Salix arctica*	85.8	<0.001***
3d CAAL	*Astragalus alpinus*	72.8	<0.001***	4d CAPA_AGVA	*Agoseris aurantiaca*	33.3	0.042*
3d CAAL	*Carex albonigra*	100	<0.001***	4d CAPA_AGVA	*Agrostis variabilis*	58.6	0.004**
3d CAAL	*Castilleja pulchella*	100	<0.001***	4d CAPA_AGVA	*Antennaria media*	37.9	0.02*
3d CAAL	*Lomatium cous*	29	0.032*	4d CAPA_AGVA	*Carex pyrenaica*	37.7	0.035*
3d CAAL	*Mertensia alpina*	29.5	0.042*	4d CAPA_AGVA	*Deschampsia cespitosa*	64.9	0.009**
3d CAAL	*Myosotis alpestris*	37.8	0.046*	4d CAPA_AGVA	*Epilobium anagallidifolium*	39.7	0.016*
3d CAAL	*Poa alpina*	29.5	0.04*	4d CAPA_AGVA	*Juncus drummondii*	34.1	0.04*
3d CAAL	*Potentilla* spp.	41.6	0.005**	4d CAPA_AGVA	*Lewisia pygmaea*	46.8	0.002**
3e CASC_CAPH	*Arenaria obtusiloba*	31.9	0.036*	4d CAPA_AGVA	*Phyllodoce glanduliflora*	50	0.002**
3e CASC_CAPH	*Carex phaeocephala*	63.2	0.002**	4d CAPA_AGVA	*Sibbaldia procumbens*	36	0.015*
3e CASC_CAPH	*Draba incerta*	36.1	0.018*	4d CAPA_AGVA	*Veronica wormskjoldii*	96.1	<0.001***
3e CASC_CAPH	*Selaginella densa*	29.7	0.037*	4e ASAL_SIPR	*Aster alpigenus*	59.7	0.002**
3e CASC_CAPH	*Silene acaulis*	38.9	0.021*	4e ASAL_SIPR	lichen *(Lepraria cacuminum)*	83.2	<0.001***
				4e ASAL_SIPR	*Polygonum bistortoides*	45.3	0.011*
				4e ASAL_SIPR	*Salix reticulata*	83.8	0.002**

[1] Signif. codes: "***"≤ 0.001 "**"≤ 0.01 "*"< 0.05.

Table 4.7. Percent relative cover[1] of families and functional groups within 15 community types. "+" indicates cover between 0.1% and 1%, "tr" indicates cover < 0.1%.

	LEDGE	TALUS				TURF					LATE-SNOWMELT				
	ARRY EPCL (1)	EPCL ARABIS (2a)	ELSC CIEA (2b)	ELSC ERCO (2c)	SABR POVI (2d)	ERCO ASKE (3a)	RAES ASFO (3b)	CAEL PHMU (3c)	CAAL (3d)	CASC CAPH (3e)	RAPY CAHA (4a)	CAPA ARSC (4b)	GERO SAAR (4c)	CAPA AGVA (4d)	ASAL SIPR (4e)
Functional group															
All Anthophyta	100	93	100	98	97	94	93	90	88	82	82	62	85	88	61
Annuals	tr	3	+	2	+	+	2	+	tr	+	.	+	+	tr	tr
Cushion plants	.	.	6	21	22	36	5	19	11	13	.	+	3	5	.
Fern allies	.	.	.	2	.	3	.	7	.	6	.	.	+	.	7
Ferns	tr	.	.	tr	.	.	.	.	.	.	.	.	.	.	.
Forbs	91	72	49	35	26	24	35	34	36	33	19	32	15	26	26
Graminoids	9	22	44	42	49	34	48	36	41	32	62	29	20	52	14
Grasses	6	18	30	38	45	30	42	18	13	14	33	9	14	28	2
Lichens	.	.	.	.	.	.	.	.	.	6	.	.	.	.	32
Mosses	.	7	+	+	3	3	6	4	12	6	18	38	14	12	.
Rushes	tr	.	+	+	2	Tr	3	4	1	3	2	3	2	5	+
Sedges	3	4	14	3	1	3	3	14	27	16	28	17	4	19	11
Trees/shrubs	.	.	.	.	tr	.	6	.	.	3	+	+	48	5	20
Family															
Apiaceae	+	.	.	3	2	1	.	+	+	.	.	+	.	.	.
Aspleniaceae	tr	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Asteraceae	89	27	43	17	9	17	24	13	9	13	6	15	8	8	14
Boraginaceae	.	.	.	+	+	2	+	5	4	+	+	2	tr	.	.
Brassicaceae	+	7	+	6	4	2	+	2	+	1	.	+	+	tr	.
Bryophyta	.	7	+	+	3	3	6	4	12	6	18	38	14	12	.
Caryophyllaceae	.	2	.	2	7	11	4	9	9	11	3	2	2	1	1
Crassulaceae	+	+	2	2	+	3	+	3	3	1	.	+	tr	tr	+
Cyperaceae	3	4	14	3	1	3	3	14	27	16	28	17	4	19	11
Ericaceae	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.

Table 4.7 (cont.)

	ARRY EPCL (1)	EPCL ARABIS (2a)	ELSC CIEA (2b)	ELSC ERCO (2c)	SABR POVI (2d)	ERCO ASKE (3a)	RAES ASFO (3b)	CAEL PHMU (3c)	CAAL (3d)	CASC CAPH (3e)	RAPY CAHA (4a)	CAPA ARSC (4b)	GERO SAAR (4c)	CAPA AGVA (4d)	ASAL SIPR (4e)
Fabaceae	.	.	2	8	6	22	2	8	6	6	.	.	.	+	.
Hydrophyllaceae	.	.	+	1	.	+	.	.	.	.	.	.	.	.	.
Juncaceae	tr	.	+	+	2	tr	3	4	1	3	2	3	2	5	+
Liliaceae	.	.	.	.	+	.	.	.	5	.	.	1	.	.	.
Onagraceae	1	18	1	+	tr	.	+	.	.	.	.	1	.	1	.
Ophioglossaceae	.	.	.	tr	.	.	.	.	.	.	.	.	.	.	.
Pinaceae	.	.	.	.	tr	.	1	.	.	.	.	+	.	.	.
Poaceae	6	18	30	38	45	30	42	18	13	14	33	9	14	28	2
Polemoniaceae	.	.	tr	10	4	2	tr	9	3	.	.	.	.	.	.
Polygonaceae	.	4	.	.	+	tr	+	+	.	1	4	.	tr	+	1
Portulacaceae	.	+	.	+	tr	.	.	.	.	.	.	.	.	+	tr
Primulaceae	tr	.	+	2	+	+	2	+	tr	+	.	+	+	tr	tr
Ranunculaceae	tr	13	+	2	.	.	3	.	+	tr	6	1	+	+	.
Rosaceae	+	.	+	+	tr	tr	+	1	4	10	.	6	6	10	10
Salicaceae	.	.	.	.	.	.	5	.	.	3	+	+	48	5	20
Saxifragaceae	.	.	4	.	12	tr	+	1	+	tr	+	+	1	+	+
Scrophulariaceae	tr	.	+	.	.	.	+	+	2	+	tr	+	+	3	.
Selaginellaceae	.	.	.	2	.	3	.	7	.	6	.	.	+	.	7
Violaceae	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.

[1] Percent of relative cover refers to the percentage of total vegetation cover contributed by each taxon.

Table 4.8. Percent relative richness[1] of functional groups and families within 15 community types.

	LEDGE	TALUS				TURF					LATE-SNOWMELT				
	ARRY EPCL (1)	EPCL ARABIS (2a)	ELSC CIEA (2b)	ELSC ERCO (2c)	SABR POVI (2d)	ERCO ASKE (3a)	RAES ASFO (3b)	CAEL PHMU (3c)	CAAL (3d)	CASC CAPH (3e)	RAPY CAHA (4a)	CAPA ARSC (4b)	GERO SAAR (4c)	CAPA AGVA (4d)	ASAL SIPR (4e)
Functional group															
Annual	4	4	3	2	2	6	5	2	2	2	.	7	6	3	5
Graminoid	39	35	29	22	22	21	25	23	21	26	30	24	33	31	33
All Anthophyta	96	96	97	93	96	96	95	96	98	93	95	95	94	98	90
Cushion plant	.	.	10	9	11	13	11	13	12	7	.	2	8	3	.
Fern	4	.	.	2	.	.	.	.	.	.	.	.	.	.	.
Fern ally	.	.	.	2	.	2	.	2	.	2	.	.	3	.	5
Forb	57	61	58	63	62	63	57	60	65	57	60	66	50	60	52
Graminoid	39	35	29	22	22	21	25	23	21	26	30	24	33	31	33
Grass	25	26	23	15	16	17	16	17	14	14	20	15	19	16	14
Lichen	.	.	.	.	.	.	.	.	.	2	.	.	.	.	5
Moss	.	4	3	2	2	2	2	2	2	2	5	2	3	2	.
Rush	4	.	3	2	2	2	2	2	2	5	5	2	6	9	5
Sedge	11	9	3	4	4	2	7	4	5	7	5	7	8	7	14
Tree/shrub	.	.	.	.	2	.	5	.	.	2	5	5	3	3	5
Family															
Apiaceae	4	.	.	2	2	2	.	2	2	.	.	2	.	.	.
Aspleniaceae	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Asteraceae	29	22	29	24	22	25	25	26	23	19	25	22	14	26	14
Boraginaceae	.	.	.	2	2	4	2	2	5	2	5	2	3	.	.
Brassicaceae	4	9	3	7	7	8	5	9	5	7	.	2	6	2	.
Bryophyta	.	4	3	2	2	2	2	2	2	2	5	2	3	2	.
Caryophyllaceae	.	4	.	9	11	10	9	11	9	10	10	10	8	10	5
Crassulaceae	4	4	3	2	2	2	2	2	2	2	.	5	3	2	5
Cyperaceae	11	9	3	4	4	2	7	4	5	7	5	7	8	7	14
Ericaceae	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.

Table 4.8 (cont.)

	ARRY EPCL (1)	EPCL ARABIS (2a)	ELSC CIEA (2b)	ELSC ERCO (2c)	SABR POVI (2d)	ERCO ASKE (3a)	RAES ASFO (3b)	CAEL PHMU (3c)	CAAL (3d)	CASC CAPH (3e)	RAPY CAHA (4a)	CAPA ARSC (4b)	GERO SAAR (4c)	CAPA AGVA (4d)	ASAL SIPR (4e)
Fabaceae	.	.	6	4	4	6	2	2	5	2	.	.	.	2	.
Hydrophyllaceae	.	.	3	2	.	4	.	.	.	.	.	.	.	.	.
Juncaceae	4	.	3	2	2	2	2	2	2	5	5	2	6	9	5
Lichen	.	.	.	.	.	.	.	.	.	2	.	.	.	.	5
Liliaceae	.	.	.	.	2	.	.	.	2	.	.	2	.	.	.
Onagraceae	4	9	3	2	2	.	2	.	.	.	.	2	.	2	.
Ophioglossaceae	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.
Pinaceae	.	.	.	.	2	.	2	.	.	.	.	2	.	.	.
Poaceae	25	26	23	15	16	17	16	17	14	14	20	15	19	16	14
Polemoniaceae	.	.	3	7	4	2	2	2	2	.	.	.	.	.	.
Polygonaceae	.	4	.	.	4	4	2	2	.	2	5	.	3	2	5
Portulacaceae	.	4	.	2	2	.	.	.	.	.	.	.	.	2	5
Primulaceae	4	.	3	2	2	2	2	2	2	2	.	5	6	2	5
Ranunculaceae	4	4	3	2	.	.	2	.	2	2	5	2	3	2	.
Rosaceae	4	.	3	4	2	2	2	4	9	10	.	5	6	3	10
Salicaceae	.	.	.	.	.	.	2	.	.	2	5	2	3	3	5
Saxifragaceae	.	.	3	.	2	2	5	4	5	2	5	5	3	2	5
Scrophulariaceae	4	.	3	.	.	.	5	4	2	2	5	2	6	3	.
Selaginellaceae	.	.	.	2	.	2	.	2	.	2	.	.	3	.	5
Violaceae	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.

[1] Percent relative richness refers to the percentage of total richness contributed by each taxon.

Comparison of Communities--Environment

The severe environmental gradients of alpine environments are probably more important than biological interactions in determining alpine plant community composition (Billings 1979). Alpine gradients were depicted by correlating distributions of plots in the ordination with environmental variables (Fig. 4.4, Table 4.3). Correlation strength with axis scores is indicated by vector arrow length, while arrow bearing indicates the direction of most rapid gradient change across the scatterplot (Fig. 4.4). Increasing cover and richness across the first axis (from talus to turf to snowmelt) is due to decreasing stress (due to dehydration, extreme temperatures, and exposure), increasing soils (which retain water and nutrients), and increasing substrate stability (decreasing slope). The second axis which separates talus and snowmelt subtypes is strongly associated with elevation (Fig. 4.4). The third axis which separates the ledge community from other types due its unique composition is mostly associated with slope and solar radiation (Fig. 4.4).

Permutation testing showed that all variables except soil clay content were significantly related to scatterplot configurations of both dimensions 1 and 2 and dimensions 1 and 3 (Table 4.3). The six best predictors of ordination scatter were: soil and rock cover, pH, %N, %C, and elevation (Table 4.3). Since four of these variables (soil, rock, C, N, and pH) were strongly correlated to each other, a simpler interpretation is that the best measured predictors of vegetation composition were the accumulation and development of soils and elevation. While unmeasured in the N. Absarokas, the importance of soil moisture to community composition can be deduced by the importance of this variable at the nearby Washburn range, and by the importance of pH in the N. Absarokas since pH is strongly negatively correlated with soil water in alpine areas worldwide (Körner 2003).

Most individual environmental variables were also significantly associated with cover and richness (Table 4.9). Highly significant positive correlates were C, N, P, conductivity, soil cover, and silt content (Table 4.9). Significant negative correlates were pH, rock cover, sand content of soil, and slope (Table 4.9).

A surprisingly strong positive correlate of richness was elevation ($r = 0.5$, $p < 0.001$; Table 4.9). Previously Gottfried et al. (1998) found that highest levels of alpine plant richness were at the upper altitudinal limits of alpine vegetation (alpine/nival interface) in the Austrian Alps. While this ecotone is not approached in the Absarokas Volcanics (elev. < 3300m, Lat ≅ 45° N), richness may generally increase in alpine communities with increasing environmental stress since such pressures prevent monodominance (Nilsson et al. 2002).

Soil Accumulation

Four potential sources for accumulation of soil exist in alpine environments. These are: 1) on-site decomposition of parent rock, 2) downslope movement, 3) deposition of snow or water, and 4) deposition by wind (Körner 2003). Two seem particularly important in the Absaroka Volcanics. That decomposition of parent material may be the source of soils in talus areas is suggested by the high sand content of soils under talus (Tables 4.1b, 4.2b). Similarly, high concentrations of silt in turf and snowbank sites (Tables 4.1b, 4.2b) suggest that soils in these communities are derived largely from wind deposited loess. Positive environmental correlates to soil accumulation (cover) were silt and conductivity ($r = 0.5$, $p < 0.01$). Negative correlates to soil accumulation were slope (negatively associated with substrate stability) and pH ($r = -0.68, -0.4$, $p < 0.01$).

Soil Organic Matter

Soil nitrogen strongly affects photosynthetic rates (Lambers et al. 1998). While soil N and C are products of biologically driven soil formation, it is difficult to discern what part of soil N is a product of local plant communities or the product of topography (i.e. leaching creating N accumulations in water sinks, and/or wind deposition). A trend of increasing nitrogen in humus soils/moisture sinks (e.g. late snowmelt sites) has been previously documented in alpine literature (Körner 2003).

Soil C and N concentration increases with vegetation cover from talus to ridge south-facing turf to snowbank sites reflecting the higher productivity and subsequent decomposition for turf and snowmelt communities (Table 4.2b). In accordance with other studies highest C/N ratios were present in acidic Absaroka snowmelt soils with high soil organic matter (cf. Körner 2003).

Soil Phosphorous

Trends of phosphorus are more difficult to discern across community types although a general tendency for enrichment on loess-rich drift sites seems to be evident (Tables 4.1b, 4.2b). Specific peaks of phosphorous may be due to high concentrations of animal droppings at particular sites (i.e. bird droppings at ledge sites, and mountain goat urine and droppings on CAHA-CAPY sites on Cutoff peak). Such additions of phosphorous to soils can double community biomass in alpine environments (Seastedt and Vaccaro 2001).

pH and Conductivity

Conductivity and pH reflect salinity and water movement but probably have little direct effect on plant performance (Lambers 1998). Acidic soils under snowbanks (pH = 5.6; Table 4.1b) are due to leaching of bases by melt water (Bridges 1978). Similarly, high conductivity at these sites (0.17 mmhos cm^{-1}; Table 4.1b) is due to leaching and subsequent accumulation of salts.

Soil Water

Plants in alpine areas may be less constrained by moisture shortages than those at lower altitudes. This is due to at least two factors. First, although extreme water shortages occasionally occur, precipitation generally increases with altitude in mountainous areas (Weaver 1980). Secondly, natural selection coupled with occasional extreme water shortages has resulted in alpine plants, which even under very dry conditions, show little evidence of drought stress (Körner 2003).

Soil water indices listed in Tables 4.1b and 4.2b are based on locally tested indicator species from Mount Washburn 50km to the southeast (Chapter 2). Like Washburn, soils in the N. Absarokas appear to be driest on wind-swept ridges and dry *Carex elynoides* meadows and highest on talus sites (where water in soils is not absorbed by plants), and late snowmelt sites (where drying is postponed) (Tables 4.1b, 4.2b).

Soil Temperature

Temperature differences commonly affect vegetation distributions in alpine environments (Körner 2003). As with Washburn, N. Absaroka soil temperatures appeared to be lowest at late melt sites (note the low temperature index responses of RAPY-CAHA, CAPA-ARSC, and CAPA-AGVA; Table 4.2b), and highest on rocky south facing talus, and ridgetop sites (ELSC-CIEA, ELSC-ERCO, and ERCO-ASKE; Table 4.2b).

While not directly measured, the importance of soil water to the Absaroka alpine can be demonstrated in a number of ways. First, pH (which is a strong negative correlate of soil water) is an important explanatory variable for community composition (Table 4.3). Second our moisture index suggests that similar soil water patterns (e.g. dry ridges, wet talus, wet snowbanks) exist for the Absarokas and Washburn Range where soil water strongly controls community composition. Similarly, the importance of soil temperature can be inferred from the importance of incident solar radiation (a positive correlate of soil temperature) in the Absarokas (Table 4.3), and by the apparent soil temperature similarities (e.g. warm ridges) between the Absarokas and the Washburn range.

Table 4.9. Pearson product moment correlations for environmental variables versus cover and richness. *P*-values[1] are the result of a test of the hypothesis of no correlation between cover or richness and environmental responses.

	Cover		Richness	
	r	*p*-val.	*r*	*p*-val.
%Soil cover	0.859	<0.001***	0.662	<0.001***
%Rock cover	-0.859	<0.001***	-0.662	<0.001***
Soil %N	0.764	<0.001***	0.486	<0.001***
Soil %C	0.755	<0.001***	0.447	<0.001***
pH	-0.744	<0.001***	-0.473	<0.001***
Cond. (mmhos cm^{-1})	0.474	<0.001***	0.305	0.001***
%Silt content of soil	0.462	<0.001***	0.347	<0.001***
Slope	-0.443	<0.001***	-0.427	<0.001***
P (mg kg^{-1})	0.413	<0.001***	0.372	<0.001***
%Sand content of soil	-0.378	<0.001***	-0.353	<0.001***
C/N	0.336	<0.001***	0.186	0.056
Elevation	0.278	0.013*	0.502	<0.001***
%Clay content of soil	-0.196	0.025*	0.048	0.882
Aspect (degrees from N)	-0.152	0.137	-0.179	0.050*
Solar radiation (MJ cm^{-2} yr^{-1})	0.09	0.575	-0.005	0.829

[1] Signif. codes: "***"≤ 0.001 "**"≤ 0.01 "*"< 0.05.

Flora of Volcanic Substrates

Despite climatic differences, the flora of the Absarokas is more similar to distant volcanic areas than to a number of intervening non-volcanic areas. This is according to Hadley (1987) who compared alpine floras of thirteen areas in the Rocky Mountains. This study found that the andesitic Sangre de Cristo Range was more similar to the Absarokas than several other much closer non-andesitic ranges e.g. the Gros Ventre, San Francisco, Teton and Wasatch Ranges.

Absaroka-Volcanic vegetation sampled at our study area is distinguished by the absence of at least three species and one genus common to surrounding alpine areas. These are: *Dryas octopetala, Eritrichium nanum, Bupleurum americanum,* and the genus *Trifolium*.

The andesitic substrates of the Absaroka Volcanics exclude *Dryas octopetala,* as do andestic alpine areas throughout North America, including Carter Mountain in the eastern Absarokas (Thilenius and Smith 1985), the Sangre de Cristo and San Juan mountains in the Southern Rockies (Rottman and Hartman 1985, Baker 1983), the Sweetwater Mountains in the Sierra Nevada (Hunter and Johnson 1983), and volcanic sites in the Copper Basin in Idaho (Caicco 1983). In contrast *Dryas* is prevalent on non-volcanic scree in all major alpine areas surrounding the Absarokas, including the Beartooths (personal observation 2003), the Gallatin Range (J. Whipple personal communication 2004), the Bridger Range (personal observation), the Flint Creek Mountains (Bamberg and Major 1968), the major ranges of Southwestern Montana (Cooper et al. 1999), and the mountains of Glacier National Park (Bamberg and Major 1968). *Dryas* is a well-documented calciophile in many arctic and alpine areas (Cooper 1989), and occurs on calcareous substrates throughout northern (Bamberg and Major 1968), central (Komárková 1979, Willard 1979) and southern Rocky Mountains (Weber 1965).

Likewise, both *Eritrichium nanum* and *Bupleurum americanum* are missing from the Absaroka Volcanics and other andesitic alpine throughout North America including the Sangre de Cristo, San Juan, and Sweetwater mountains (Rottman and Hartman 1985, Baker 1983, Hunter and Johnson 1983). *E. nanum* and *B. americanum* are both circumpolar (Lackschewitz 1994), and are widespread throughout the northern, central, and southern Rockies on non-andesitic substrates (Pemble 1965, Willard 1979, Komárková 1979, Hartman and Rottman 1988 Damm 2001). *E. nanum* has also been well documented as a calicicole (Komárková 1979, Kershaw et al. 1998).

The cause for the absence of the genus *Trifolium* in the Northern Absarokas is less clear, though it appears unrelated to substrate. While *Trifolium* spp. (e.g. *T. haydenii, T. dasyphyllum,* and *T. parryi*) is common in the non-volcanic Beartooth, Bridger, Pioneer, Tobacco Root, Anaconda, Pintlar, Madison and Beaverhead Ranges in Southern Montana (Cooper 1997) it is also common in the andesitic-volcanic western Absarokas (personal observation), and the southeastern Absarokas (Thilenius and Smith 1985). *Trifolium* spp. is also common on andesitic substrates from the Mosquito Range and San Juan Mountains in Colorado (Seagrist and Taylor 1998 and Rottman and Hartman 1985) and the Sweetwater Mountains in California (Hunter and Johnson 1983). Strangely, *Trifolium* spp. is also notably absent from the granitic Teton alpine (Spence and Shaw 1981).

Conclusions

In this chapter we describe alpine communities of the Absaroka Volcanics. Consequently we provide ecological information for a substrate which is essentially unstudied in the Northern, and North-central Rocky Mountains. We identify and describe the vegetation and environment of fifteen communities nested hierarchically within four supergroups (i.e. ledge, talus, ridge/turf and snowbank). Among measured environmental factors the best predictors of alpine community composition were soil accumulation, soil development, and elevation. An analysis of our data accompanied with a thorough literature search indicates that Absaroka Volcanic alpine vegetation is unexpectedly similar to distant andesitic-alpine areas in Colorado and New Mexico.

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Literature Cited

Aho, K., Huntly N., Moen J., and T. Oksanen. 1998. Pikas (*Ochotona princeps*: Lagomorpha) as allogenic engineers in an alpine ecosystem. Oecologia. 114(3): 405-409.

Aho, K. 2006. Multivariate clustering for objective classification of vegetation data. *In* 2006 Billings Land Reclamation Symposium, June 5-8, 2006, Billings MT . Jointly published by BLRS and ASMR 3134 Montavista Rd., Lexington KY 40502.

Aayd, M., and R. Dix. 1964. An analysis of a vegetation-microenvironment on prairie slopes in Saskatchewan. Ecological Monographs 34: 421-442.

Baker, W. L. 1983. Alpine vegetation of Wheeler Peak, New Mexico U.S.A: gradient analysis, classification and biogeography. Arctic and Alpine Research. 15(2) 223-240.

Bamberg, S. A., and J. Major. 1968. Ecology of the vegetation and soils associated with calcareous parent materials in three alpine areas in Montana. Ecological Monographs. 38: 127-167.

Bazely, D. R., and R. L. Jefferies. 1985. Goose faeces: a source of nitrogen for plant growth in a grazed salt marsh. Journal of Applied Ecology. 22: 693 – 703.

Begon, M., Harper, J. L., and C. R. Townsend. 1996. Ecology: individuals, populations and communities 3rd edition. Blackwell Science. Oxford, UK.

Billings, W. D. 1979. Alpine ecosystems of Western North America, pp. 6-21. In D. A. Johnson (ed.). Special management needs of alpine ecosystems. Society for Range Management. Denver, CO.

Billings, W. D. 2000. Alpine Vegetation of North America. pp. 537- 572. *In* North American Terrestrial Vegetation 2nd edition, Barbour, M. D. and Billings, W. D. eds. Cambridge Univ. Press, Cambridge.

Billings, W. D., and L. C. Bliss. 1959. A snowbank alpine environment and its effects on vegetation, plant development, and productivity. Ecology 40(3): 388-397.

Bliss, L. C. 1969. Alpine community pattern in relation to environmental parameters. In: Essays in plant geography and ecology. Nova Scotia Museum, Halifax, Nova Scotia, 167-184.

Bockheim, J. G. 1997. Pedogenesis of alpine ecosystems of the eastern Uinta Mountains, U.S.A. Arctic and alpine research. 29 (2): 164-172.

Bowman, D., Theodose, T. A., Schart, J. C., and R. T. Conant. 1993. Alpine tundra primary production constrained by nutrient availability. Ecology 24: 2085-2098.

Bowman, D., Schardt, J. C., and Schmidt S. K. 1996. Symbiotic N_2 fixation in alpine tundra: ecosystem input and variation in fixation rates among communities. Oecologia. 108: 345 – 350.

Bray J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities in southern Wisconsin. Ecological Monographs. 27: 325-349.

Bremner, J. 1996. Total nitrogen, pgs. 1085-1133, *in* Klute, A. (ed.) 1996. Methods of soil analysis I: physical and mineralogical methods. Soil Sci. Soc. America. Madison WI. 1188 pgs.

Briggs, G. M., and J. A. MacMahon. 1983. Alpine and subalpine plant communities of the Uinta Mountains, Utah. Great Basin Naturalist 43(4): 523-530.

Bridges, E. M. 1978. World soils. Cambridge University Press. London, UK.

Brogden, H. E. 1949. A new coefficient: application to biserial correlation and to estimation of selective efficiency. Psychometrika. 14: 169-182.

Caicco, S. L. 1983. Alpine vegetation of the Copper Basin area, South-Central Idaho. Master's Thesis, University of Idaho. 99 pages.

Chambers, J. C., MacMahon, J. A., and R. W. Brown. 1990. Alpine seedling establishment: the influence of disturbance type. Ecology 71(4): 1323-1341.

Cooper, D. J. 1989. Geographical and ecological relationships of the arctic-alpine vascular flora and vegetation, Arrigetch Peaks region, Brooks Range, Alaska. Journal of Biogeography. 16: 279-295.

Cooper, S. V., Lessica, P., and D. Page-Dumroese. 1997. Plant community classification for alpine vegetation on the Beaverhead National Forest, Montana. Gen. Tech. Rep. INT-GTR -362. Ogden UT: U.S. Department of Agriculture, Forest Service Intermountain Research Station. 61 pgs.

Cooper, S. V., Jean, C., Heidel, B. L. 1999. Plant association and related botanical inventory of the Beaverhead Mountains, Section Montana. Montana Natural Heritage Program, Helena, MT. 243 pgs.

Damm, C. 2001. A phytosociological study of Glacier National Park, Montana, USA, with notes on syntaxonomy of alpine vegetation in the western United States. Doctoral dissertation. University of Göttingen. Göttingen, Germany. 305 pgs.

Dorn, R. D. 1992. Vascular Plants of Wyoming. Mountain West Publishing. Cheyenne WY.

Douglas, G. W., and L. C. Bliss. 1977. Alpine and high subalpine plant communities of the North Cascades range, Washington and British Columbia. Ecological Monographs. 47: 113-150.

Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetric approach. Ecological Monographs. 67(3): 345-367.

Ehleringer, J. A., and P. C. Miller. 1975. Water relations in selected plant species in the alpine tundra, Colorado. Ecology 56-370-380.

Faith, D. P., Minchin P. R., and L. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 88: 57-68.

Feeley, T. C. 2003. Origin and tectonic implications of across-strike geochemical variations in the Eocene Absaroka-Volcanic Province, United States. The Journal of Geology. 111: 329- 346.

Galen, C., and M. L. Stanton. 1995. Responses of snowbed plant species to changes In growing season length. Ecology 75(5):1546-1558.

Gauslaa, Y. 1984. Heat resistance and energy budget in different Scandinavian plants. Holarctic ecology 7: 1-78.

Gee, G., and J. Bauder. 1986. Particle size analysis. Pgs. 383-412. In: Klute, A. (ed.). 1996. Methods of soil analysis I: physical and mineralogical methods. Soil Sci. Soc. America. Madison, WI. 1188 pgs.

Geiger, R., R. H. Aeon & P. Todhunter. 2003. The Climate Near the Ground. 6th edition. Rowman and Littlefield. Lanham, MD., U.S.A.

Goodall, D. W. 1973. Numerical classification. Handbook of Vegetation Science. 5: 575-615.

Gottfried, M., Pauli, H., and G. Grabherr. 1998. Prediction of vegetation patterns at the limits of plant life: a new view of the Alpine-Nival ecotone. Alpine and Arctic Research. 30: 207-221.

Gregory, S. 1983. Subalpine forb community types of the Bridger-Teton National Forest, Wyoming. Masters thesis, Montana State University, Bozeman MT.

Hadley, K. S. 1987. Vascular alpine distributions within the central and southern Rocky Mountains, U.S.A. Arctic and Alpine Research. 19(3): 242-251.

Harrison, S. 1997. How natural habitat patchiness affects the distribution of diversity in Californian serpentine chaparral. Ecology 78: 1898-1906.

Hartman, E. L., and M. L. Rottman. 1988. The vegetation and alpine vascular flora of the Sawatch Range, Colorado. Madrono. 35(3): 202-225.

Hayward, C. L. 1952. Alpine biotic communities of the Uinta Mountains, Utah. Ecological Monographs. 22(2): 94-120.

Hitchcock, A. S. 1950. Manual of the grasses of the United States. USDA Miscellaneous publication No. 200 U.S. Government Printing Office. 1051 pgs.

Hiza, M. M. 1999. Geochemistry and geochronology of the Eocene Absaroka Volcanic province, northern Wyoming and southwest Montana, USA. Doctoral thesis, Montana State University. 46 pgs.

Houston, D. B., Schriener E. G., and B. B. Moorhead. 1994. Mountain goats in Olympic National Park: biology and management of an introduced species. Scientific Monographs. NPS/NROLYM/NRSM-94125.

Hrapko, J. O. 1970. An ecological study of the alpine plant communities of Signal Mountain, Jasper national Park, Alberta. PhD thesis. University of Alberta, Edmonton, Alberta.

Hrapko, J. O., LaRoi, G. H. 1978. The alpine tundra vegetation of Signal Mountain, Jasper National Park. Canadian Journal of Botany. 56: 309-332.

Hubert, L. J. and J. R. Levin. 1976. A general framework for assessing categorical clustering in free recall. Psychol. Bull. 83: 1072-1080.

Hunter, K. B., and R. E. Johnson. 1983. Alpine flora of the Sweetwater Mountains, Mono County, California. Madrono. 30: 89-105.

Islebe, G. A., and A. Velázquez. 1994. Affinity among mountain ranges in Megamexico: A phytogeographical scenario. Vegetatio. 115: 1-9.

Johnson, P. L., and W. D. Billings. 1962. The alpine vegetation of the Beartooth Plateau in relation to cryptogenic processes and patterns. Ecolog. Monographs. 32: 105-135.

Keefer, W. R. 1976. The geologic story of Yellowstone National Park. Geological Survey Bulletin 1347 USGS. 92 pgs.

Kershaw, L., MacKinnon, A., and Pojar, J. 1998. Plants of the Rocky Mountains. Lone Pine Publishing, Edmonton Alberta. Pg. 203

Knapik, L. J., Scotter, G. W., and W. W. Paettapiece. 1973. Alpine soil and plant community relationships of the Sunshine area, Banff National Park. Arctic and Alpine Research 5: 161-170.

Komárková, V. 1979. Alpine vegetation of the Indian Peaks area, Front Range Colorado Rocky Mountains. PhD dissertation University of Colorado, Boulder. 591 pgs.

Komárková, V., and P. J. Weber. 1978. An alpine vegetation map of Niwot Ridge, Colorado. Alpine and Arctic Research. 10(1): 1-29.

Körner, C. 2003. Alpine plant life: Functional plant ecology of high mountain Ecosystems, 2nd edition. Springer-Verlag, Berlin. 338 pgs.

Körner, C., and De Moraes, J. A. P. V. 1979. Water potential and diffusion resistance in alpine cushion plants on clear summer days. Oecol. Plant. 14: 109-120.

Kruskal, J. B. 1964. Nonmetric Multidimensional Scaling: a numerical method. Psychometrica. 29: 115-129

Lackschewitz, K. H. 1994. Beartooth alpine flora, pgs. 105-113. *In*: Anderson, B. (ed). Beartooth Country: Montana’s Absaroka and Beartooth Mountains. Unicorn Publishing, Helena MT.

Lambers, H., Chapin, F. S., and T. L. Pons. 1998. Plant physiological ecology. Springer-Verlag. New York.

Lance, G. N., and W. T. Williams. 1967. A general theory of classification sorting strategies II clustering systems. Computer Journal 10: 271-277.

Langenheim, J. H. 1962. Vegetation and environmental patterns in the Crested Butte area, Gunnison County, Colorado. Ecological Monographs 32(3): 249-285.

Lemke, T. O. 2004. Origin, expansion, and status of mountain goats in Yellowstone National Park. Wildlife Society Bulletin. 32(2): 532-541.

Lewis, M. E. 1970. Alpine rangelands of the Uinta Mountains: Ashley and Wasatch National Forests. USDA U. S. Forest Service Publication. 75 pgs.

Loope, L. L. 1970. Subalpine and alpine vegetation of northeastern Nevada. PhD thesis, Duke University, Durham NC. 307 pgs.

MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. Ecology. 42: 594-598.

Mattson W. J. Jr. 1980. Herbivory in relation to plant nitrogen content. Annual Review of Ecological Systematics. 11: 119-161.

McCune B., and J. B. Grace. 2002. Analysis of ecological communities. MJM software design, Glendale Beach, Oregon.

McCune, B., and D. Keon. 2002. Equations for potential annual direct radiation and heat load. Journal of Vegetation Science. 13: 603-606.

McCune B., and M. S. Mefford. 1999. PC-ORD: Multivariate analysis of ecological data, ver. 4. Mjm Software Design, Glendale Beach, Oregon.

Mellman-Brown, S. 2002. The regeneration of whitebark pine in the timberline ecotone of the Beartooth Plateau, Montana and Wyoming. Doctoral Dissertation. University of Münster, Germany. 157 pgs.

Minchin, P.R. 1987. An evaluation of relative robustness of techniques for ecological ordinations. Vegetatio. 71: 145-156.

Nelson, D. W., and L. E. Sommers. 1996. Total carbon, organic carbon, and organic matter, pgs 961-1010, *in* D. L. Sparks (ed.). Methods of soil analysis, Part 3. Chemical methods. Soil Science Society of America book series number 5. American Society of Agronomy, Madison WI

Nilsson, M. C., Wardle, D. A., Zackrisson, O., and A. Jaderlund. 2002. Effects of the alleviation of ecological stresses on an alpine tundra community over an eight year period. Oikos. 97: 3-17.

Norton D., and C. J. Burrows. 1979. Adventive plants at Temple basin ski field, Arthur's Pass National Park. Mauri Ora. 7: 103-115.

Oksanen, J. 2005. Community ecology package, vegan ver. 1.6-6. http://www.cran.r-project.org

Olsen, S. R., and L. E. Sommers. 1982. Phosphorous, pgs 416-418, *in* Page, A. L. et al. (eds.). Methods of soil analysis Part 2. Agron Mongr. 9. 2nd ed. ASA and SSSA. Madison, WI.

Pemble, R. H. 1965. A survey of distribution patterns in the Montana alpine flora. Masters Thesis, University of Montana, Missoula. 146 pages.

Porembski, S., Szarzynski, J., Mund, J. P., and W. Barthlott. 1996. Biodiversity and vegetation of small-sized insulbergs in a West African rain forest (Taï, Ivory Coast). Journal of Biogeography. 23: 47-55.

Protska, H. J., Ruppel, E.T., and R.L. Christiansen. 1975. Geologic map of the Abiathar Peak quadrangle, Yellowstone National Park, Wyoming and Montana. U.S. Geological Survey, Denver CO.

R Development Core Team. 2006. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Reynolds, D. N. 1984. Alpine annual plants: phenology, germination photosynthesis, and growth of three Rocky Mountain species. Ecology. 65: 759-766.

Richardson, C. A., and D. M. Henderson. 1999. Classification and ordination of the alpine plant communities of Railroad Ridge, White Cloud Peaks, Idaho. Great Basin Naturalist. 59(1): 63-78.

Roberts, D. W. 2005. Laboratory for Dynamic Synthetic Vegephenomenology, labdsv ver. 1.2-1, http://www.cran.r-project.org

Rottman, M. L., and E. L. Hartman. 1985. Tundra vegetation of three cirque basins in the Northern San Juan Mountains, Colorado. Great Basin Naturalist. 45: 87-93.

Rousseeuw, P. J. 1987. Silhouettes: A graphical aid to the interpretation and validation of cluster analysis. J. Comput. Appl. Math. 20: 53-65.

Scott, R. W. 1966. The alpine flora of northwestern Wyoming. M. A. Thesis. University of Wyoming, Laramie, Wyoming.

Seagrist, R. V., and K. J. Taylor. 1998. Alpine vascular flora of Buffalo Peaks, Mosquito Range, Colorado USA. Madrono. 45(4) 319-325.

Seastedt, T. R., and L. Vaccaro. 2001. Plant species richness, productivity, and nitrogen and phosphorus limitations across a snowpack gradient in alpine tundra, Colorado, USA. Arctic, Antarctic and Alpine Research. 33: 100-106.

Simpson, E. H. 1949. Measurement of diversity. Nature. 163: 688.

Smedes, H. W., and Protska, H. J. 1972. Stratigraphic framework of the Absaroka Volcanic Supergroup in the Yellowstone National Park region: U.S.G.S. Prof. Pap. 720-C, US Gov. Print. Office, Wash. DC, 33 pgs.

Spence, J. R. and R. J. Shaw. 1981. A checklist of the alpine vascular flora of the Teton Range, Wyoming, with notes on biology and habitat preferences. Great Basin Naturalist. 41(2): 232-241.

Tateno, M., and T. Hirose. 1987. Nitrification and nitrogen accumulation in the early stages of primary succession on Mt. Fuji. Ecological Research. 2: 113-120.

Taye, A. C. 1995. Alpine Vascular flora of the Tushar Mountains, Utah. Great Basin Naturalist. 55(3): 225-236.

Thilenius, K. F., and D. R. Smith. 1985. Vegetation and Soils of an Alpine Range In the Absaroka Mountains, Wyoming. USDA Forest Service General Technical Report RM-121, 18 pgs. Rocky Mountain Forest and Range Experiment Station, Fort Collins Colo.

Thomas, G. 1996. Soil pH and acidity. Pgs 475-490. *In* Methods of soil analysis I: Physical and minerogical methods. Klute, A. (ed.). 1996. Soil Sci. Soc. America. Madison WI. 1188 pgs.

Titus, J. H., and S. Tsuyuzaki. 1999. Ski slope vegetation on Mount Hood, Oregon, USA. Arctic, Antarctic and Alpine Research. 31(3): 283-292.

Urbanczyk, S. A., and D. A. Henderson. 1994. Classification and ordination of alpine plant communities, Sheep Mountain, Lemhi County, Idaho. Madrono. 41(3): 205-223.

USGS. 1972. Geologic Map of Yellowstone National Park. Miscellaneous Geologic Investigations Map 1-711. USGS, Department of Interior, Reston, VA, USA.

Velland, M. 2001. Do commonly used indices of β-diversity measure species turnover? Journal of Vegetation Science. 12: 545-552.

Venables S., and B. Ripley. 2005. MASS ver. 7.2-20. http://cran.r-project.org

Walter, H., and H. Leith. 1967. Klimadiargramm-Weltaltas. Gustav Fisher, Jena.

Weber, W. A. 1965. Plant geography in the southern Rocky Mountains. *In* H. E. Wright and D. C. Frey eds., The Quaternary of the United States. P. 458-468. Princeton Univ. Press, Princeton NJ.

Weaver, T. 1980. Climates of vegetation types of the northern Rocky Mountains and adjacent plains. American Midland Naturalist 103: 392-398.

Weaver, T. 1990. Climates of subalpine pine woodlands. p 72-79 IN W Schmidt and K McDonald ed 1990 Proceedings-- Symposium on whitebark pine ecosystems: ecology and management of a high mountain resource. USDA Forest Service General Tech Report INT-270. Ogden UT.

Weaver, T., Gustafson, D., and J. Lichthardt. 2001. Exotic plants in early and late seral vegetation of fifteen northern Rocky Mountain environments (HTs). Western North American Naturalist. 61(4): 417-427.

Western Regional Climate Center (WRCC). 2006. Reno NV. 89512.

Whittaker, R. H. 1960. Vegetation of the Sisikyou Mountains, Oregon and California. Ecological Monographs. 30: 279-338.

Whipple, J. 2005. YNP herbarium curator/plant taxonomist.

Willard, B. E. 1979. Plant Sociology of alpine tundra, Trail Ridge, Rocky Mountain National Park, Colorado. Quarterly of the Colorado school of mines. 74: 4.

Wishart, D. 1969. An algorithm for hierarchical classifications. Biometrics 25: 165-170.

Young, T. P., and M. M. Peacock. 1992. Giant senecios and alpine vegetation Mt. Kenya. Journal of Ecology. 80: 141-148.

CHAPTER 5

LOCAL AND REGIONAL VARIATION IN ALPINE VEGETATION (NORTH-CENTRAL ROCKIES)

Introduction

Vegetation composition is controlled by climate (e.g. temperature and water; Holdridge 1947), topography (e.g. exposure, microclimate; Hanson and Churchill 1961), substrate (e.g. parent material, nutrients, toxins; Rorison 1969) dispersal and succession (Daubenmire 1968), and biotic interactions (e.g. competition, facilitation; Tilman 1988). These controls parallel the soil forming factors of Jenny (Jenny 1941) i.e. climate, topography, substrate, vegetation and time.

Within a localized area where climate and substrate are uniform, vegetation varies primarily with topographic influences on microclimate. For instance, in an alpine environment, vegetation on north faces, south faces, nivation hollows, scree slopes, and ridgetops are very different from each other due to microclimatic differences in temperature, moisture, and exposure (Billings 1998, Chapters 3 and 4).

On a broad scale topographic factors are confounded by the influence of climate (Holdridge 1947) and substrate (Küchler 1975). Indeed, these factors largely control the distribution of the major terrestrial biomes (Begon et al. 1996).

Studies which simultaneously address both local (e.g. topography) and regional (substrate and climatic) influences on vegetation are rare. To our knowledge such scale considerations have never been directly and quantitatively applied to alpine vegetation in the Rocky Mountains. Most studies of Rocky Mountain alpine vegetation concentrate on areas within a single climatic regime (e.g. Hrapko and LaRoi 1978, Seagrist et al. 1998, Komárková 1979, and Willard 1979) and/or substrate (e.g. Bamberg and Major 1968, Johnson and Billings 1962). In addition these studies generally describe communities and their environments rather than the vegetation and environment of specific topographic regions in an alpine landscape.

The objects of this paper are to 1) describe and compare the vegetation and environments of alpine topographic environments (local habitats/microsites) located in the Northern Rockies but extendable throughout the world. 2) To describe regional variation in alpine vegetation and environments across three substrates (andesite, granite, limestone) and two climatic regimes (dry and wet). 3) To examine interactions of local and regional environmental factors to determine whether substrate and climate have different effects among different habitats.

Study Area

Four mountain ranges in south-central Montana and northwestern Wyoming were used in the study. The ranges varied widely with respect to geology/substrate and climate.

Geology/Substrate

Washburn Range Surfaces of the Washburn Range consist largely of rock and soils deposited 49-47 MYBP by Eocene volcanoes of the Absaroka Volcanic Supergroup (Figs. 5.1a, 5.1b). The dominant formation (Langford) consists of light colored lava flows and alluvial facies composed of hornblende and pyroxene andesite fragments (Smedes and Prostka 1972; Chapter 3). Planar area above treeline is approximately 0.76 km^2.

Northern Absaroka Volcanics The substrate for this area is the Lamar River and Wapiti Formations from the Absaroka Volcanic Supergroup (Smedes and Prostka 1972; Chapter 4). Both formations were deposited 49-47 million years ago and include sheer vertical faces of conglomerate breccia, alluvial volcanoclastics, and minor mafic flows (Smedes and Protska 1972). The mineralogical composition is mostly andesitic, though flows often contain diverse inclusions. The planar area above treeline for the Absaroka Mountains is about 2384 km^2 (Hadley 1987).

Beartooth Plateau The substrate of the Beartooth Plateau is exposed granitic basement rock (Anderson 1984; Figs. 5.1a, 5.1b). During the Laramide revolution 65 MYBP, three distinct Archean blocks were thrust upward from the Bighorn Basin to the east. The largest of these, the Beartooth Block, comprises the current Beartooth Plateau. Most recently during the Quaternary period, the Beartooths were heavily sculpted by ice which caused deep U-shaped canyons and created an alternating plateau-canyon landscape (Anderson 1984). The planar area above treeline for the Beartooth Mountains is 768 km^2 (Hadley 1987). Alpine vegetation for the Beartooth Plateau encompasses approximately 190 km^2 (Johnson and Billings 1962).

Beartooth Butte Substrates of Beartooth Butte are primarily sedimentary limestones (Figs. 5.1a, 5.1b). These are the last remnants of sedimentary strata which covered the entire Beartooth Plateau when it formed at the bottom of an inland sea 400 MYBP. Strata on Beartooth Butte include Cambrian quartzite, Ordovician dolomite, and Devonian limestone (Anderson 1984). The limestone alpine area that includes Beartooth Butte contains several summits above 3150m and is approximately 4 km^2 in area.

Climate

While summer temperature patterns are relatively similar at the four sites, precipitation varies strongly (Figs. 5.1c, 5.2). Warmest summer temperatures at the four sites occur in July (average max. = 17º- 22º C), while coldest temperatures (average min. = -14º to -17º) occur in December or January (Fig. 5.2). While the Beartooths and the N. Absarokas appear to have three month growing seasons, the stations closest to Mt. Washburn (Canyon Village and Parker Peak) both indicate 4 month growing seasons (Fig. 3.2, Fig. 5.2). Annual precipitation increases from the Washburn region [278mm yr^{-1} at Canyon Village (elev. 2489m); 784 mm yr^{-1} at Parker Pk. (elev. 2867m); Figs. 3.2, 5.1c, 5.2] through the Northern Absarokas [659 mm yr^{-1} at NE entrance (elev. 2241); 1279 mm yr^{-1} at Fisher Creek (elev. 2775m); Figs. 4.2a, b, 5.1c, 5.2] and the Beartooth region [843 mm yr^{-1} at Beartooth Lake (2853m); Figs. 5.1c, 5.2]. Patterns of precipitation also vary (Fig. 5.2). At southern weather stations nearer to Washburn precipitation is relatively low and constant (Canyon Village) or occurs mostly in the early spring (Fisher Creek; Figs. 3.2a). In the Northern Absarokas and Beartooth region precipitation occurs mostly as snow during winter months (Fig. 5.2).

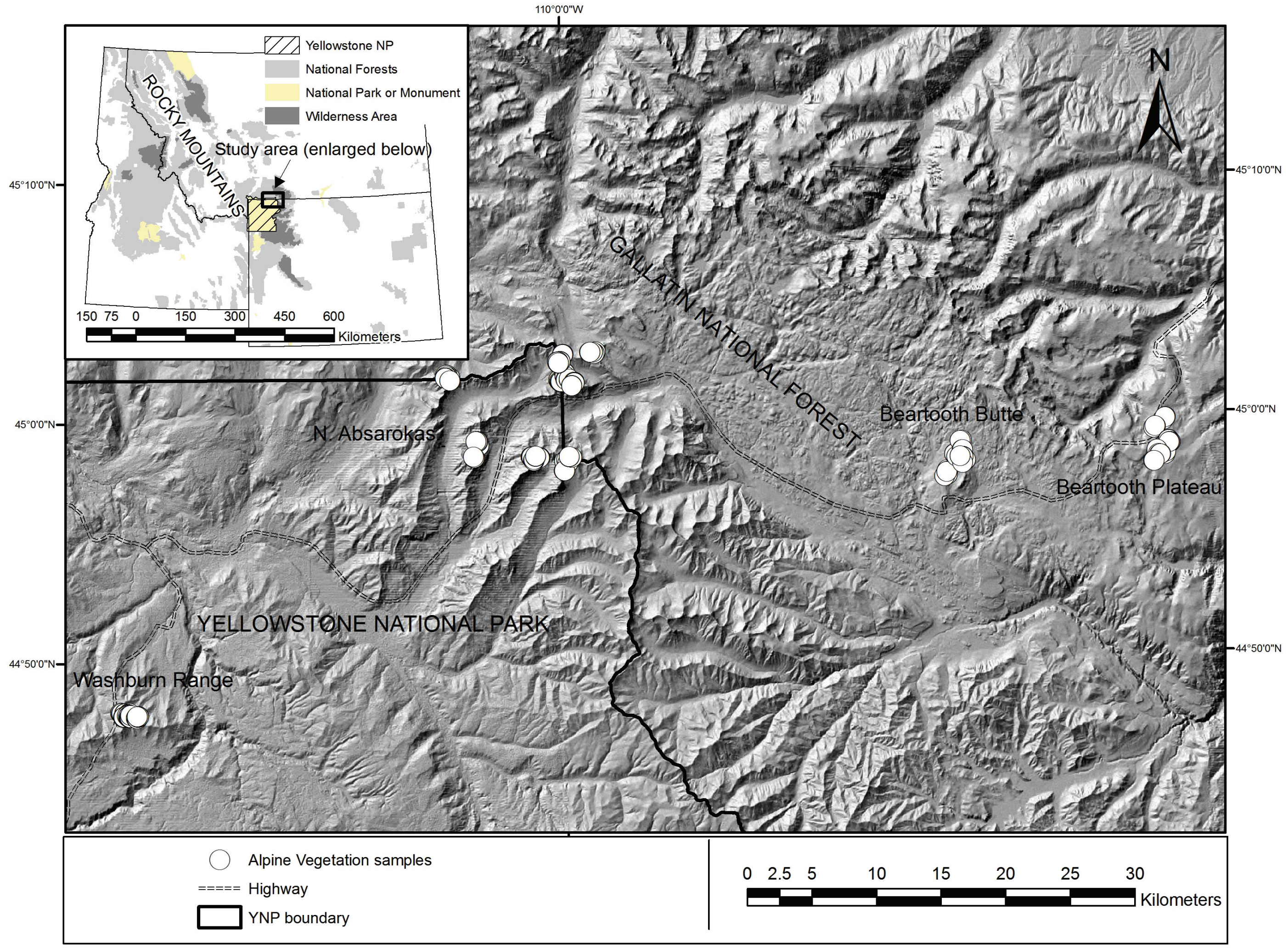


Figure 5.1a. Overview of study area. Digital information from USGS (1999).

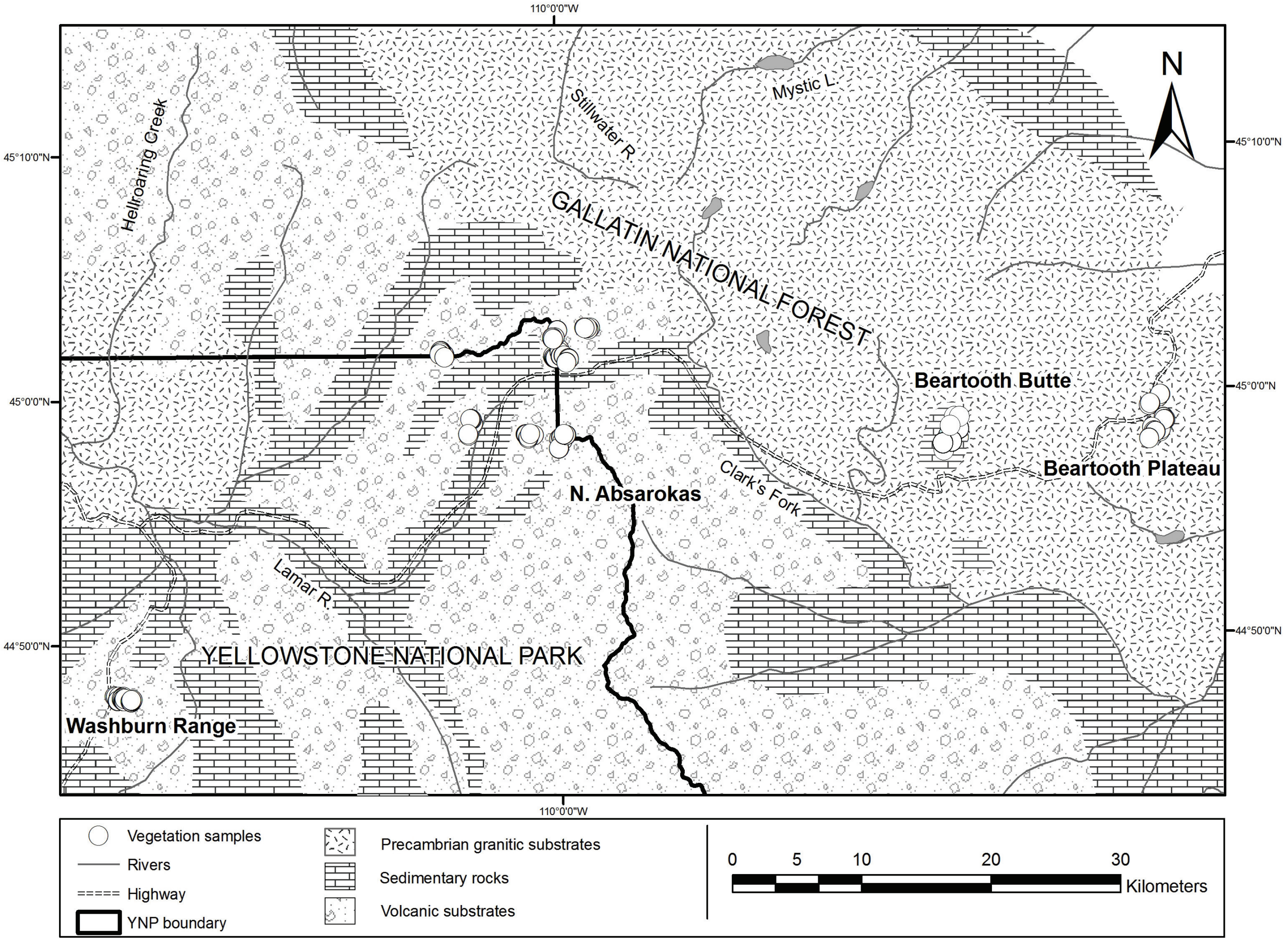


Figure 5.1b. General geology of study area. Map follows Anderson (1984).

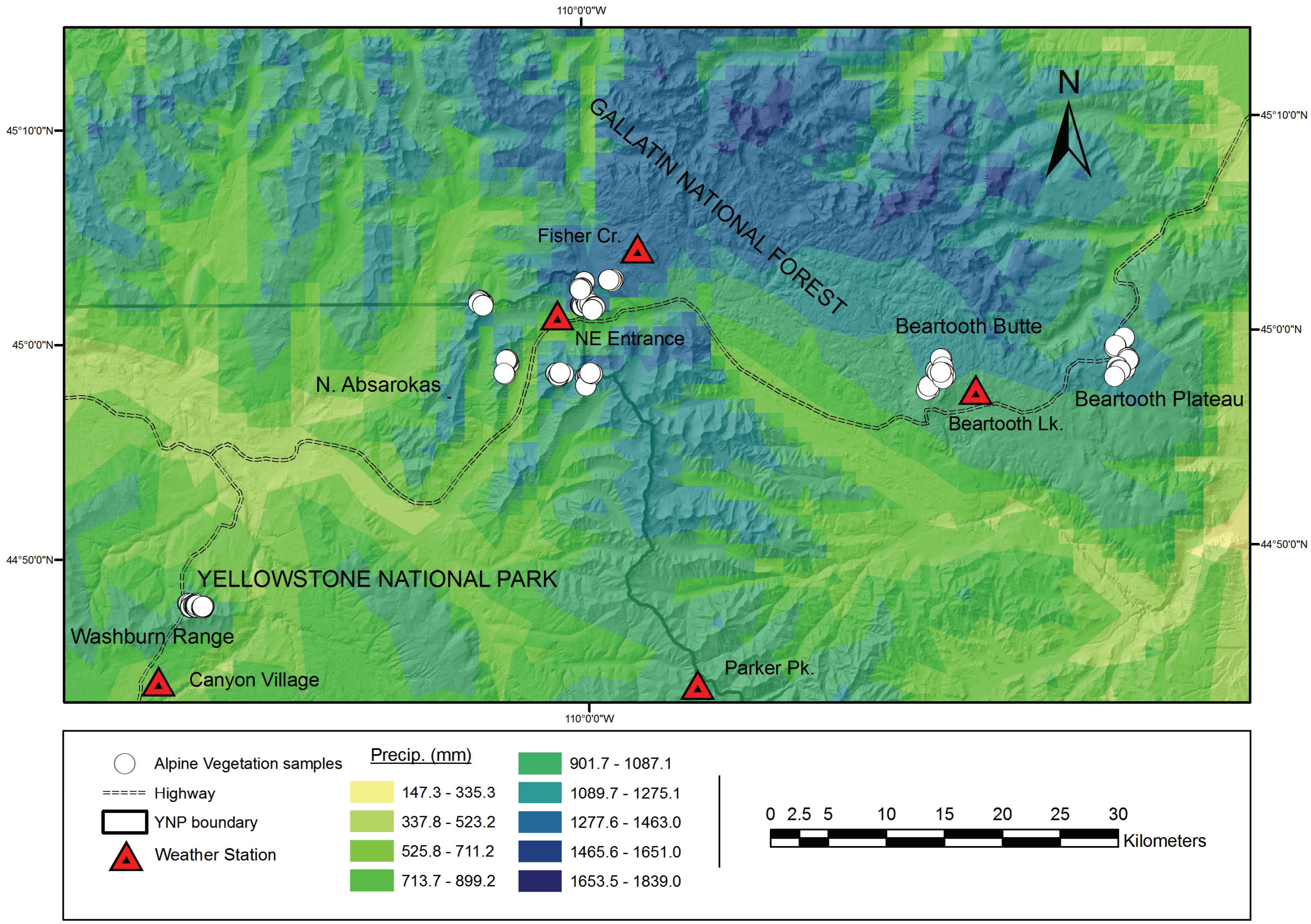


Figure 5.1c. Generalized precipitation patterns for the study area, and weather stations used in the dissertation. Digital information was provided by USGS (1999) and is based on NOAA snotel data from 1966-1990.

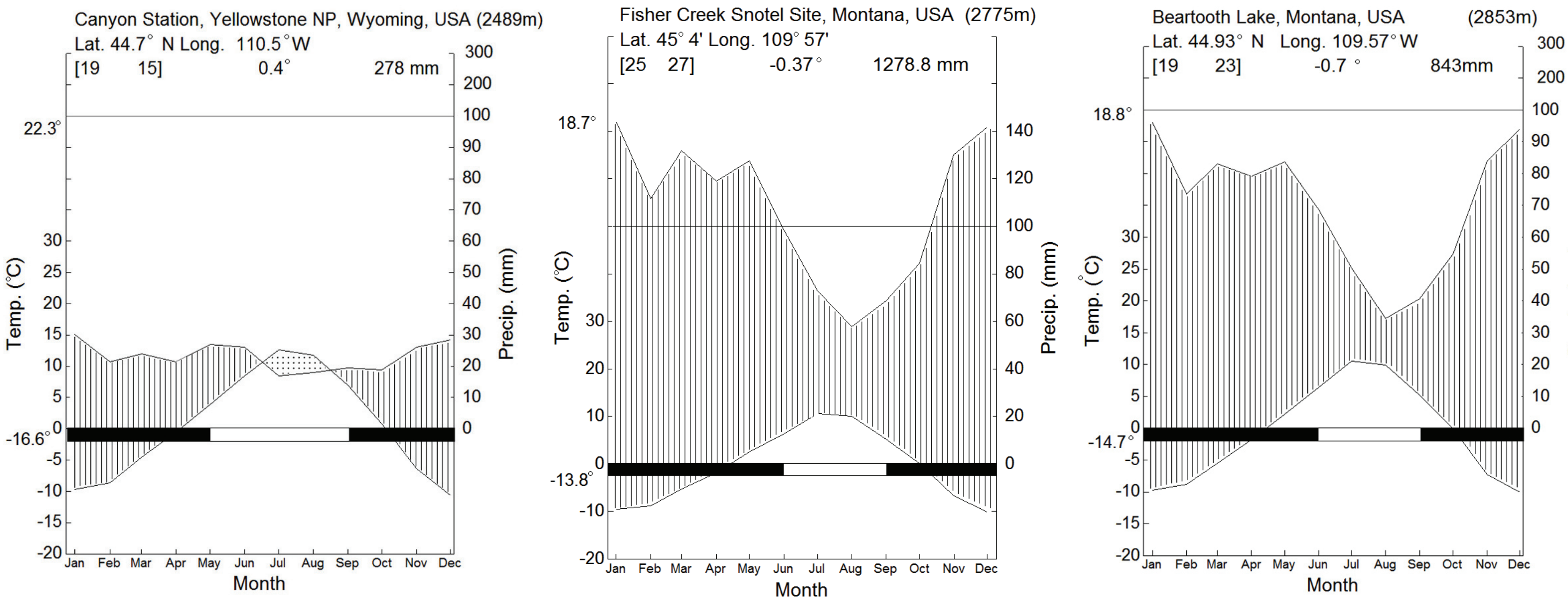


Figure 5.2. Climatic diagrams (cf. Walter and Leith 1967) for weather stations adjacent to study sites. The Canyon Village weather station is adjacent to Mt. Washburn (for additional climate data on Washburn see Fig. 3.2). The Fisher Creek Station is close to Northern Absaroka sites. The Beartooth Lake station is close to Beartooth Plateau and Beartooth Butte sites (see Fig. 5.1c). The upper plotted line indicates average monthly precipitation; the lower humped line indicates average mean monthly temperature. The vertically hatched area indicates the months that precipitation exceeds evaporation. The dotted area on the Canyon Station diagram indicates months when evaporation exceeds precipitation. Text at the top of the figure gives general information about the site: the length of records in years for temperature and precipitation data respectively (in brackets), the latitude and longitude, the name of the station, the elevation, and the average yearly precipitation and overall mean temperature. Average daily maximum temperature of the warmest month and average daily minimum temperature of the coldest month are also indicated on the temperature axis. The blackened area of the long rectangle near the bottom of the figure indicates the frost period (i.e. the months when average minimum temperature was < 0ºC). Raw climate data was provided by the Western Regional Climate Center (WRCC 2006).

Methods

Field Methods

Four unnamed summits from the andesitic Washburn Range, nine mountains from the andesitic Northern Absarokas, three summits from the granitic Beartooth Plateau, and three calcareous summits from Beartooth Butte were sampled for the study (Figs. 5.1a, 5.1b). All mountains were located on federal lands in Yellowstone National Park and Gallatin National Forest (Figs. 5.1a, 5.1b). From each of the nineteen mountains five major physical environments (topographic types) were sampled: talus, ridgetops, south facing slopes, ridgetops, north facing slopes, and snowbank sites. Vegetation of each of the five environments was sampled with two replicates. Each replicate consisted of ten 20 x 50cm frames placed at one meter intervals along a ten meter sampling tape. The ten frames summed to a $1m^2$ sampling unit. Replicate locations were established using a stratified random design (Ch. 4). The vegetation of each frame was characterized by listing the plant species present and ocularly estimating the cover of each (Daubenmire 1959). A total of 178 of these plots were sampled. One hundred and eighty-one plant species were identified within plots (Appendix D.3). Voucher specimens were deposited at the Yellowstone National Park herbarium in Gardiner MT. Nomenclature follows Dorn (1992).

Environmental data were recorded at each plot. Elevations were determined using Trimble™ GeoExplorer 3, and Trimble™ Pro XR receivers. Readings were differentially corrected at the Montana State University, and Idaho National Engineering and Environmental Laboratory (INEEL) GPS base stations. Magnetic aspect and slope were measured with a Brunton compass. Surface rock cover was measured as a percentage by placing a meter stick perforated with eight nails at 1 meter intervals along the 10m vegetation transect line and reading the number of rock/nail hits. Soil samples were taken in plots to measure elemental constituents (i.e. N, C), pH, soil salinity (conductivity), and soil texture (i.e. % sand, % clay, % silt). Soil carbon and nitrogen were determined using LECO ignition (Nelson and Sommers 1996). Conductivity and pH were measured on 1:1 water slurries with appropriate meters (Thomas 1996). Soil texture was measured with the Boyoucous hydrometer method (Gee and Bauder 1986).

Soil moisture and soil temperature were measured at a depth of 15 cm at each plot on the Washburn Range. Temperatures were gauged with thermocouples (Taylor and Jackson 1986). Soil water availability was determined with data gathered from Bouyoucos gypsum blocks (Gardner 1986). Gypsum block sensor responses were converted to soil water potentials using methods discussed in Chapter 9. Water and temperature indices of "treatments" were calculated using water/temperature indicator species identified from Washburn soils data (see Ch. 2). Indicator species were given soil water and temperature scores which ranged from 0 to 1. Species with water index (WI) responses near 0 indicated dry soils, while those near 1 indicated wet soils. Temperature index (TI) responses near 0 indicated frigid soils, while those near 1 indicated relatively hot soils (Ch. 2).

Data Analysis

Ordination Non-Metric Multidimensional Scaling ordinations (NMDS; Kruskal 1964) were used to compare vegetation samples. Bray-Curtis dissimilarity (Bray and

Curtis 1957, Faith et al. 1987) was used to create dissimilarity matrices. Although random starting points were also tried, the best (lowest stress) solutions resulted from using PCoA (Principal Coordinates Analysis) scores as initial starting points (e.g. Roberts 2005). A tolerance of $1 \bullet 10^{-7}$ was used with 200 iterations.

Environmental Vectors and Environmental Correlations with NMDS Axes

Vectors which describe the direction and strength of maximum correlation between continuous environmental variables and ordination axes were calculated and plotted into ordinations (Oksanen 2005). Environmental vectors were scaled within NMDS ordinations by their correlation to configurations. The correlation of vectors to ordination axes was tested for significance with a Monte Carlo procedure which permuted responses from environmental variables using 1000 iterations. The relationship of categorical variables to ordination solutions was quantified with Eq. 5.1 (Oksanen 2005).

$$r^2 = 1 - SSW / SSTO \qquad (5.1)$$

where *SSW* = within-group sums of squares (scatter with respect to treatment centroids for two dimensions of interest) and *SSTO* = total sums of squares (overall scatter with respect to the scatterplot centroid for the same two dimensions of interest).

Indicator Species and Murdoch's Index We adapted Murdoch's index of prey preference (Jacobs 1974) to identify species which indicated particular topographic zones, major alpine areas, and/or topographic zone within alpine areas. Murdoch's index was originally designed to measure an animal's preference between two prey species. We modified the algorithm so that the "animal" was a plant species making a binary choice between belonging and not belonging to a "treatment" type (Eq. 5.2).

$$C_M = \log\{(r_A / r_{A'})(n_A / n_{A'})\} \tag{5.2}$$

C_M = Modified Murdoch's index of preference,

$r_A / r_{A'}$ = The proportion of treatment choice A or A' (i.e. NOT A) in species "diet"
$n_A / n_{A'}$ = The proportion of treatment choice A or A' in species environment

Murdoch index responses span the range from $-\infty$ (the species *never* occurs at the "treatment" type) to ∞ (the species *only* occurs at the "treatment" type). Calculation of for p values for the test of the null hypothesis: "species affiliation to a treatment was no greater than expected by chance" were calculated using the probability distribution function for the Hypergeomentric distribution (Eq. 5.3). Only species which were present in 5% of the plots in a dataset or data subset were included in the analysis.

$$p\text{-}val_{aB} = \frac{\binom{n_B}{x_B}\binom{n_{B'}}{x_{B'}}}{\binom{N}{X}} \quad \text{where} \quad \binom{n}{x} = \frac{n!}{x!(n-x)!} \tag{5.3}$$

Where $p\text{-}val_{aB}$ = The p value for the null hypothesis: "the affiliation of species a to treatment B is not greater than expected by chance". n_B = the number of samples in community B. x_B = The number of samples in community B which contain species a. $n_{B'}$ = the number of samples NOT in community B which contain species a. $x_{B'}$ = The number of samples NOT in community B which contain species a. N = The total number of samples, X = the total number of samples containing species a.

Software NMDS ordinations were run in R using MASS (Venables and Ripley 2004) and vegan (Oksanen 2005) libraries. Vector analyses were in R using vegan. Algorithms for the Murdoch's index were written in the R language (R Development Core Team 2005).

Results/Overview

A three dimensional NMDS ordination of all sampled data illustrates several patterns useful for analysis of local and regional alpine vegetation patterns. When samples are labeled by environmental/topographic type (Fig. 5.3a) one sees a scatter of points representing the range of upland vegetation (south facing and north facing slopes) and three relatively distinct clusters representing more specialized conditions (i.e. talus, ridge and snowbank). When in the same ordination samples are labeled by geographic location (Fig. 5.3b) clusters are apparent indicating regional climatic and substrate differences. The environmental variables which were best correlated with scatterplot variation across all samples were soil cover ($r^2 = 0.74$, $p < 0.001$) and measures soil of soil development (e.g. %C and %N; $r^2 = 0.43$ and 0.47 respectively, $p < 0.001$).

Neither local topography nor regional assignments explained a great deal of variation in ordination scatter (In the first two dimensions $r^2 = 0.37$ for topographic types while $r^2 = 0.31$ for regional assignments) though both were statistically significant ($p < 0.001$; Table 5.1). However, combining topographic assignments with the four major alpine regions explained 73% of variance in the first two NMDS dimensions (Table 5.1). This indicated that local and regional factors acted collectively in controlling vegetation composition.

The remainder of this chapter examines vegetation patterns from three scale perspectives: local (e.g. topography and microclimate), regional (substrate and macroclimate) and local/regional interactions. Summary tables help characterize local and regional patterns. Table 5.2 compares topographic, regional, and combination categories with respect to cover, richness and diversity. Table 5.3 describes and compares the environments of local, regional, and combinatorial categories. Finally three summary relevé tables (Tables 5.4-5.6) list sorted species of local, regional, and

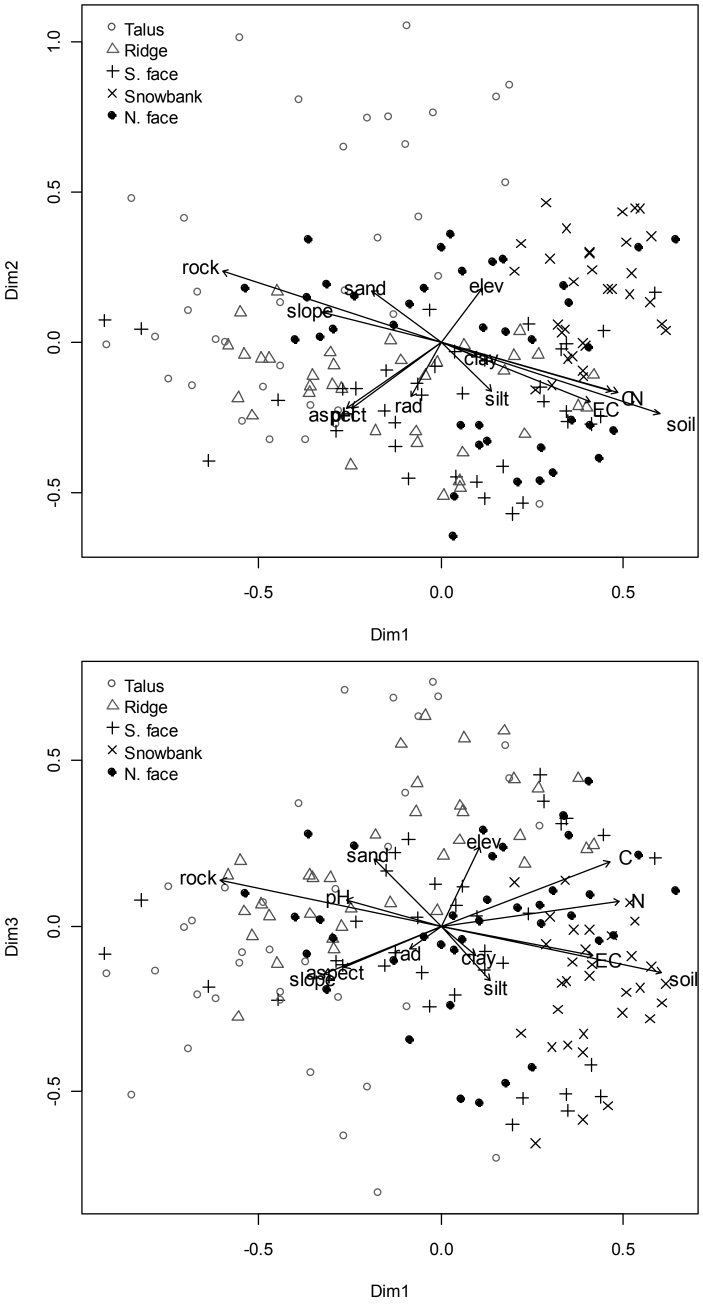


Figure 5.3a. Effect of topography. Three dimensional NMDS solution using all 178 samples. The five topographic types also indicated. Final stress = 18.13. For relationship of vectors to configurations see Table 5.1. Environmental variables are: P = Phosphorous (mg kg^{-1}), C = % soil carbon, N = % soil nitrogen, elev = elevation (m), slope = slope(degrees), aspect = degrees from N, rad = solar radiation (MJ · cm^2/yr.), soil = % cover of surface soil, EC = soil conductivity (mmhos cm^{-1}), sand = % sand content of soil, clay = % clay content of soil, silt = % silt content of soil.

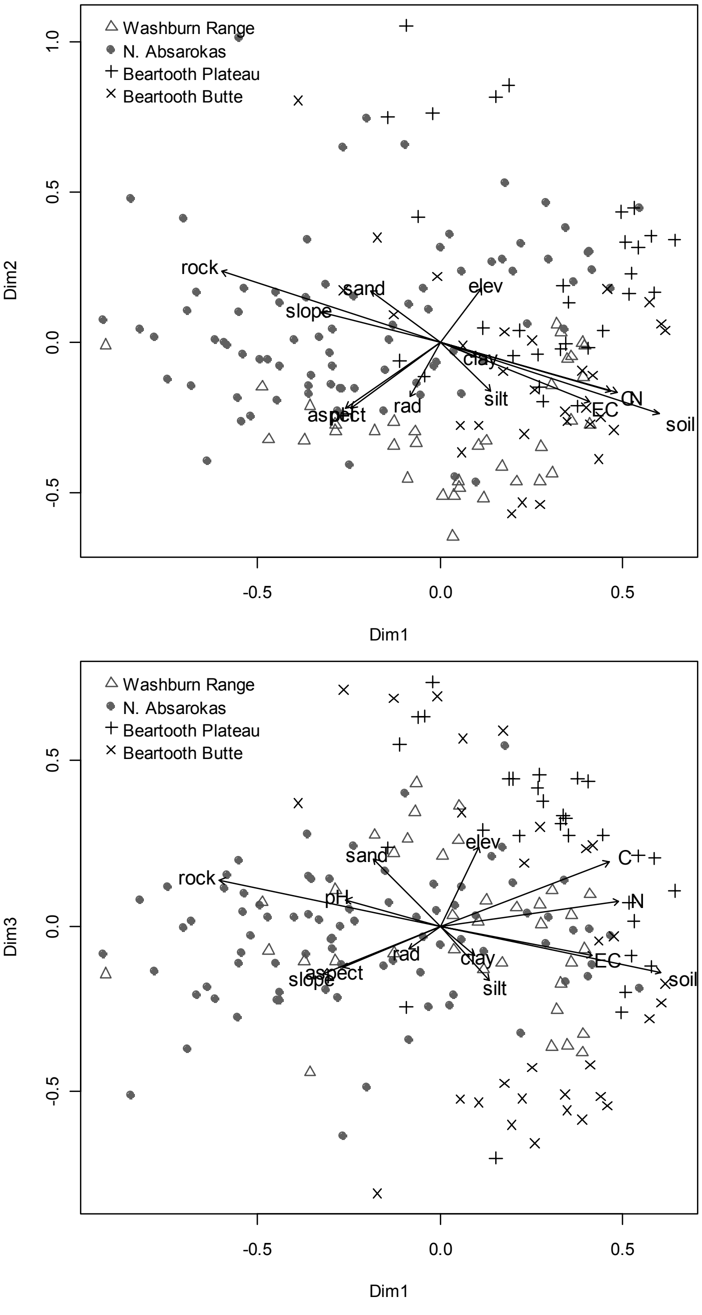


Figure 5.3b. Effect of region. Identical three dimensional NMDS solution to Fig. 5.3a but with the four major alpine areas indicated. For a summary of the relationship of vectors to configurations see Table 5.1. For explanation of vector acronyms see Fig. 5.3a.

Table 5.1. Vector and factor fitting analysis showing relationship of environmental variables to 3D ordination solutions.

	All Plots				**Talus**				**Ridgetop**			
	Dim 1 and 2		Dim 1 and 3		Dim 1 and 2		Dim 1 and 3		Dim 1 and 2		Dim 1 and 3	
	r^2	P*r*(>*r*)	r^2	P*r*(>*r*)	r^2	P*r*(>*r*)	r^2	P*r*(>*r*)	r^2	P*r*(>*r*)	r^2	P*r*(>*r*)
Continuous variables												
%C	0.44	<0.001	0.45	<0.001	0.40	<0.001	0.01	0.868	0.59	<0.001	0.56	<0.001
%N	0.47	<0.001	0.44	<0.001	0.11	0.141	0.05	0.468	0.58	<0.001	0.43	<0.001
Radiation (MJ cm^{-2} yr^{-1})	0.07	0.001	0.02	0.129	0.39	<0.001	0.28	0.002	0.02	0.710	0.01	0.822
Elev (m)	0.08	<0.001	0.12	<0.001	0.12	0.126	0.11	0.166	0.39	<0.001	0.04	0.521
Slope (degrees)	0.21	<0.001	0.22	<0.001	0.12	0.14	0.09	0.202	0.12	0.103	0.07	0.308
Aspect (degrees from N)	0.20	<0.001	0.15	<0.001	0.48	<0.001	0.41	<0.001	0.07	0.320	0.07	0.274
Soil (percent cover)	0.74	<0.001	0.69	<0.001	0.05	0.457	0.07	0.308	0.60	<0.001	0.60	<0.001
Rock (percent cover)	0.74	<0.001	0.69	<0.001	0.05	0.457	0.07	0.308	0.60	<0.001	0.60	<0.001
pH	0.19	<0.001	0.13	<0.001	0.26	0.009	0.07	0.305	0.42	0.001	0.22	0.017
EC (mmhos cm^{-1})	0.37	<0.001	0.33	<0.001	0.14	0.068	0.04	0.551	0.63	<0.001	0.73	<0.001
%Sand	0.12	<0.001	0.13	<0.001	0.07	0.294	0.05	0.456	0.28	0.004	0.02	0.783
%Clay	0.02	0.167	0.03	0.088	0.06	0.370	0.01	0.782	0.35	<0.001	0.15	0.075
%Silt	0.08	0.001	0.08	0.001	0.08	0.244	0.07	0.276	0.11	0.141	0.16	0.047
Categorical variables												
Topographic type[1]	0.37	<0.001	0.32	<0.001								
Alpine area[2]	0.31	<0.001	0.24	<0.001	0.47	<0.001	0.31	0.001	0.83	<0.001	0.80	<0.001
Combination[3]	0.73	<0.001	0.67	<0.001								
	South face				**North face**				**Snowbank**			
Continuous variables												
%C	0.64	<0.001	0.48	<0.001	0.74	<0.001	0.61	<0.001	0.16	0.074	0.13	0.154
%N	0.68	<0.001	0.52	<0.001	0.74	<0.001	0.58	<0.001	0.16	0.08	0.07	0.375
Radiation (MJ cm^{-2} yr^{-1})	0.027	0.628	0.04	0.516	0.76	<0.001	0.25	0.004	0.24	0.015	0.21	0.040
Elev (m)	0.57	<0.001	0.14	0.075	0.74	<0.001	0.65	<0.001	0.09	0.251	0.12	0.120
Slope (degrees)	0.56	<0.001	0.43	<0.001	0.73	<0.001	0.04	0.480	0.09	0.217	0.25	0.020
Aspect (degrees from N)	0.09	0.221	0.09	0.255	0.68	<0.001	0.41	<0.001	0.27	0.015	0.20	0.038
Soil (percent cover)	0.65	<0.001	0.45	<0.001	0.78	<0.001	0.20	0.021	0.11	0.157	0.01	0.834
Rock (percent cover)	0.65	<0.001	0.45	<0.001	0.78	<0.001	0.76	<0.001	0.11	0.157	0.01	0.834
pH	0.68	<0.001	0.07	0.310	0.30	<0.001	0.76	<0.001	0.46	<0.001	0.48	<0.001
EC (mmhos cm^{-1})	0.60	<0.001	0.64	<0.001	0.53	<0.001	0.16	0.038	0.36	0.001	0.41	<0.001
%Sand	0.05	0.483	0.32	0.001	0.09	0.199	0.47	<0.001	0.41	<0.001	0.26	0.006
%Clay	0.08	0.222	0.05	0.440	0.01	0.904	0.39	0.001	0.83	<0.001	0.58	<0.001
%Silt	0.08	0.286	0.34	0.001	0.10	0.152	0.27	0.006	0.02	0.708	0.04	0.571
Categorical variables												
Alpine area[1]	0.59	<0.001	0.68	<0.001	0.77	<0.001	0.74	<0.001	0.73	<0.001	0.60	<0.001

[1] i.e. talus, ridge, south face, north face, snowbank.; [2] i.e. Washburn Range, N. Absarokas, etc.; [3] i.e. Washburn talus, Washburn ridge, etc.

Table 5.2. Vegetation summary statistics for local topographic types, alpine regions, and topographic/regional combinations. Intervals are standard errors.

		Sub.[1]	Plots	Total rich.	Mean rich.[2]	Mean cover (%)[2]	Simpson diversity[3]	SW diversity[4]	Beta diversity[5]
Topographic type									
	Talus		38	73	6.6 ± 0.8	6.7 ± 1.0	0.94	3.37	0.91
	Ridge		36	91	16.4 ± 0.8	43.3 ± 4.0	0.96	3.51	0.82
	S_face		36	111	20.1 ± 1.1	63.4 ± 4.4	0.98	3.99	0.82
	N_face		38	115	20.1 ± 0.8	60.8 ± 5.8	0.97	3.91	0.83
	Snowmelt		32	120	22.2 ± 1.0	106.6 ± 5.2	0.93	3.35	0.82
Region									
	Washburn Range	A	36	78	19.7 ± 1.1	68.7 ± 5.9	0.95	3.48	0.75
	N. Absarokas	A	82	118	15.0 ± 0.8	41.9 ± 4.4	0.97	3.86	0.87
	Beartooth Plateau	G	30	77	17.5 ± 1.5	61.3 ± 6.8	0.93	3.21	0.77
	Beartooth Butte	L	30	105	19.0 ± 1.3	69.2 ± 8.7	0.96	3.51	0.82
Combination (Topographic type/Region)									
Talus	Washburn Range	A	8	27	7.5 ± 2.2	8.0 ± 2.6	0.91	2.73	0.72
	N. Absarokas	A	18	43	6.7 ± 1.1	7.9 ± 1.4	0.92	3.02	0.84
	Beartooth Plateau	G	6	14	3.3 ± 0.7	1.6 ± 0.9	0.77	1.79	0.76
	Beartooth Butte	L	6	28	8.7 ± 1.7	6.7 ± 2.1	0.87	2.44	0.69
Ridge	Washburn Range	A	6	30	18.0 ± 0.7	59.6 ± 8.3	0.83	2.39	0.4
	N. Absarokas	A	18	51	13.7 ± 1.0	29.3 ± 4.0	0.93	3.01	0.73
	Beartooth Plateau	G	6	36	20.5 ± 1.6	55.2 ± 7.6	0.86	2.56	0.43
	Beartooth Butte	L	6	43	18.8 ± 1.4	56.9 ± 11.8	0.89	2.67	0.56
South face	Washburn Range	A	6	43	17.8 ± 1.8	61.6 ± 10.1	0.95	3.24	0.59
	N. Absarokas	A	18	74	18.7 ± 1.7	55.1 ± 7.0	0.97	3.62	0.75
	Beartooth Plateau	G	6	43	23.3 ± 0.9	71.8 ± 7.7	0.90	2.73	0.46
	Beartooth Butte	L	6	47	23.2 ± 2.3	81.8 ± 6.3	0.91	2.71	0.51
North face	Washburn Range	A	10	47	22.4 ± 1	97.8 ± 6.4	0.95	3.17	0.52
	N. Absarokas	A	16	59	16.1 ± 1	27.1 ± 4.3	0.93	3.17	0.73
	Beartooth Plateau	G	6	46	23.3 ± 1.6	86.7 ± 11.0	0.91	2.86	0.49
	Beartooth Butte	L	6	51	23.5 ± 1.6	63.3 ± 4.3	0.93	3.05	0.54
Snowmelt	Washburn Range	A	8	55	26.1 ± 1.7	87.9 ± 6.3	0.79	2.48	0.53
	N. Absarokas	A	12	84	22.8 ± 1.7	111.4 ± 7.1	0.92	3.24	0.73
	Beartooth Plateau	G	6	33	16.8 ± 0.8	91.3 ± 5.9	0.74	2.08	0.49
	Beartooth Butte	L	6	48	21.0 ± 1.7	137.3 ± 14.8	0.90	2.78	0.56

[1] Substrate, [2] per 1m^2 plot, [3]Simpson (1949), [4]MacArthur and MacArthur (1961), [5]Whittaker (1960).

Table 5.3. Mean environmental responses ± SE for topographic types (TA = talus, RT = ridgetop, SF = south face, NF = north face, and SM = snowmelt) alpine regions (WA=Washburn Range, NA = Northern Absarokas, BP =Beartooth Plateau, BB = Beartooth Butte), and topographic/regional combinations.

		%C	%N	Elev. (m)	Slope (deg.)	Aspect (dg. f/N)	Ann. solar rad. MJ cm^{-2} yr^{-1}	% Soil cover	% Rock cover	pH	Conduct. mmhos cm^{-1}	% Sand in soil	% Clay in soil	% Silt in soil
Topographic type														
	TA	2.1 ± 0.5	0.1 ± 0.01	3120 ± 16	27.4 ± 1.5	110 ± 7	0.85 ± 0.02	7 ± 2	93 ± 2	7.0 ± 0.1	0.10 ± 0.01	69 ± 1.4	5 ± 0.5	26 ± 1.2
	RT	4.4 ± 0.8	0.3 ± 0.1	3180 ± 17	9.2 ± 1.2	104 ± 10	0.88 ± 0.02	42 ± 4	58 ± 4	7.1 ± 0.1	0.17 ± 0.02	62 ± 1.5	8 ± 1.6	31 ± 1.2
	SF	5.5 ± 0.9	0.5 ± 0.1	3160 ± 17	19.1 ± 1.1	142 ± 4	0.94 ± 0.01	64 ± 5	36 ± 5	6.8 ± 0.1	0.23 ± 0.03	64 ± 1.5	4 ± 0.3	32 ± 1.5
	NF	5.2 ± 0.7	0.4 ± 0.1	3122 ± 14	22.4 ± 1.4	33 ± 4	0.67 ± 0.02	63 ± 6	37 ± 6	6.7 ± 0.1	0.20 ± 0.02	61 ± 1.5	6 ± 0.9	33 ± 1.4
	SM	5.7 ± 0.5	0.5 ± 0.04	3114 ± 14	16.0 ± 1.1	56 ± 7	0.77 ± 0.02	89 ± 3	11 ± 3	5.9 ± 0.1	0.25 ± 0.03	59 ± 1.9	7 ± 1.6	34 ± 1.6
Region														
	WA	5.0 ± 0.6	0.4 ± 0.04	3047 ± 5	21.8 ± 1.4	89 ± 8	0.82 ± 0.02	60 ± 5	40 ± 5	6.5 ± 0.1	0.18 ± 0.01	63 ± 1.6	3 ± 0.3	34 ± 1.5
	NA	1.6 ± 0.2	0.1 ± 0.01	3143 ± 8	22.5 ± 1.1	94 ± 6	0.80 ± 0.02	35 ± 3	65 ± 3	6.7 ± 0.1	0.10 ± 0.01	64 ± 0.9	5 ± 0.3	31 ± 0.8
	BP	9.0 ± 1.0	0.8 ± 0.1	3282 ± 11	9.5 ± 1.2	79 ± 11	0.87 ± 0.01	69 ± 7	31 ± 7	6.1 ± 0.1	0.23 ± 0.02	68 ± 1.5	4 ± 0.4	28 ± 1.4
	BB	7.4 ± 0.5	0.5 ± 0.05	3105 ± 8	15.5 ± 1.3	88 ± 9	0.83 ± 0.02	75 ± 7	25 ± 7	7.7 ± 0.1	0.39 ± 0.04	56 ± 2.1	14 ± 2.1	30 ± 1.7
Combination (Topographic type/Region)														
TA	WA	0.9 ± 0.2	0.1 ± 0.0	3047 ± 12	34.1 ± 2.5	139 ± 2	0.94 ± 0.01	4 ± 2	96 ± 2	6.8 ± 0.2	0.09 ± 0.02	70 ± 4.1	4 ± 0.7	26 ± 3.5
	NA	0.5 ± 0.1	0.05 ± 0.01	3101 ± 16	30.2 ± 1.2	118 ± 9	0.84 ± 0.04	9 ± 3	91 ± 3	7.0 ± 0.1	0.08 ± 0.02	68 ± 1.4	4 ± 0.6	28 ± 1.1
	BP	1.5 ± 0.2	0.2 ± 0.0	3296 ± 24	13.3 ± 3.5	86 ± 26	0.87 ± 0.03	3 ± 1	97 ± 1	6.3 ± 0.1	0.07 ± 0.01	70 ± 5.2	7 ± 1.3	24 ± 4.1
	BB	9.1 ± 1.2	0.2 ± 0.1	3100 ± 15	24.0 ± 3.7	71 ± 10	0.75 ± 0.03	9 ± 5	91 ± 5	8.3 ± 0.1	0.19 ± 0.03	72 ± 3.3	5 ± 1.4	23 ± 2.2
RT	WA	4.6 ± 1.5	0.4 ± 0.1	3066 ± 6	12.3 ± 1.9	89 ± 23	0.85 ± 0.05	46 ± 6	54 ± 6	6.9 ± 0.2	0.15 ± 0.02	64 ± 2.8	4 ± 0.8	33 ± 2.1
	NA	1.0 ± 0.1	0.1 ± 0.01	3180 ± 18	10.3 ± 2.1	120 ± 13	0.87 ± 0.03	24 ± 3	76 ± 3	6.9 ± 0.1	0.08 ± 0.01	62 ± 1.8	6 ± 0.8	33 ± 1.5
	BP	11.0 ± 3	0.9 ± 0.2	3341 ± 6	2.3 ± 0.6	89 ± 28	0.90 ± 0.01	68 ± 8	32 ± 8	6.7 ± 0.1	0.28 ± 0.05	69 ± 1.4	3 ± 0.4	28 ± 1.2
	BB	7.9 ± 0.8	0.4 ± 0.1	3137 ± 20	9.5 ± 1.9	87 ± 25	0.89 ± 0.02	68 ± 8	32 ± 8	8.2 ± 0.0	0.34 ± 0.02	53± 4.4	23 ± 6.3	24 ± 4
SF	WA	4.9 ± 1.9	0.4 ± 0.2	3037 ± 16	20.3 ± 3.1	136 ± 6	0.95 ± 0.01	56 ± 11	44 ± 11	6.5 ± 0.2	0.22 ± 0.04	57 ± 4.0	4 ± 0.9	38 ± 3.9
	NA	2.4 ± 0.5	0.2 ± 0.04	3166 ± 19	23.4 ± 1.0	138 ± 6	0.93 ± 0.01	49 ± 8	51 ± 8	6.8 ± 0.1	0.13 ± 0.02	66 ± 1.7	4 ± 0.5	31 ± 1.7
	BP	12.4 ± 2	1.0 ± 0.2	3307 ± 13	12.7 ± 0.4	146 ± 6	0.95 ± 0.01	82 ± 3	18 ± 3	6.2 ± 0.1	0.25 ± 0.04	70 ± 4.3	3 ± 0.5	27 ± 4.0
	BB	8.7 ± 1.4	0.8 ± 0.1	3118 ± 10	11.3 ± 1.4	155 ± 8	0.95 ± 0.00	97 ± 1	3 ± 1	7.6 ± 0.2	0.54 ± 0.08	60 ± 2.5	4 ± 0.6	36 ± 3.1
NF	WA	8.0 ± 0.4	0.6 ± 0.0	3048 ± 10	20.7 ± 1.6	60 ± 2	0.74 ± 0.02	85 ± 3	15 ± 3	6.7 ± 0.1	0.25 ± 0.02	63 ± 2.8	2 ± 0.4	35 ± 2.7
	NA	1.0 ± 0.3	0.1 ± 0.03	3127 ± 18	28.9 ± 1.5	24 ± 3	0.56 ± 0.02	25 ± 3	75 ± 3	6.7 ± 0.1	0.07 ± 0.01	64 ± 1.9	6 ± 0.8	31 ± 2.1
	BP	11.6 ± 2	0.9 ± 0.1	3253 ± 15	11.0 ± 2.9	5 ± 1	0.78 ± 0.03	94 ± 1	6 ± 1	6.1 ± 0.1	0.3 ± 0.04	65 ± 2.2	3 ± 0.4	32 ± 2.3
	BB	5.5 ± 0.7	0.5 ± <0.1	3103 ± 13	19.3 ± 1.1	41 ± 6	0.72 ± 0.00	99 ± 0	1 ± 0	7.4 ± 0.2	0.34 ± 0.06	50 ± 2.4	14 ± 2.6	36 ± 3.9
SM	WA	6.0 ± 0.7	0.5 ± 0.05	3038 ± 9	18.9 ± 1.1	40 ± 9	0.73 ± 0.01	86 ± 4	14 ± 4	5.6 ± 0.1	0.16 ± 0.01	59 ± 3.1	2 ± 0.5	39 ± 3.0
	NA	4.1 ± 0.9	0.3 ± 0.1	3138 ± 18	19.2 ± 1.9	47 ± 14	0.71 ± 0.04	81 ± 6	19 ± 6	5.6 ± 0.2	0.16 ± 0.03	61 ± 3.2	4 ± 0.8	35 ± 3.2
	BP	8.7 ± 0.7	0.7 ± 0.1	3213 ± 27	8.2 ± 1.3	68 ± 9	0.86 ± 0.01	98 ± 1	2 ± 1	5.5 ± 0.0	0.22 ± 0.04	67 ± 2.9	2 ± 0.5	31 ± 3.1
	BB	5.7 ± 0.9	0.5 ± 0.1	3070 ± 20	13.3 ± 0.4	85 ± 12	0.85 ± 0.02	100 ± 0	0 ± 0	7.1 ± 0.2	0.54 ± 0.11	47 ± 1.3	23 ± 1.4	30 ± 2.1

Table 5.3 cont.

		Soil Water and Temperature [1]	
		Avg. water index (WI) (0 = dry, 1 = wet)	Avg. temp. index (TI) (0 = frigid, 1 = hot)
Topographic			
	TA	0.57 ± 0.09	0.35 ± 0.08
	RT	0.31 ± 0.10	0.47 ± 0.09
	SF	0.46 ± 0.09	0.38 ± 0.08
	NF	0.46 ± 0.10	0.27 ± 0.06
	SM	0.81 ± 0.08	0.13 ± 0.05
Alpine region			
	WA	0.38 ± 0.08	0.38 ± 0.07
	NA	0.56 ± 0.11	0.30 ± 0.08
	BP	0.64 ± 0.14	0.16 ± 0.07
	BB	0.53 ± 0.12	0.30 ± 0.08
Combination (Topographic type/alpine region)			
TA	WA	0.34 ± 0.09	0.54 ± 0.10
	NA	0.67 ± 0.10	0.29 ± 0.09
	BP	0.88 ± 0.12	0 ± 0
	BB	0.17 ± 0.08	0.43 ± 0.15
RT	WA	0.16 ± 0.08	0.61 ± 0.09
	NA	0.36 ± 0.12	0.48 ± 0.11
	BP	0.33 ± 0.14	0.33 ± 0.11
	BB	0.33 ± 0.12	0.42 ± 0.13
SF	WA	0.25 ± 0.08	0.53 ± 0.08
	NA	0.47 ± 0.10	0.36 ± 0.09
	BP	0.50 ± 0.15	0.16 ± 0.09
	BB	0.64 ± 0.14	0.25 ± 0.06
NF	WA	0.21 ± 0.08	0.34 ± 0.07
	NA	0.83 ± 0.09	0.25 ± 0.09
	BP	0.67 ± 0.14	0.11 ± 0.07
	BB	0.63 ± 0.11	0.23 ± 0.08
SM	WA	0.83 ± 0.08	0.08 ± 0.02
	NA	0.79 ± 0.09	0.13 ± 0.06
	BP	0.83 ± 0.12	0.06 ± 0.03
	BB	0.93 ± 0.07	0.16 ± 0.05

[1] See Chapter 2 for explanation of the temperature and water indices. 30% used as minimum within-group constancy for indicator of all treatments except talus. Because of the heterogeneity of talus environments no constancy threshold was imposed.

combination categories respectively. Indicator species quantitatively identified with the modified Murdoch index are also indicated in Table 5.4-5.6.

Vegetation and Environmental Variation Among Local Topographic Types

Vegetation

Cover increased from talus (7%) to ridge (43%) to north and south slopes (63-61%) to snowbanks (106%). Percentages above 100% occurred in snowbanks due to the consistent occurrence of multiple vegetation layers in samples.

Average richness and diversity generally paralleled cover and increased from talus (7 spp. plot^{-1}, Simpson's div. = 0.93) to ridge (16 spp. plot^{-1}, Simpson's div. = 0.96), to north and south slopes (20 spp. plot^{-1}, Simpson's div. = 0.98 - 0.97) to snowbanks (22 spp. plot^{-1}, Simpson's div. = 0.93).

We use soil carbon and nitrogen as an index of net productivity across types (see Chapter 3 discussion). This is reasonable because life forms of the study area plants were generally similar (short herbs), and because sites have had similar times for biologically driven carbon and nutrient accumulation. Thus, net production indices (%C, %N) increased from talus (2.1%, 0.1%) to ridge (4.4%, 0.3%), and was highest on south face (5.5%, 0.5%), north face (5.2%, 0.4%) and snowbank sites (5.7%, 0.5%). The fact that C/N ratios were higher under talus (21) and ridges (14) than under north and south slopes and snowbank sites (11-12) suggests that decomposition was lower in talus and ridge than in other environments (cf. Frank et al. 1994).

Indicators Species composition varied greatly among topographic types (Table 5.4). Most species (72%) occurred in less than 10% of plots. Ubiquitous species were generally graminoids e.g. *Trisetum spicatum, Festuca brachyphylla, Poa pattersonii,* and *Luzula spicata*. Ubiquitous forbs included *Cerastium arvense* and *Sedum lanceolatum* (Table 5.4).

The heterogeneity of talus is demonstrated by its high beta diversity (Table 5.2), and by the fact that no species occurred with greater than 50% constancy within its samples (Table 5.4). Across the four alpine regions significant Murdoch Indicators of talus were *Elymus scribneri, Antennaria microphylla*, *Arabis* spp. *Epilobium clavatum,* and *Polemonium viscosum* (Table 5.4, Fig. 5.4a).

The ridge community has several constants shared to some extent with warm talus and south facing sites (Table 5.4). Significant ridgetop associates were often cushion plants: e.g. *Eritrichium nanum, Trifolium nanum, Astragalus kentrophyta, Phlox pulvinata,* and *Sedum lanceolatum* (Table 5.4, Fig. 5.4b).

The variability of south and north slopes across the four regions is illustrated by the scatter of north and south samples across all three dimensions of ordination diagrams (Fig. 5.3a). Significant Murdoch associates of south facing slopes included *Antennaria umbrinella, Arenaria obtusiloba, Bupleurum americanum, Mertensia alpina,* and *Selaginella densa* (Table 5.4, Fig. 5.4c). North slope indicators included *Astragalus alpinus, Besseya wyomingensis, Poa alpina, Saxifraga bronchialis,* and mosses (Table 5.4, Fig. 5.4d).

Snowbank plots tended to be dominated by similar key species across the four regions (note low Simpson's and Shannon-Wiener diversity responses; Table 5.2). A large number of plants occurred largely or solely on snowbank sites, making this topographic type very distinct (Table 5.4). Significant indicators included multi-headed sedges *Carex paysonis* and *Carex phaeocephala* along with *Agrostis variabilis, Poa reflexa, Salix arctica, Sibbaldia procumbens,* and *Veronica wormskjoldii* (Table 5.4, Fig. 5.4e).

Environment

At a local scale (within a consistent substrate and climate) vegetation composition varies largely with respect to topographic influences on microclimate. Prairie vegetation varies with temperature and moisture as determined by slope and aspect in the plains of North Dakota (Aayd and Dix 1964). In the alpine, topographic control of vegetation is even more pronounced because (1) slopes are generally steeper, and (2) wind, sun and precipitation tend to interact more dramatically with topographic characteristics (Körner 2003).

Talus sites were very rocky (90% rock cover vs. 10-60% in other types; Table 5.3, Fig. 5.3a) and steep/unstable providing a poor environment for plant establishment and growth. Soils temperatures were intermediate compared to other types (Temperature Index (TI) = 0.35; where 0 = frigid and 1 = hot), average aspects were east/west (110^{o}), although incident radiation was fairly high (0.85 MJ cm^{-2} yr^{-1}; Table 5.3) due to the steep (27^{o}) southern aspect of some sites. Soils under talus were often moist all summer long (Water Index (WI) = 0.57; where 0 = dry, 1 = wet) because of low evaporation (due to rock cover) and low transpiration (little plant cover). Soils were poorly developed (%C = 2.1%, %N = 0.1%), sandy (69% sand), with low conductivity (0.01 mmhos cm^{-1}), but relatively high pH (Table 5.3; Fig. 5.3a).

Ridgetop sites were generally wind-swept and dry. The temperature index of ridgetops was higher than other topographic types (TI = 0.47) due to uninterrupted solar radiation inputs (0.88 MJ cm^{-2} yr^{-1}; Table 5.3). Ridges were also the driest of the five environments (WI = 0.31). High winds that sweep away snow from ridgetops also generate evaporation which further depletes soil water. Note that cushion plants (often associated with this type) are well adapted to exposed, dry environments since their morphology traps heat and reduces transpiration (Gauslaa 1984, Körner and De Moraes 1979). Ridge soils were rocky (58% cover), clayey (7.6% clay) poorly devloped (4.4% C, 0.3% N) with low conductivity (0.17 mmhos cm^{-1}) and relatively alkaline pH (7.1; Table 5.3).

South slopes were warmer than north slopes (TI = 0.38, TI = 0.27 respectively), and had much higher radiation totals (0.94 compared to 0.67 MJ cm^{-2} yr^{-1}). Other than these differences, however, north and south slopes were highly similar. Water index responses were identical (WI = 0.46) reflecting similar soil rock content (63%-61%), sand content (64%-61%) slope (19°-22°), C and N content [%C (5.5-5.2), %N (0.5-0.4)] pH (6.8-6.7) and vegetation cover (63%-61%).

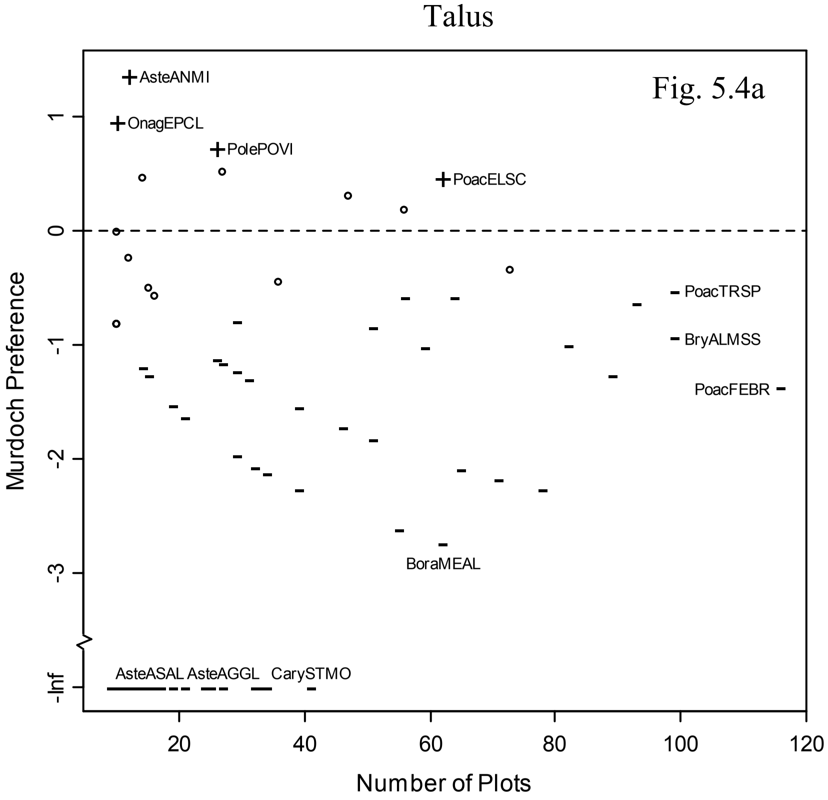
Snow collection sites had abundant soils and short cool/moist growing seasons. Temperature index response was lower than other environments (TI = 0.13, compared to 27-47; Table 5.3) due to late melt, northern aspect (56° from north) and low incident solar radiation (0.8 MJ cm^{-2} yr^{-1}). While only measured on the Washburn Range growing seasons were much shorter on snowbanks than other topographic types (19 days with soils warmer than 10ºC versus 39-69 days in other communities; Ch. 3, Table 3.3). Water index measures (WI = 0.81) were much higher than those of other types (WI = 0.31-0.57; Table 5.3) due to accumulated snow and gradual melt. Nitrogen on snowbank sites was relatively high (0.5% vs. 0.1-0.5% on other sites), although cool site decomposers may recycle it poorly (Bridges 1978). Higher nutrient content on north and south slopes and snowbanks may be a product of dense vegetation and biologically driven soil development (Körner 2003). Silt concentrations were particularly high at snowbank sites (34%; Table 5.3, Fig. 5.3a) due to windblown soil (loess) collecting in the same lee locations where snow collects. Acid soil under snowbanks (pH = 5.9 vs. 6.7-7.1 in other environments) was due to leaching of bases by melt water (cf. Bridges 1978).

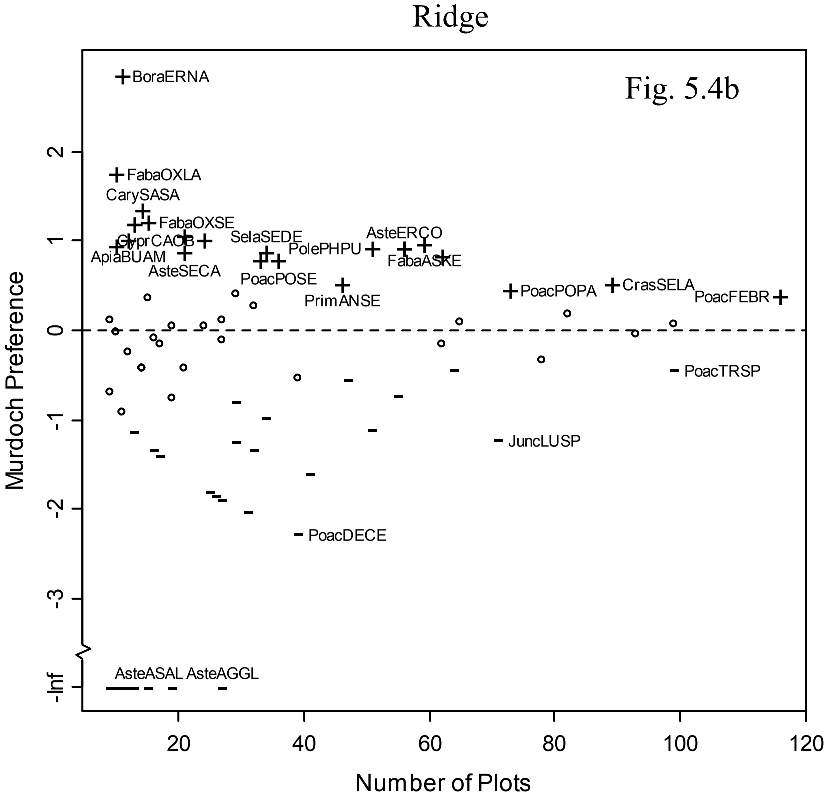
Table 5.4. Summarized relevé table for topographic habitats. Only species which occurred with constancy ≥ 30% with at least one topographic type are included in the table. A two character cipher[1] is included in each cell which indicates constancy (percentage of sites that contain the species), and cover. Asterisked cells indicate a significant positive Murdoch index association ($\alpha = 0.05$) between the designated species and topographic type (see Fig. 5.4). Bolded cells have constancy ≥ 30%

	LF[2]	Talus	Ridge	S. face	N. face	Snowbank
Elymus scribneri	Gr	**4B***	**6B***	2A	2A	..
Erigeron compositus	Fo	**3A***	**6B***	**3A**	2A	..
Lomatium cous	Fo	**3A**	1A	**3A***	2A	2A
Poa secunda	Gr	1A	**3A***	1A	2A*	+A
Astragalus kentrophyta	Cu	1A	**6C***	**5C***	2A	+A
Smelowskia calycina	Fo	1A	**6B***	**4A**	2A	+A
Poa pattersonii	Gr	2A	**5B***	**4B**	**4A**	2A
Phlox pulvinata	Cu	1A	**5C***	**3A**	**3C**	..
Androsace septentrionalis	Fo/An	+A	**3A***	2A	**3A**	2A
Festuca brachyphylla	Gr	1A	**8C***	**7B**	**6B**	**7C**
All mosses	Mo	2A	**5C**	**4B**	**7C***	**8D***
Sedum lanceolatum	Cu	1A	**7B***	**6B**	**5A**	**3A**
Arenaria obtusiloba	Cu	1A	**5B**	**6B***	**4B**	**4A**
Cerastium arvense	Fo	2A	**4A**	**6B**	**7C***	**3A**
Trisetum spicatum	Gr	**3A**	**3A**	**7B***	**6B**	**6A**
Potentilla diversifolia	Fo	+A	**3A**	**5B**	**5C***	**7C***
Erigeron simplex	Fo	+A	**3A**	**4A**	**3A***	**6B***
Poa rupicola	Gr	..	**3A***	2B	2B	+A
Selaginella densa	Fe	..	**3C***	**3B***	2B	..
Antennaria umbrinella	Fo	+A	2A	**3B***	+A	+A
Mertensia alpina	Fo	++	2A	**4B***	**5A***	2A
Achillea millefolium	Fo	2A	2A	**5B***	**3B**	**4B**
Luzula spicata	Gr	+A	1A	**5A***	**6B***	**5A***
Polygonum bistortoides	Fo	++	1A	**4A***	**3A**	**5B***
Polemonium viscosum	Fo	2A*	++	+A	**3B***	++
Besseya wyomingensis	Fo	+A	++	2A	**4A***	+A
Astragalus alpinus	Fo	..	+A	2A	**4A***	1A
Stellaria monantha	Fo	..	++	1A	**3A**	**6A***
Poa alpina	Gr	+A	1A	2A	**5B***	**4B***
Carex paysonis	Gr	+A	++	+A	+A	**7D***
Artemisia scopulorum	Fo	++	1A	1B	2A	**5C***
Sibbaldia procumbens	Fo	++	+A	1A	..	**5C***
Antennaria media	Fo	..	++	+A	1A	**5B***
Deschampsia cespitosa	Gr	+A	+A	2B	2B	**4D***
Ranunculus eschscholtzii	Fo	+A	++	1A	1A	**3A***
Carex phaeocephala	Gr	+A	+A	1B	1A	**3A***
Lupinus argenteus	Fo	+A	+A	2B*	2B	**3C***
Salix arctica	Sh	..	..	..	1C	**4C***
Agoseris glauca	Fo	..	..	2A*	+A	**3B***
Veronica wormskjoldii	Fo	..	..	..	+A	**3A***

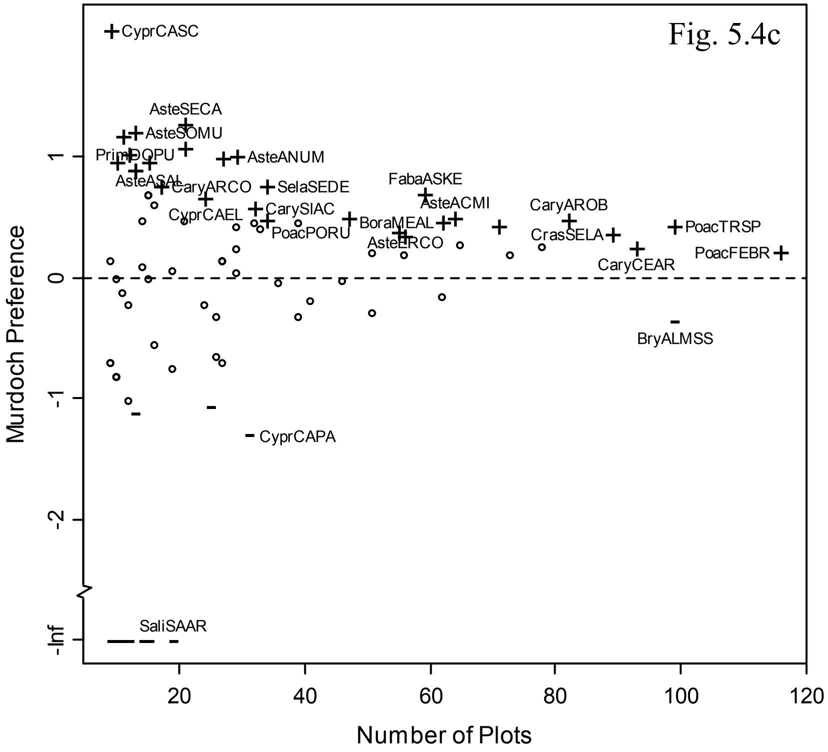
[1] For each cell in the body of the table, constancy is indicated by the first symbol, while cover is indicated by the second symbol. For constancy: 0% = “.”, 0-10% = +, 10-20% = 1, 20-30% = 2, 30-40% = 3, 40-50% = 4, 50-60% = 5, 60-70% = 6, 70-80% = 7, 80-90% 8, 90-100% = 9. For cover: 0% = “.”, 0-0.01% = +, 0.01-1% = A, 1-2% = B, 2-5% = C, 5-25% = D, >25% = E.

[2] LF = Life form: An = Annual, Cu = Cushion plant, Fe = Fern Ally, Fo =Upright forb, Gr = Graminoid, Mo = Moss, Sh = Shrub.

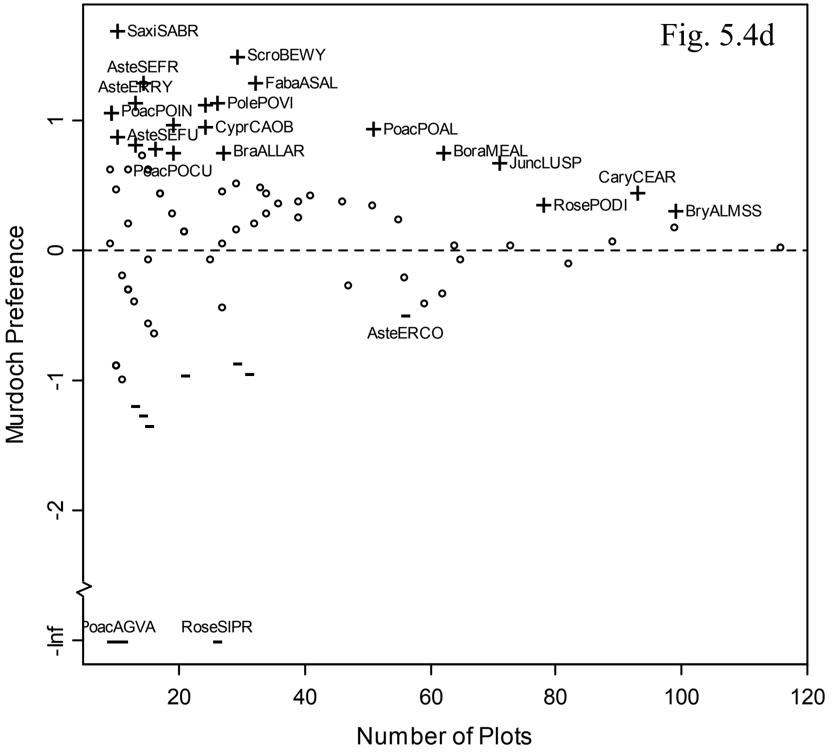




For figure descriptions see next page



S. Face



N. Face

For figure description see next page

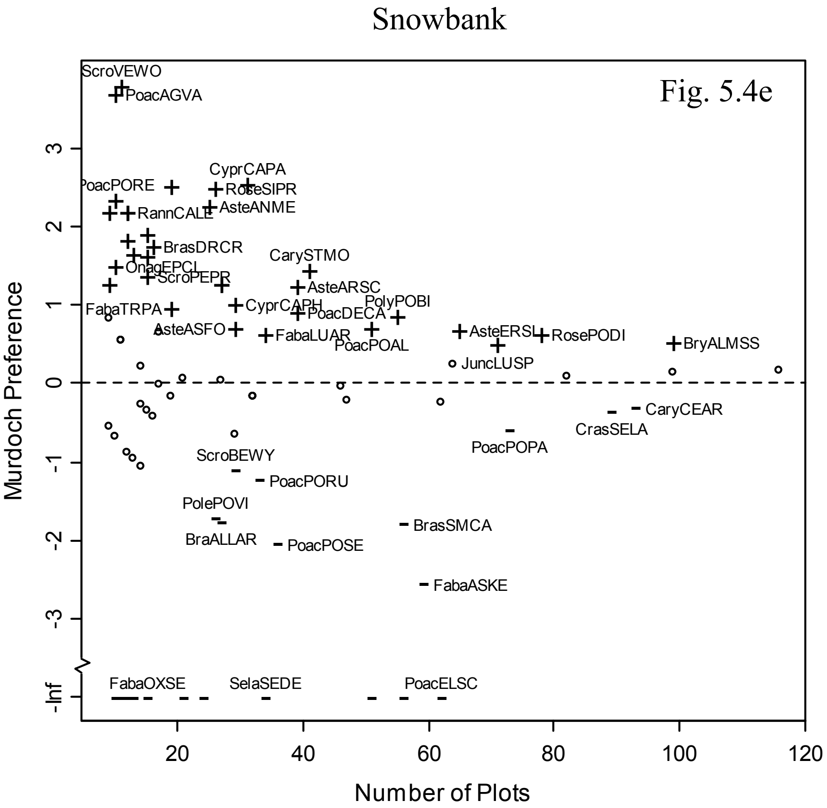


Figure 5.4. Murdoch analysis results for topographic types: (a) talus, (b) ridge, (c) south face, (d) north face, and (e) snowbank. Eighty-six species which occurred in at least 5% of the 178 plots across the 4 alpine regions were analyzed. Significant positive and negative species are identified where space on the graph allows, "+" indicates a positively significant Murdoch species, "-" indicates a negatively significant Murdoch species, "0" indicates neither significantly positive nor negative. Due to overlaying species not all species can be identified in graphs. For species codes see Appendix D.1. For complete summary of Murdoch analyses for topographic types see Appendix D.2, Table D.2.1.

Ecosystem Variation Across Regions

In addition to variation with topography, alpine ecosystems (vegetation and environment) varied among regions with different substrates (andesite, granite, and limestone) and climates (wet and relatively dry).

Vegetation

We expected little variation between regions with respect to general vegetation characteristics (e.g. cover, richness, and productivity) because these attributes were averaged across very different topographic types. Nonetheless, vegetation cover was lower in the Northern Absaroka volcanics (42%) compared to other ranges (61- 69%), as was richness (15 spp plot^{-1}) compared to (18-19 spp plot^{-1}), and production as indexed by soil organic matter (1.6% C, 0.1 %N) versus (5-9% C, 0.4-0.8% N). Note that these differences may have been partially due to a slightly lower percentage of snowmelt sites sampled in the Northern Absarokas compared to other ranges.

Indicators In contrast to cover and richness, we expected large phytosociological differences among regions because regional differences were summed (not averaged) across topographic types. These phytosociological trends are summarized in a relevé format (Table 5.5) which lists species important in at least one region (constancy ≥ 30%), and by Murdoch analyses (Fig. 5.5).

A large number of species distinguished the Washburn Range (Table 5.5). Significant Murdoch indicators included *Poa cusickii, Poa rupicola Cerastium arvense, Erigeron rydbergii, Eriogonum ovalifolium, Oxytropis lagopus, Pedicularis* *cystopteridifolia, Penstemon procerus, Saxifraga rhomboidea, Sedum lanceolatum, Senecio canus,* and *Senecio integerrimus* (Table 5.5, Fig. 5.5a)

Vegetation of the Northern Absarokas was more heterogeneous than that of other regions; note the high alpha and beta diversity responses (Table 5.2). Significant indicators included *Agrostis variabilis, Elymus scribneri, Androsace septentrionalis, Antennaria microphylla, Arnica rydbergii, Astragalus kentrophyta, Lloydia serotina,* and *Senecio fremontii,* (Table 5.5, Fig. 5.5b).

Beartooth Plateau vegetation was relatively homogenous across topographic types; note high richness but low diversity measures for the region (Table 5.2). Significant Murdoch species included *Bupleurum americanum, Caltha leptosepala, Carex pyrenaica, Deschampsia cespitosa, Geum rossii, Senecio fuscatus, Trifolium nanum* and *Trifolium parryi* (Table 5.5, Fig. 5.5c).

Beartooth Butte was also distinguished by a large number of species. Significant indicators included *Carex atrata*, *Elymus trachycaulus, Festuca idahoensis, Stipa lettermanii, Dryas octopetala*, *Gentianella amarella*, *Geum triflorum*, *Oxytropis sericea, Pedicularis bracteosa, Phleum alpinum, Solidago multiradiata, Trollius laxus, Valeriana edulis,* and *Zigadenus elegans* (Table 5.5, Fig. 5.5d).

Environment

Vegetation differences among the four major alpine regions are undoubtedly largely due to major environmental differences including substrate and climate. We also consider several other potential regional factors including grazing, isolation, and dispersal.

Climatic Controls Precipitation increases from the Washburn Range through the Northern Absarokas and the Beartooths (Figs. 5.1c, 5.2). Plant indicators substantiated the aridity of the Washburn Range [WI = 0.38 (where 0 = dry, 1 = wet)] compared to other regions (WI = 0.53 to 0.64; Table 5.3). Predicted soil temperatures fell with increasing mean elevation from Washburn [TI = 0.38 (where 0 = frigid, 1 = hot); 3047m] to Beartooth Butte (TI = 0.3, 3105m) to the N. Absarokas (TI = 0.3, 3143m) to the Beartooth Plateau (TI = 0.16, 3282m). Incident solar radiation totals were approximately equal for the four regions (0.80 – 0.87 MJ cm^{-2} yr^{-1}, Table 5.3)

Regional climatic effects are probably best deduced from vegetation differences between the drier Washburn Range and the wetter North Absarokas since they have similar (andesitic) substrates (Fig. 5.1b). Dry *Carex elynoides* turf occurred primarily on north facing slopes in the Washburn Range, but occurred on south facing slopes in the Northern Absarokas and other regions. Xeric species were often dominant on the Washburn Range including *Carex elynoides* (cf. Komárková 1979, Hitchcock and Cronquist 1973), *Carex obtusata* (cf. Komárková 1979, Hitchcock and Cronquist 1973), Lupinus *argenteus* (cf. Kershaw et al. 1998), *Oxytropis lagopus* (cf. Hitchcock and Cronquist 1973), *Poa rupicola* (cf. Kershaw et al. 1998), *Sedum lanceolatum* (cf. Hitchcock and Cronquist 1973, Kershaw et al. 1998) and *Selaginella densa* (cf. Kershaw et al. 1998). In contrast, species occurring solely or primarily in the N. Absarokas were often hydrophiles including *Androsace septentrionalis* (Ch. 2), *Deschampsia cespitosa* (cf. Johnson and Billings 1969, Komárková 1979), *Erigeron simplex* (Ch. 2) and *Phleum alpinum* (cf. Kershaw et al. 1998, Bamberg and Major 1968; Table 5.5).

Several frequently occurring species on Beartooth Butte including *Festuca idahoensis, Bromus inermis* (var. *purpurescens*), *Geum triflorum, Stipa lettermanii*, *Senecio crassulus*, and *Salix glauca* generally do not occur in alpine environments (Dorn 1992). This suggests a relatively mild alpine climate on Beartooth Butte due to its relatively low altitude and large, habitable southern aspects.

Substrate Controls Across all 178 plots (i.e. all topographic types from all regions) the environmental variables most strongly correlated with NMDS scatter were soil cover and development. Because limestone substrates break down into clayey soils, the sand content of Beartooth Butte soils were lower (56%) than other regions (62%-68%) while clay contents were higher (14% vs. 3%-5%, Table 5.3). Soils were most acidic on the granitic Beartooth Plateau (pH = 6.1) slightly acidic on the andesitic Washburn Range and N. Absarokas (pH = 6.5 – 6.7), and highly alkaline on Beartooth Butte (pH = 7.7) due to H^+ buffering characteristics of calcite.

In the N. Absarokas soils were particularly scarce compared to the other regions (soil cover = 35% vs. 60% - 67%) and poorly developed (0.1% N vs. 0.4%-0.8%). Species distinguishing the N. Absarokas were often those preferring rocky nutrient-poor soils including *Elymus scribneri, Androsace septentrionalis, Saxifraga bronchialis,* and *Senecio fremontii* (cf. Dorn 1992).

The andesitic N. Absarokas and Washburn Range are notable in the absence of at least three species and one genus which occur frequently in adjacent alpine areas including Beartooth Butte and the Beartooth Plateau. These were: *Bupleurum americanum Eritrichium nanum, Dryas octopetala,* and the genus *Trifolium* (e.g. *T.*

dasyphyllum, T. haydenii, T. nanum and *T. parryi*). *Dryas octopetala, B. americanum*, and *E. nanum* are missing from other andesitic alpine areas in the southern Rockies and coastal cordilleras (Rottman and Hartman 1985, Baker 1983, Hunter and Johnson 1983). The presence/absence of *Trifolium* appears unrelated to andesitic substrates since it is also missing from the granitic Tetons (Spence and Shaw 1981) while occurring in the andesitic southern Absarokas (Thilenius and Smith 1985). Species favoring the andesitic Washburn Range and N. Absarokas over other regions included a number of widespread, often low altitude species: *Astragalus kentrophyta, Erigeron compositus, Lomatium cous* and *Phlox multiflora* (Table 5.5, Figs. 5.5b, 5.5c).

At least four species which occurred primarily or solely on limestone Beartooth Butte are documented calciophiles. These include *Carex nardina* (Komárková 1979, Sørenson 1933), *Carex rupestris* (Komárková 1979, Gjaerevoll 1953) *Dryas octopetala* (Bamberg and Major 1968, Komárková 1979, Willard 1979), and *Eritrichium nanum* (Bamberg and Major 1968).

Other Regional Controls: Grazing *Geum rossii* is extremely dominant on the Beartooth Plateau (10% cover, 80% constancy), though it rarely occurs elsewhere in the study area (Table 5.5, Fig. 5.5d). Since *G. rossii* is dominant through the Rockies (Mellman-Brown 2002) and unpalatable to domestic livestock (Billings 2000) this suggests that it may come to dominate frequently grazed areas like the Beartooth Plateau (Fig. 5.6; cf. Milton 1940, 1947, Jones 1933). The lack of *Geum rossii* on Washburn and in the N. Absarokas may be due to the prevention of domestic grazing in Yellowstone National Park over the last 125 years. Indeed, the southeastern Absarokas, where domestic grazing has been frequent and continuous, have much higher quantities of *G. rossii* (Thilenius amd Smith 1985), as do local heavily grazed areas in the Pioneer, Tobacco Root, and Flint Creek Mountains in southern Montana (Cooper et al. 1997, Bamberg and Major 1968). The hypothesis that *G. rossii* dominance is simply the result of grazing is countered on the heavily grazed Beartooth Butte area where *G. triflorum* is dominant but *G. rossii* is missing (Table 5.5).

<u>Other Regional Controls: Isolation and Dispersal</u> The distinctiveness of the Washburn flora may be due in part to its small size and isolation, i.e. island characteristics (Fig. 5.1a, also see Ch. 3). Immigration may be reduced by isolation, preserving community patterns that would disappear in the face of increased dispersal and competition (Hubbell 2001). Of particular note, *Erigeron rydbergii* often dominates dry turf areas in the Washburn Range though it seldom occurred in plots elsewhere in the study area (Table 5.5, Fig. 5.5a). *Erigeron rydbergii* is endemic to the Greater Yellowstone Ecosystem, and limited in range to southern Montana and northwestern Wyoming (Pemble 1965, Lackschewitz 1994).

Table 5.5. Summarized relevé table for species common[1] in the four major alpine areas. A two character cipher is included in each cell which indicates constancy (percentage of sites that contain the species), and cover[2]. Asterisked cells indicate a significant positive Murdoch index association (α = 0.05) between the designated species and alpine region (see Fig. 5.5). Bolded cells indicate constancy ≥ 30%.

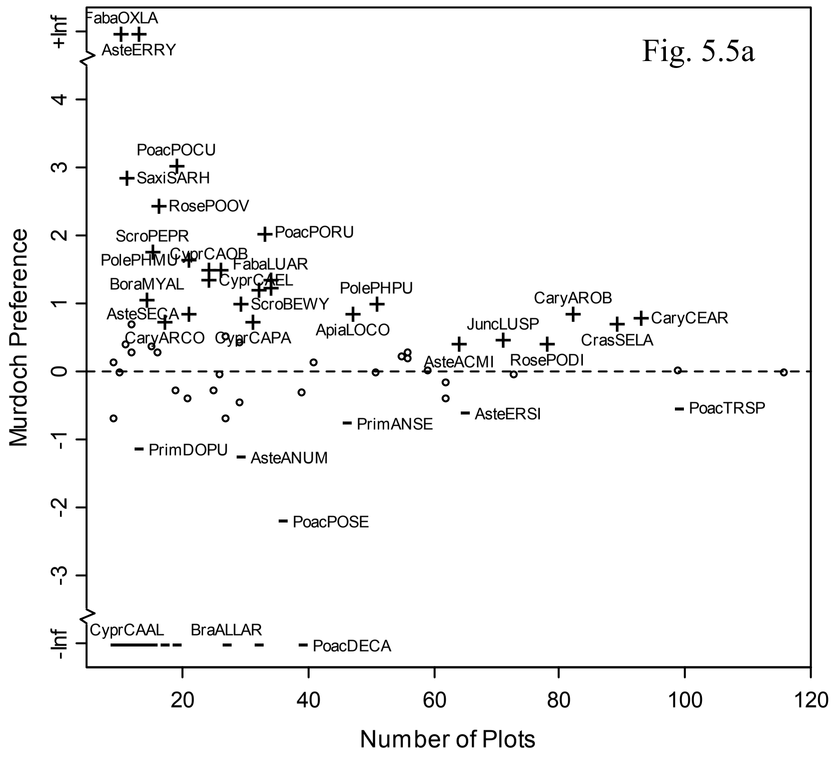
	LF[2]	Washburn Range	Northern Absarokas	Beartooth Plateau	Beartooth Butte
Erigeron rydbergii	Fo	**3B***	..	..	..
Potentilla ovina	Fo	**3A***	+A	..	..
Phlox multiflora	Fo	**3A***	+A	..	..
Poa rupicola	Gr	**6C***	+A	+A	..
Selaginella densa	Fe	**4D***	1A	2A	..
Carex elynoides	Gr	**3C***	+A	1C	1B
Poa cusickii	Gr	**4A***	++	..	+A
Astragalus alpinus	Fo	**4B***	1A	..	2A
Polemonium viscosum	Fo	**3B***	+A	+A	+A
Sedum lanceolatum	Cu	**8B***	**5A**	2A	2A
Lomatium cous	Fo	**4A***	**3A***	..	+A
Erigeron compositus	Fo	**3A**	**4A***	..	+A
Astragalus kentrophyta	Cu	**3B**	**5C***	..	++
Elymus scribneri	Gr	2A	**5B***	+A	+A
Androsace septentrionalis	Fo/An	1A	**4A***	..	++
Festuca brachyphylla	Gr	**6B**	**7B***	**7C***	2A
Arenaria obtusiloba	Cu	**8C***	**3A**	**5A**	2A
Luzula spicata	Gr	**5B***	**3A**	**5A***	+A
Trisetum spicatum	Gr	**3A**	**5B**	**5A**	**7B***
Cerastium arvense	Fo	**9C***	**4A**	**3A**	**4A**
All mosses	Mo	**5C**	**4C**	**7C***	**5D**
Poa alpina	Gr	2A	**3A***	+A	**3A**
Erigeron simplex	Fo	2A	**4A**	**4A**	1A
Mertensia alpina	Fo	2B	2A	**4A***	**3A**
Carex paysonis	Gr	2D*	1B	2D	..
Carex obtusata	Gr	**3C***	..	**3B***	..
Lupinus argenteus	Fo	**4C***	+A	..	**3C***
Besseya wyomingensis	Fo	**3A***	+A	..	**4A***
Poa pattersonii	Gr	**3A**	**5B***	..	**3A**
Achillea millefolium	Fo	**4B***	**3A**	..	**5B***
Polygonum bistortoides	Fo	**3A**	+A	**6A***	**5A***
Potentilla diversifolia	Fo	**6C***	1A	**6B***	**7B***
Phlox pulvinata	Cu	**5C***	+A	**4A**	**3C**
Smelowskia calycina	Fo	**3A**	2A	**4B***	**3A**
Stellaria monantha	Fo	2A	1A	**3A***	2A
Artemisia scopulorum	Fo	1A	1A	**6C***	..
Geum rossii	Fo	..	+A	**7D***	..
Silene acaulis	Cu	..	2A	**3B***	..
Trifolium nanum	Cu	..	..	**4C***	..
Bupleurum americanum	Fo	..	..	**3A***	..
Senecio fuscatus	Fo	..	..	**3A***	..
Trifolium parryi	Fo	..	..	**3A***	2A*
Deschampsia cespitosa	Gr	..	1B	**5C***	**3C***
Aster foliaceus	Fo	1A	1A	+A	**4C***
Ranunculus eschscholtzii	Fo	+A	1A	++	**3A***
Agoseris glauca	Fo	2A	+A	..	**4C***
Dodecatheon pulchellum	Fo	+A	+A	..	**3A***
Phleum alpinum	Gr	..	+A	..	**3A***
Oxytropis sericea	Fo	..	..	1A	**3A***
Solidago multiradiata	Fo	..	..	..	**4C***
Elymus trachycaulus	Gr	..	..	..	**5C***

Table 5.5 cont.

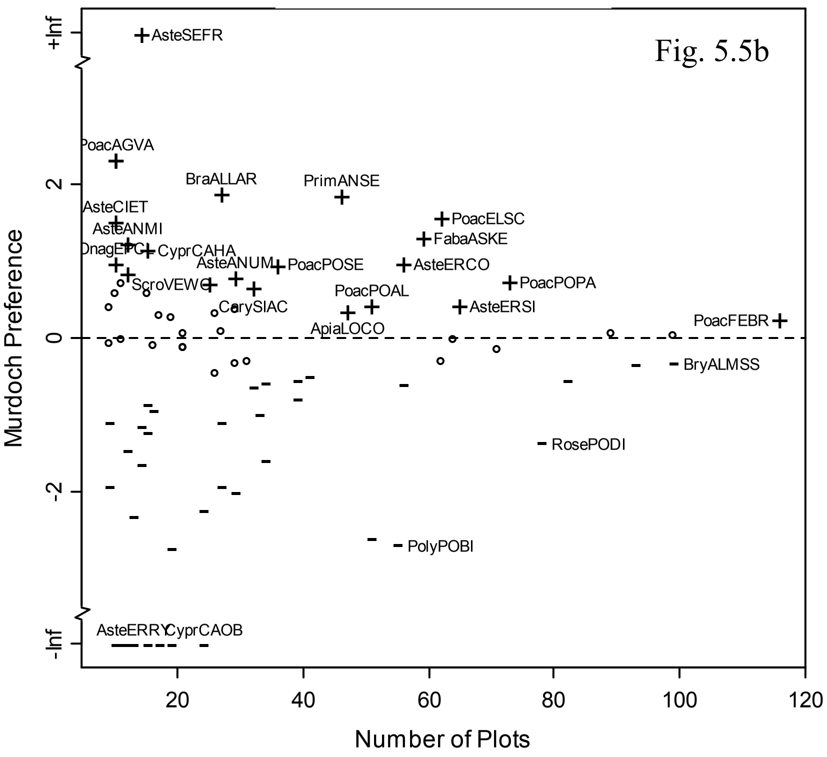
[1] Only species which occurred with ≥ 30% constancy within at least one of the four alpine regions are included in the table.

[2] For each cell in the body of the table, constancy is indicated by the first symbol, while cover is indicated by the second symbol. For constancy: 0% = ".", 0-10% = +, 10-20% = 1, 20-30% = 2, 30-40% = 3, 40-50% = 4, 50-60% = 5, 60-70% = 6, 70-80% = 7, 80-90% 8, 90-100% = 9. For cover: 0% = ".", 0-0.01% = +, 0.01-1% = A, 1-2% = B, 2-5% = C, 5-25% = D, >25% = E. [2] LF = Life form: An = Annual, Cu = Cushion plant, Fe = Fern Ally, Fo = Upright forb, Gr = Graminoid, Mo = Moss, Sh = Shrub.

Washburn Range



Northern Absarokas



For figure description see next page

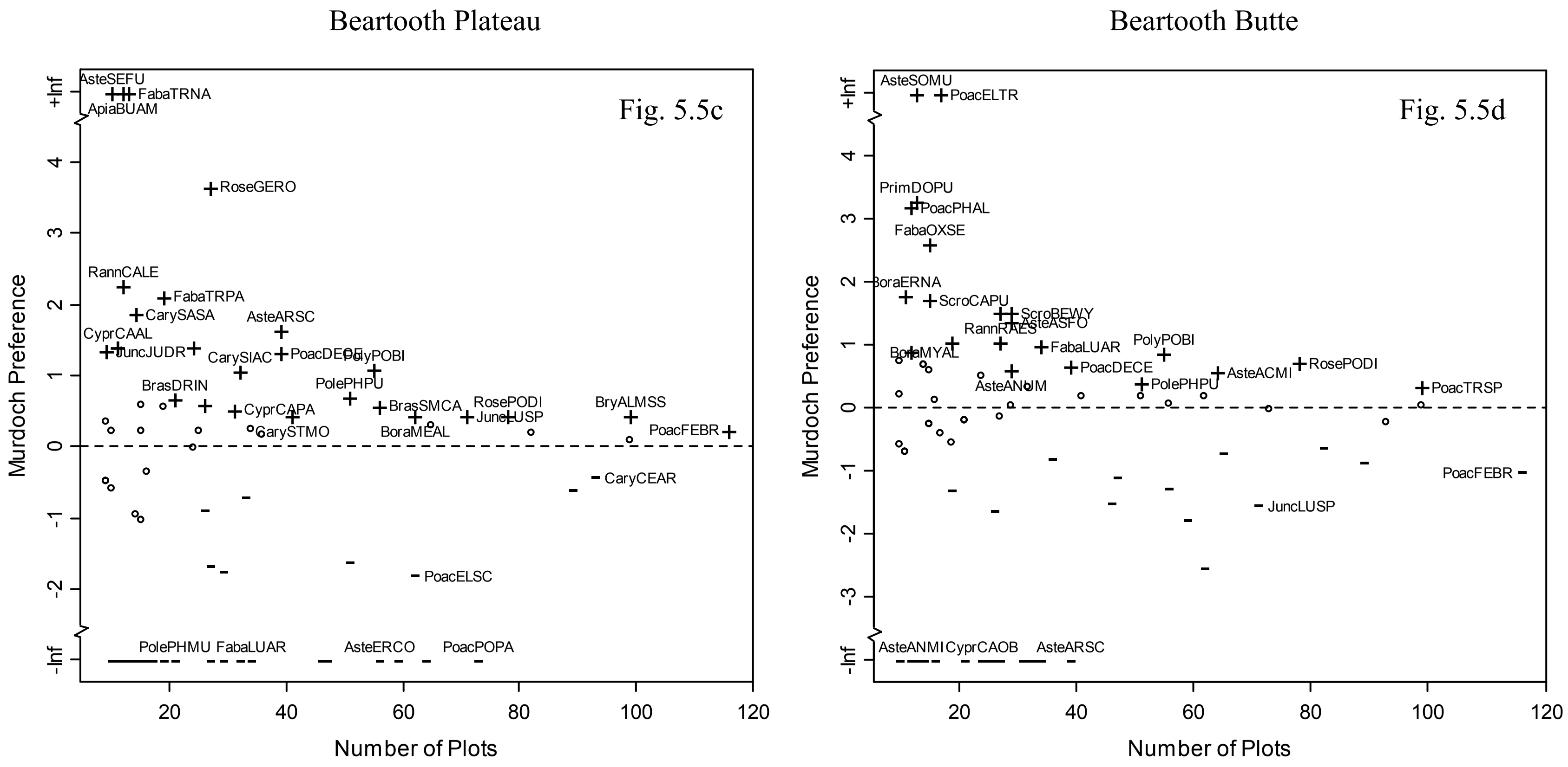


Figure 5.5. Murdoch analysis results for alpine areas: (a) Washburn Range, (b) N. Absarokas, (c) Beartooth Plateau, (d) Beartooth Butte. The eighty-six species which occurred in at least 5% of the 178 plots across the 4 alpine areas were analyzed. Significant positive and negative species are identified where space on the graph allows, "+" indicates a positively significant Murdoch species, "-" indicates a negatively significant Murdoch species, "0" indicates neither significantly positive nor negative. Due to overlaying species not all species can be identified in graphs. For species codes see Appendix D.1. For complete summary of Murdoch analyses for alpine areas see Appendix D.2, Table D.2.2.

Figure 5.6. Domestic sheep grazing on the Beartooth Plateau (Anderson 1984). Domestic grazing may account for particularly high levels of unpalatable *G. rossi* on the Beartooth Plateau.

Interaction of Topographic and Regional Factors on Ecosystems.

While we have described how local and regional factors act alone in determining vegetation composition, our analyses indicate that these factors act strongly together. As noted earlier, combinations of local and regional treatments (demonstrated in Tables 5.2 and 5.3) explained 73% of scatter in the two most important ordination dimensions (Fig. 5.3, Table 5.1). In contrast local topography explained 37% while regional assignments explained only 31% of ordination variation (Table 5.1). A summary of vegetation patterns with respect to local/regional interactions is provided by Table 5.6, individual ordinations of topographic types (Figs. 5.7, 5.9, 5.11, 5.13, 5.15), and Murdoch analyses (Figs. 5.8, 5.10, 5.12, 5.14, 5.16).

Talus Variation Across Regions

Vegetation While talus vegetation cover and richness were low in all regions (7% cover, 7 spp. plot^{-1}), these responses were much lower on the granitic Beartooth

Plateau (2% cover, 3 spp. plot^{-1}) compared to other regions (7-8% cover, 7-9 spp. plot^{-1}). Talus productivity (as indexed by soil organic matter) was much higher on calcareous Beartooth Butte (C = 9.1%, N = 0.2%) compared to other regions (C = 0.5-1.5%, N = < 0.1-0.2%).

Ubiquitous indicators of talus across all regions included *Elymus scribneri, Antennaria microphylla, Arabis* spp., and *Epilobium clavatum* (Fig. 5.4a, Table 5.1). A number of species which occur in talus including *Carex paysonis, Carex phaeocephala Deschampsia cespitosa*, *Draba crassifolia*, and *Sibbaldia procumbens* also occur on moist late-melt sites (Table 5.4, 5.6). The frequently hydric character of talus soils was demonstrated on the Washburn Range (Chapter 3).

Due to vegetation heterogeneity, clusters separating alpine regions in talus ordination space were poorly defined, and explained relatively little variation in ordination scatter ($r^2 = 0.48$, $p = 0.001$, Table 5.1, Fig. 5.7). Regardless of this, several species were significantly associated with talus of a particular region. Species which distinguished Washburn talus from talus of other areas included *Sedum lanceolatum* and *Phlox pulvinata* (Fig. 5.8a, Table 5.6). Species distinguishing N. Absaroka talus included *Carex phaeocephala, Draba crassifolia, and Epilobium anagallidifolium* (Fig. 5.8b, Table 5.6). Species distinguishing the Beartooth Plateau included *Carex paysonis, Deschampsia cespitosa, Geum rossii,* and *Sibbaldia procumbens* (Fig. 5.8c, Table 5.6). Species distinguishing Beartooth Butte included *Castilleja pulchella* and the calcicole *Dryas octopetala* (Fig. 5.8d, Table 5.6).

Environment The environmental variables most strongly correlated with the talus ordination scatter were aspect, solar radiation, and soil carbon content (Fig. 5.7, Table 5.1). Washburn talus soils were much warmer than other regions (TI = 0.54 versus 0.0 to 0.43) and had higher incident radiation totals (0.94 MJ cm^{-2} yr^{-1} versus 0.75 to 0.84 MJ cm^{-2} yr^{-1}) due to their steep (34.1º versus 13 to 30º slopes) southern aspects (139º from north versus 78 to 118º). Beartooth Plateau talus soils were very cold (TI = 0.0) due to their high altitude (3296m compared to 3047 - 3100m) and more northern aspects (Table 5.3, Fig. 5.7). Scree slopes not continually exposed to sun may be particularly cold for plants because roots are forced deeper and radiant soil warming is reduced by rock cover (Körner 2003). These characteristics may explain the poor productivity of Beartooth Plateau talus. With the exception of Beartooth Butte (WI = 0.17) talus soils were predicted to be wet, particularly on the Beartooth Plateau (WI = 0.88; Table 5.3). Talus soils of the granitic Beartooth Plateau were more acidic than other regions (pH = 6.3), while those of the calcareous Beartooth Butte were markedly alkaline (pH = 8.3). The higher productivity of Beartooth Butte talus may be due to the relatively high availability of nutrient bases (e.g. N = 0.2%; Table 5.3).

Table 5.6. Summarized relevé table for five topographic types within four alpine regions (i.e. 20 combination treatments). Only species which occurred with ≥ 30% constancy within at least one of the 20 treatments are included in the table. A two character cipher is included in each cell which indicates constancy (percentage of sites that contain the species), and cover[1]. Asterisked cells indicates that, within a particular topographic type (e.g. talus), the species is significantly associated ($\alpha = 0.05$) with the indicated alpine region (e.g. Washburn) using the modified Murdoch's index (see Figs. 5.8, 5.10, 5.12, 5.14, 5.16). Bolded cells indicate constancy ≥ 30%.

		Talus				Ridgetop				South-face				North-face				Snowbank			
	LF[2]	WA	NA	BP	BB	WA	NA	BP	BB	WA	NA	BP	BB	WA	NA	BP	BB	WA	NA	BP	BB
Claytonia megarhiza	Fo	..	1A	..	**3A***	..	+A	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Dryas octopetala	Cu	..	..	..	**3B***	..	..	..	1A	..	..	..	..	..	..	..	..	..	..	..	..
Draba oligosperma	Fo	..	..	..	**4A***	..	..	..	**3A***	..	..	..	..	..	..	..	..	..	..	..	..
Antennaria microphylla	Fo	**3A***	2A	..	..	..	1A*	..	..	..	+A	..	..	+A	++	..	..	..	+A	..	..
Elymus scribneri	Gr	**8B***	**7B***	..	..	**3A**	**9C***	**3A**	1A	**3A**	**4B***	..	..	..	**6B***	..	..	..	..	..	..
Potentilla nivea	Fo	..	..	..	..	..	..	**3A***	..	..	..	..	..	..	..	..	..	..	..	..	..
Erigeron compositus	Fo	**8A***	**4A**	..	..	**4A**	**8C***	..	**4A**	**4B**	**5B***	..	..	2A	**3A***	..	..	..	..	..	..
Saxifraga oppositifolia	Cu	..	..	..	**4A***	..	..	..	1A	..	..	..	..	..	..	..	..	..	+A	..	..
Calamagrostis purpurascens	Gr	..	..	..	..	..	..	1A	**3B***	..	..	..	..	..	..	..	..	..	..	..	..
Oxytropis lagopus	Fo	..	..	..	..	**9C***	..	..	..	1A	..	..	..	2A*	..	..	..	..	..	..	..
Eritrichium nanum	Cu	..	..	..	..	..	..	**4A***	**9C***	..	..	**3A***	..	..	..	..	..	..	..	..	..
Astragalus kentrophyta	Cu	1A	2A*	..	..	**8C**	**9D***	..	**3A**	**6C**	**8D***	..	..	1A	**4A***	..	..	..	+A	..	..
Senecio canus	Fo	1A	..	..	..	**3A**	1A	..	**4A***	**6C***	**3A**	..	..	++	+A	..	..	..	..	..	..
Eriogonum ovalifolium	Cu	..	..	..	..	**6A***	++	..	..	..	..	..	..	1A*	..	..	..	1A	..	..	..
Smelowskia calycina	Fo	1A	1A	..	**6A***	**9B***	**2A**	**9C***	**9B***	**4B**	**3A**	**8C***	..	2A	1A	**6A***	..	..	1A*	..	..
Lomatium cous	Fo	**6A***	**4A***	..	..	1A	2A*	..	..	**9C***	**4A**	..	..	**5A***	1A	..	..	1A	2A	..	**4A***
Arabis spp.		..	**4A***	..	..	..	2A*	..	..	..	1A*	..	..	..	**4A***	..	**4A***	..	..	..	1A
Polemonium viscosum	Fo	**6A***	2A	..	1A	..	++	..	..	**3C***	++	..	..	**6C***	1A	**3B**	..	1+	..	..	..
Erigeron rydbergii	Fo	..	..	..	..	**9C***	..	..	..	1A	..	..	..	**5B***	..	..	..	..	..	..	..
Poa secunda	Gr	1A	1A	1A	1A	..	**5A***	**4A**	..	..	**3A***	..	1+	..	**4A***	**4B***	..	..	..	..	1A
Phlox pulvinata	Cu	**4A***	..	..	**3A***	**9D***	1A	**9C***	**9D***	**6C***	+A	**8B***	**3A**	**7D***	..	**6A***	**3B**	..	..	..	..
Selaginella densa	Fe	..	..	..	..	**9D***	1A	**6B***	..	**4C**	**3C**	**4A**	..	**6D***	1A	..	..	..	..	..	..
Draba incerta	Fo	1A	..	..	..	1+	2A	**3A**	**3A**	1A	1A	**3A***	..	..	1A	**3A***	1+	..	..	..	..
Carex nardina	Gr	..	..	..	..	..	..	..	**3B***	..	..	..	1A	..	..	..	..	..	..	..	..
Taraxacum ceratophorum	Fo	..	..	..	**3A***	..	..	..	1A	..	+A	..	..	+A	..	..	..	..	+A	..	..
Poa pattersonii	Gr	**6B***	2A	..	**4A**	**8B***	**5B**	..	**9B***	**3C**	**8B***	..	..	1A	**6A***	..	**4A**	1A	**5B***	..	..
Poa rupicola	Gr	..	..	..	..	**9C***	**2A**	**3A**	..	**6C***	2A	1B	..	**9D**	..	..	..	2A*	..	..	..
Senecio fremontii	Fo	..	2A*	..	..	..	1A*	..	..	..	..	..	..	..	**4A***	..	..	..	+A	..	..
Poa arctica	Gr	..	..	..	**3A***	..	..	..	..	..	..	**3A***	..	+A	..	1A	..	..	..	..	..
Trifolium nanum	Cu	..	..	..	..	..	..	**9C***	..	..	..	**8C***	..	..	..	**3B***	..	..	..	..	..

Table 5.6 cont.

	LF^2	Talus				Ridgetop				South-face				North-face				Snowbank			
		WA	NA	BP	BB	WA	NA	BP	BB	WA	NA	BP	BB	WA	NA	BP	BB	WA	NA	BP	BB
Antennaria umbrinella	Fo	1A	1A	..	..	..	2A	..	**6B***	1A	**4C***	..	**3A**	..	+A	..	**3B***	..	2A*	..	..
Carex obtusata	Gr	..	..	..	..	**6C***	..	**9D***	..	1A	..	**4A***	..	**7D***	..	**3A**	..	..	..	..	..
Bupleurum americanum	Fo	..	..	..	..	..	..	**8A***	..	..	..	**8A***	..	..	..	**3A***	..	..	..	..	..
Anemone multifida	Fo	..	..	..	..	..	..	..	**6A**	..	..	..	1+	..	..	..	1A*	..	..	..	..
Sedum lanceolatum	Cu	**6A***	+A	..	1A	**9B***	**8B***	**4A**	**3A**	**9C***	**7B**	**4A**	**3A**	**8B***	**3A**	**4A**	**3A**	**7A***	**4A**	..	..
Sagina saginoides	An	..	..	..	..	..	..	**4A***	**6A***	..	..	**6A***	..	..	..	1+	..	..	1A*	..	..
Oxytropis sericea	Fo	..	..	..	..	..	..	1A	**9C***	..	..	**3A***	**4A***	..	..	1A	**3A***	..	..	..	..
Cerastium arvense	Fo	**8A***	2A	..	**3A**	**8A***	**4A**	**3A**	**3A**	**9D***	**5B**	**6A**	**4A**	**9D***	**5A**	**6B**	**8B**	**9C***	2A	1+	1A
Castilleja pulchella	Fo	..	..	..	**3A***	..	..	**4A***	1A	..	1A	..	**4A***	..	..	..	**3A***	..	1A*	..	..
Arenaria obtusiloba	Cu	**4B***	++	..	**4A***	**9C***	2A	**8B***	**4B**	**9C***	**7B**	**8B**	..	**8C***	**3A**	..	**3A**	**8A***	2A	**9A***	..
Poa cusickii	Gr	1A	..	..	..	**4A***	+A	..	..	**4C***	..	..	1A	**6A***	..	..	..	2A*	..	..	1A
Potentilla ovina	Fo	..	..	..	..	**4B***	..	..	..	**4A***	1A	..	..	**4C***	+A	..	..	1A	++	..	..
Festuca brachyphylla	Gr	1A	1A	**3A**	1+	**8B**	**8C**	**9C***	**8A**	**9B***	**8B**	**8B**	**3A**	**3A**	**9C**	**8C**	..	**8B**	**9C***	**9B***	..
Saxifraga bronchialis	Fo	..	..	..	1+	..	1A*	..	..	..	++	..	..	..	**3B***	..	..	..	..	..	..
Oxytropis borealis	Fo	..	..	..	..	..	..	..	..	**3B***	..	..	..	1B*	..	..	..	..	..	..	..
Claytonia lanceolata	Fo	..	..	..	..	..	..	..	..	1A	..	..	**3A***	..	..	..	..	..	..	..	..
Androsace septentrionalis	An	..	1A*	..	..	..	**7A***	..	..	..	**3A**	..	**3A**	+A	**7A***	..	..	**4A***	**3A**	..	..
Carex elynoides	Gr	..	..	..	..	**3A***	..	..	**4D***	**3A**	1B	**6D***	..	**7D***	..	..	**4B***	..	..	..	..
Achillea millefolium	Fo	**4A***	2A	..	..	..	**4B***	..	1A	**6B***	**4B**	..	**9C***	**3B**	2A	..	**9C***	**8C***	2A	..	**6B***
Phlox multiflora	Fo	..	..	..	..	1A	1A	..	..	**4B***	**3C**	..	..	**3A***	++	..	..	**4A***	..	..	..
Carex scirpoidea	Gr	..	..	..	..	..	..	..	**3C***	..	1A	**3D***	**3C***	..	..	..	..	..	..	..	1B*
Silene acaulis	Cu	..	..	1A	..	..	1A	**8C***	..	..	**4B***	**3A**	..	..	**3A***	**4A***	..	..	**3B***	1A	..
Taraxacum spp.	Fo	..	..	..	..	..	..	..	1+	..	1A	1A	**3A***	..	..	..	..	..	+A	..	..
Trisetum spicatum	Gr	**4A**	2A	1A	**6A***	..	**4B**	**4A**	**3A**	**4B**	**7C**	**8A**	**9A***	**3B**	**6B**	**8A***	**6C**	**3A**	**5A**	**6A**	**9C***
Arenaria congesta	Fo	..	..	..	..	..	1A*	..	..	..	2A	..	**3A***	**3A***	+A	..	..	2A*	+A	..	..
Epilobium clavatum	Fo	..	2A*	..	..	..	..	..	..	..	..	..	..	..	++	..	..	..	1A	..	**4A***
Senecio fuscatus	Fo	..	..	..	..	..	..	**3A***	..	..	..	**6A***	..	..	..	**6A***	..	..	..	..	..
Geum triflorum	Fo	..	..	..	..	..	..	..	..	..	..	..	**3D***	..	..	..	..	..	..	..	..
Valeriana edulis	Fo	..	..	..	..	..	..	..	..	..	..	..	**6D***	..	..	..	..	..	..	..	..
All mosses	Mo	..	1A	**4A***	**4A***	**8B***	**3A**	**6B**	**9D***	1A	**3C**	**8C***	**3A**	**8D***	**6B**	**9D***	**3C**	**6C**	**9D***	**9C**	**6D**
Geum rossii	Fo	..	..	**3A***	..	..	..	**9D***	..	..	..	**9D***	..	..	1A	**9D***	..	..	+A	**6C***	..
Myosotis alpestris	Fo	1A	..	..	..	..	..	..	**3A***	1A	++	1A	..	2B*	..	..	**3A***	1A	1A*	..	..
Mertensia alpina	Fo	..	..	..	1A	1A	1A	**8A***	**3A**	1C	**5B**	**8A***	**3A**	**5B**	**4A**	**6A**	**9A***	**3A**	**3B**	1+	1+
Erigeron simplex	Fo	..	+A	1+*	..	..	2A	**8A***	**6B***	..	**6B***	**8A***	..	..	**6B***	1A	3C	**9B***	**8C***	**3A**	..
Draba cana	Fo	1A	..	..	..	..	..	..	..	..	..	..	**3A***	..	..	..	**6A***	..	..	..	..
Carex rupestris	Gr	..	..	..	..	..	..	..	1A	..	..	..	**3B***	..	..	..	**3B***	..	..	..	..
Besseya wyomingensis	Fo	1A	..	..	..	..	..	..	**3A***	1A	++	..	**9B***	**7B***	1A	..	**9B***	2A*	..	..	..
Astragalus alpinus	Fo	..	..	..	..	..	1A*	..	..	**3A**	1A	..	**6B***	**9C***	1A	..	**4A**	**3A***	1A	..	..

Table 5.6 cont.

	LF^2	Talus				Ridgetop				South-face				North-face				Snowbank			
		WA	NA	BP	BB	WA	NA	BP	BB	WA	NA	BP	BB	WA	NA	BP	BB	WA	NA	BP	BB
Carex phaeocephala	Gr	..	1A*	..	..	..	1B*	..	..	..	**3C***	..	..	+A	1A	..	**4B***	**8B***	1A	..	**3A**
Luzula spicata	Gr	1A*	+A	..	..	..	1A	**4A***	..	**4B**	**6B**	**9A***	..	**8C***	**5A**	**8A**	**3A**	**9B***	**5B**	**4A**	1A
Potentilla diversifolia	Fo	..	..	..	**3A***	**3A**	++	**6B***	**8A***	**3C**	**3A**	**9B***	**6B**	**9D***	++	**8A**	**9B***	**9D***	**4B**	**6C**	**9C***
Carex albonigra	Gr	..	..	..	..	..	++	..	..	..	1B	**4B***	..	..	..	**3B***	..	..	1D*	..	1A
Saxifraga rhomboidea	Fo	..	..	..	..	..	..	..	..	1A	1A	..	..	**4A***	..	..	..	**3A***	..	..	..
Lupinus argenteus	Fo	..	+A	..	..	**4A***	..	..	..	1A	1A	..	**9D***	**5C***	..	..	**6C***	**8C***	+A	..	**3D**
Festuca idahoensis	Gr	..	..	..	..	..	..	..	..	..	..	..	**6D***	..	..	..	**3A***	..	..	..	..
Linum lewisii	Fo	..	..	..	..	..	..	..	1A	..	..	..	..	..	..	..	**3A***	..	..	..	..
Gentiana algida	Fo	..	..	..	..	..	..	..	..	..	..	**6A***	..	..	..	**4A***	..	..	..	1A	..
Aster foliaceus	Fo	..	1A*	..	..	..	1A*	..	..	..	1A	1A	**6C***	..	**3A**	..	**6D***	**4C***	..	..	**8D***
Poa alpina	Gr	1A*	+A	..	..	..	1A	..	1+	1A	**3B***	..	1A	**3A**	**7B***	1A	**6B**	**4A**	**5B**	1A	**6C**
Solidago multiradiata	Fo	..	..	..	..	..	..	..	1A	..	..	..	**9D***	..	..	..	**8D***	..	..	..	1A
Draba crassifolia	An	..	1A*	..	..	..	++	..	..	..	..	..	**3A***	..	1A*	..	..	**4A***	1A	**3A***	1+
Epilobium anagallidifolium	Fo	..	1A*	..	..	..	..	..	..	..	..	..	..	..	1A*	..	..	**4A***	2A	..	..
Polygonum bistortoides	Fo	..	..	1A	..	1A	..	**6A***	1A	1A	1A	**9B***	**9A***	2A	++	**8A***	**8A***	**9C***	..	**8A***	**9B***
Artemisia scopulorum	Fo	..	++	..	..	..	..	**8B***	..	..	1A	**6C***	..	+A	1A	**9C***	..	**6C**	**5C**	**8B***	..
Ranunculus eschscholtzii	Fo	1A*	+A	..	..	..	++	..	..	..	+A	1+	**6A***	..	2A*	..	**3A***	2A	**4A**	..	**6B***
Deschampsia cespitosa	Gr	..	..	**3A***	..	..	..	1A	..	..	1A	**6D***	**6C***	..	1A	**9C***	**3C**	..	**4D**	**6D***	**8D***
Aster alpigenus	Fo	..	..	..	..	..	..	..	..	..	2A	..	**3A***	..	+A	..	..	**4A***	**3A**	..	..
Agoseris glauca	Fo	..	..	..	..	..	..	..	..	**3A**	1A	..	**9C***	..	..	..	**6C***	**7B***	**2A**	..	**4D**
Penstemon procerus	Fo	..	..	..	..	..	..	..	..	..	1A	1A	..	2A*	..	..	**3A***	**7A***	+A	..	..
Carex misandra	Gr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	**3C***	..	..	..	..	..
Carex nova	Gr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	**3C***	..	..	..	..	..
Lloydia serotina	Fo	..	+A	..	..	..	..	..	..	..	..	..	..	..	1A*	..	..	..	**4C**	..	..
Sibbaldia procumbens	Fo	..	..	**3A***	..	..	+A	..	..	..	2B*	..	..	..	..	..	..	**6C**	**7D***	**8D***	..
Erigeron ursinus	Fo	..	..	..	..	..	..	..	..	..	..	..	**6A***	..	..	..	..	..	+A	..	**3A***
Poa reflexa	Gr	..	+A	..	..	..	..	..	..	..	..	1A	..	..	..	1+	..	2A	**4A***	..	..
Carex atrata	Gr	..	..	..	1+	..	..	..	..	..	..	..	1A	..	..	..	**3A***	..	+B	..	**3D***
Salix reticulata	Sh	..	..	..	..	..	..	..	..	..	+A	..	..	..	..	**6D***	..	2A*	+A	..	..
Elymus trachycaulus	Gr	..	..	..	..	..	..	..	1A	..	..	..	**9D***	..	..	..	**8D***	..	..	..	**8D***
Stellaria monantha	Fo	..	..	..	..	..	++	1+*	..	1A	1A	**3A**	**3A**	+A	1A	**8A***	**6A**	**8A***	**7A**	**3B**	**3A**
Poa interior	Gr	..	..	..	..	..	..	..	..	..	+A	1A*	..	1A*	..	..	**3A***	..	..	..	**4B***
Trifolium parryi	Fo	..	..	..	..	..	..	**3A***	..	..	..	**3A***	..	..	..	**8B***	**4A***	..	..	**4A***	**6C***
Carex paysonis	Gr	..	+A	1A*	..	1A	..	..	..	1A*	+A	..	..	+A	+A	1A	..	**9E***	**7D**	**9E***	..
Pedicularis oederi	Fo	..	..	..	..	..	..	..	..	..	..	..	..	..	..	**6A***	..	..	..	1A	..
Polygonum viviparum	Fo	..	..	..	..	..	..	..	1A	..	..	..	..	..	..	**6C***	..	..	1A	..	**3A***

Table 5.6 cont.

		Talus				Ridgetop				South-face				North-face				Snowbank			
	LF[2]	WA	NA	BP	BB	WA	NA	BP	BB	WA	NA	BP	BB	WA	NA	BP	BB	WA	NA	BP	BB
Bromus inermis	Gr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	**3B***	..	..	..	..
Zigadenus elegans	Fo	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	**3A***	..	..	..	..
Carex haydeniana	Gr	..	+A	..	..	..	..	..	..	..	..	..	..	..	**3A***	..	..	..	**4C***	..	**6C***
Antennaria media	Fo	..	..	..	..	..	+A	..	..	..	1A*	..	..	..	**3A***	..	..	**4A**	**6C**	**8B***	..
Dodecatheon pulchellum	Fo	..	..	..	..	..	..	..	..	..	..	..	**8A***	..	..	..	1A*	1A	+A	..	**8A***
Antennaria lanata	Fo	..	..	..	1A	..	..	..	..	..	..	..	..	..	..	..	..	..	+A	**6A***	..
Juncus drummondii	Gr	..	..	..	..	..	..	..	..	..	+A	..	..	..	..	**3A***	..	1A	2A	**3B***	..
Pedicularis cystopteridifolia	Fo	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	**3A***	..	..	..
Salix arctica	Sh	..	..	..	..	..	..	..	..	..	..	..	..	..	1C	**3B***	..	**3A**	**5C***	**4D**	1+
Agrostis variabilis	Gr	..	..	..	..	..	..	..	..	..	+A	..	..	..	..	..	..	..	**6C***	1A	..
Veronica wormskjoldii	Fo	..	..	..	..	..	..	..	..	..	..	..	..	..	+A	..	..	**3A**	**4B***	..	1A
Sedum integrifolium	Fo	..	..	..	..	..	..	..	..	..	..	..	..	..	..	**3A***	..	..	1A	..	**3B***
Lewisia pygmaea	Fo	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	**4A***	2A	1A	..
Phleum alpinum	Gr	..	..	..	..	..	..	..	..	..	..	..	**3A***	..	..	..	**3A***	..	1A	..	**9C***
Caltha leptosepala	Fo	..	..	..	..	..	..	..	..	..	..	..	..	..	..	**6C***	..	..	..	**6A***	**6E***
Carex pyrenaica	Gr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2B	**8C***	..
Taraxacum officinale	Fo	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1A*	..	..	..	**6C***
Senecio crassulus	Fo	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	**4C***
Trollius laxus	Fo	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	**3A***

[1] For each cell in the body of the table, constancy is indicated by the first symbol, while cover is indicated by the second symbol. For constancy: 0% = “.”, 0-10% = +, 10-20% = 1, 20-30% = 2, 30-40% = 3, 40-50% = 4, 50-60% = 5, 60-70% = 6, 70-80% = 7, 80-90% 8, 90-100% = 9.
For cover: 0% = “.”, 0-0.01% = +, 0.01-1% = A, 1-2% = B, 2-5% = C, 5-25% = D, >25% = E.

[2] LF = Life form: An = Annual, Cu = Cushion plant, Fe = Fern Ally, Fo =Upright forb, Gr = Graminoid, Mo = Moss, Sh = Shrub.

Table 5.6 was sorted with the function “SORTID” (Appendix A.1).

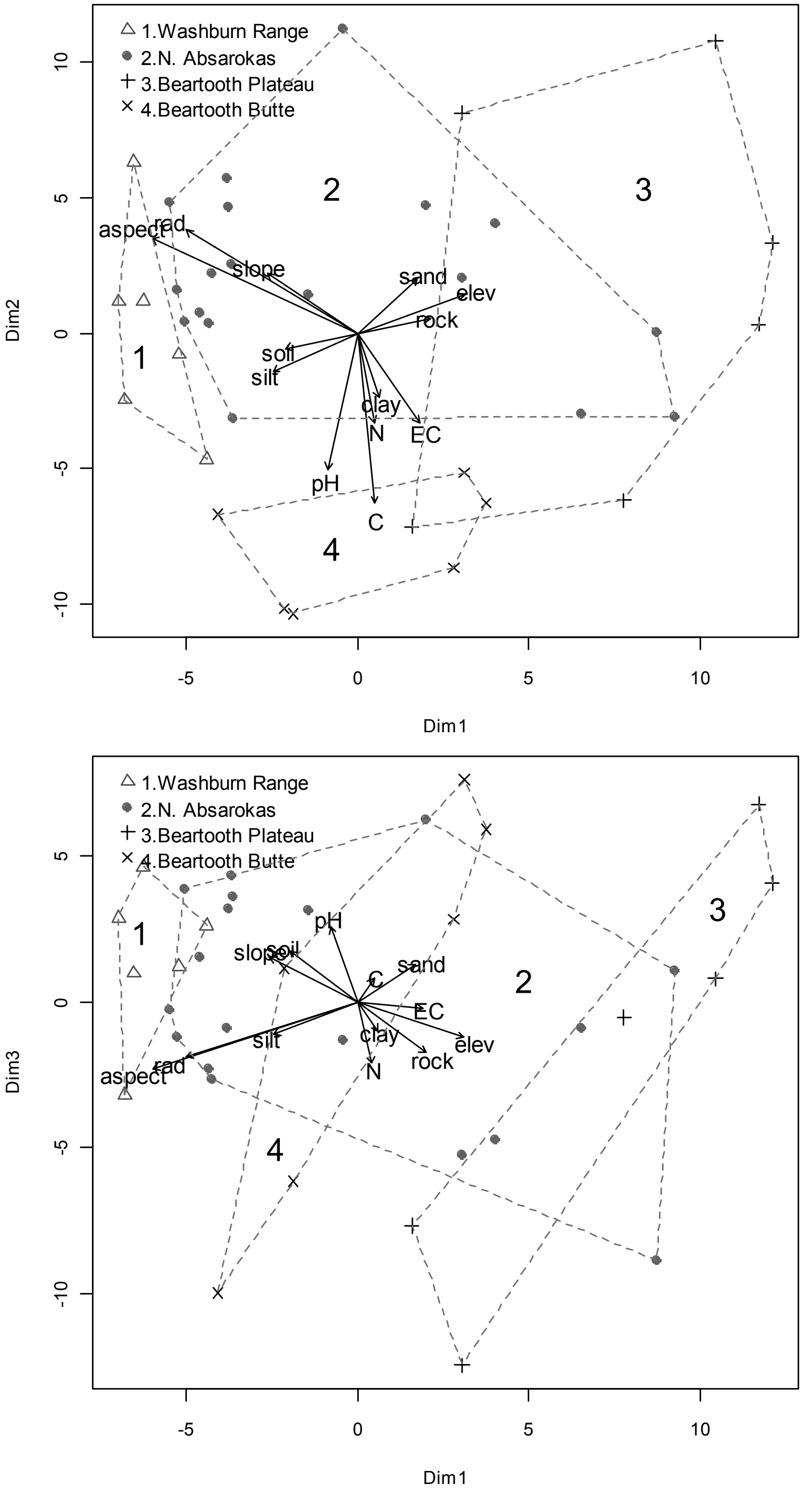


Figure 5.7. Three dimensional NMDS solution for talus plots, stress = 16.0. Environmental vectors are overlaid, and the four alpine regions are indicated by symbols and dashed lines. For exact relationship of vectors to configurations see Table 5.1. For explanation of vector annotations see Fig. 5.3.

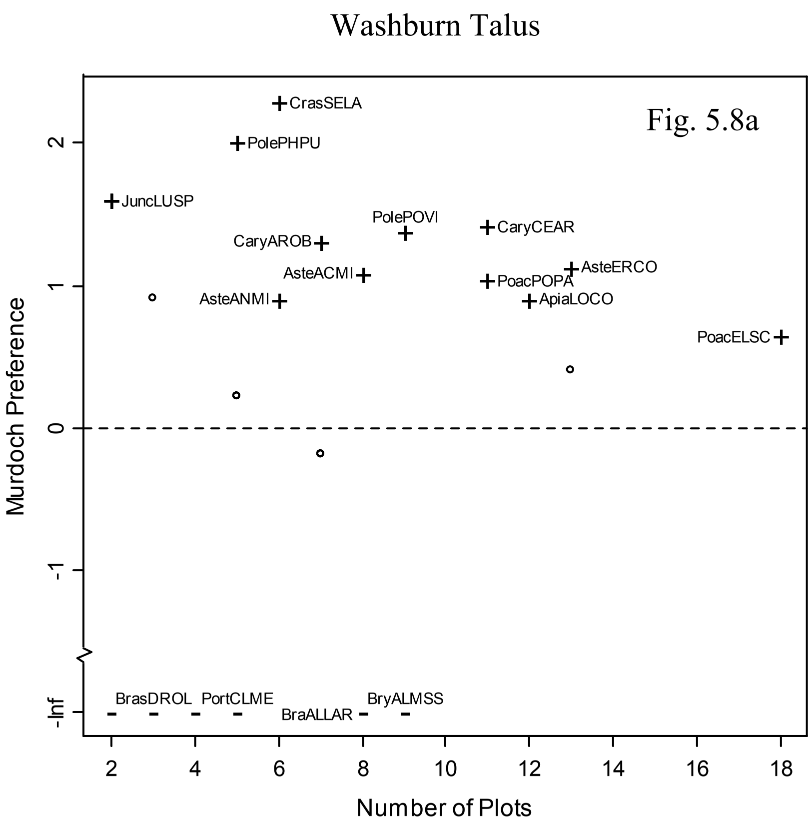

Washburn Talus

Fig. 5.8a

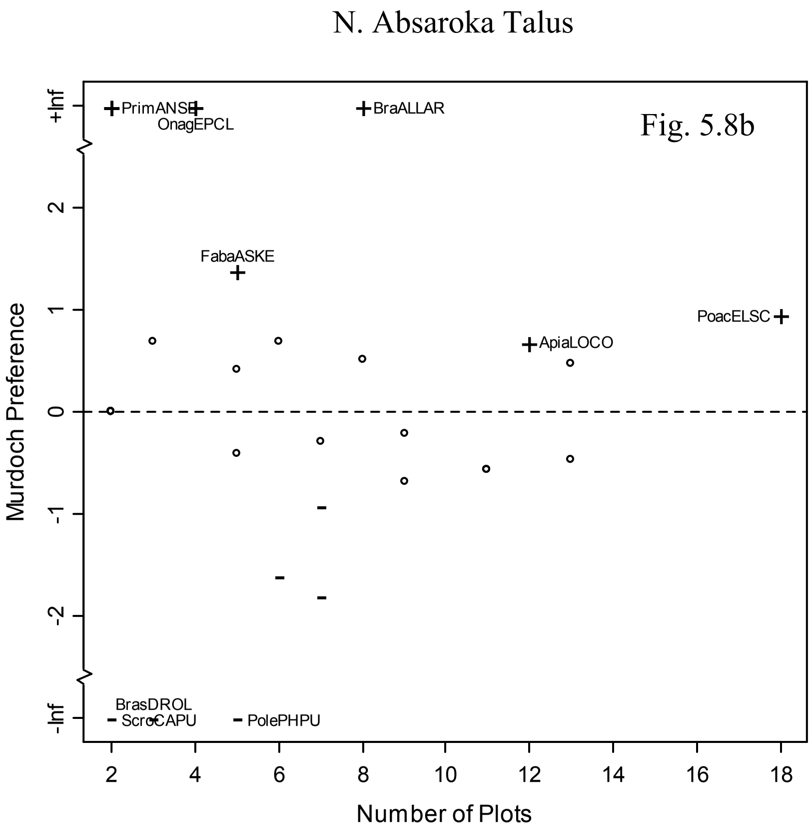

N. Absaroka Talus

Fig. 5.8b

For figure description see next page

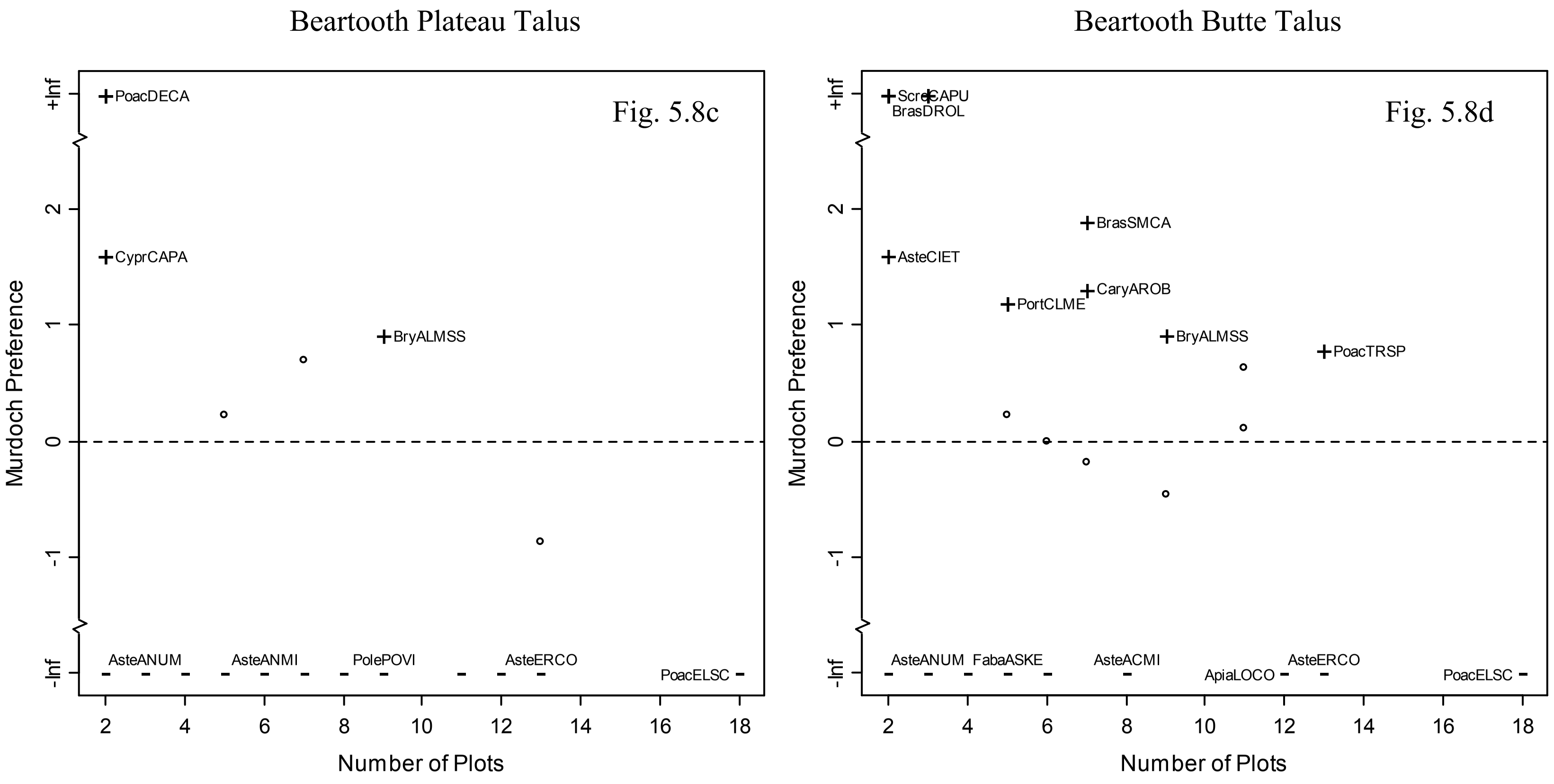


Figure 5.8. Murdoch analysis results for talus sites across alpine regions: (a) Washburn Range, (b) N. Absarokas, (c) Beartooth Plateau, (d) Beartooth Butte. Forty-five species (those which occurred in at least 5% of the 36 talus plots sampled in the 4 alpine regions) were analyzed. Significant positive and negative species are identified where space on the graph allows, "+" indicates a positively significant Murdoch species, "-" indicates a negatively significant Murdoch species, "0" indicates neither significantly positive nor negative. Due to overlaying species not all species can be identified in graphs. For species codes see Appendix D.1. For complete summary of Murdoch analysis for talus areas see Appendix D.2, Table D.2.3.

Ridgetop Variation Across Regions

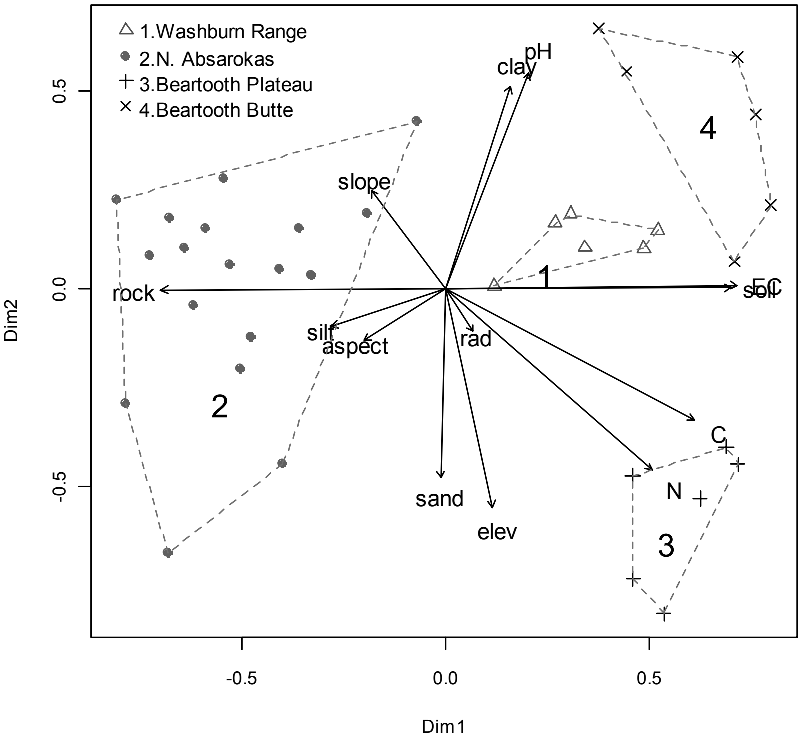
Vegetation Ridgetop vegetation cover and richness were much lower in the rocky N. Absarokas (29% cover, 13.7 spp. plot^{-1}) than ridges from other regions (50-59% cover, 18-20.5 spp. plot^{-1}; Table 5.2). Ridgetop productivity (indexed by soil organic matter) paralleled cover and richness increasing from the N. Absarokas (C = 1.0%, N = 0.1%) to the Washburn Range (4.6%, 0.4%), to Beartooth Butte (7.9%, 0.4%), to the Beartooth Plateau (11.0%, 0.9%).

Indicators of ridgetops across all regions included the upright grasses *Elymus scribneri* (often present in talus) and *Poa pattersonii*, and a large number of cushion plant species: e.g. *Eritrichium nanum, Trifolium nanum, Astragalus kentrophyta, Phlox pulvinata,* and *Sedum lanceolatum* (Table 5.1, Fig. 5.4b).

Ridgetops from the four regions were very different from each other as demonstrated by well defined regional clusters in ordination space ($r^2 = 0.83$, $p < 0.001$; Table 5.1, Fig. 5.9). Species which distinguished Washburn ridges from ridges in other areas included *Poa rupicola, Erigeron rydbergii, Eriogonum ovalifolium, Lupinus argenteus,* and *Oxytropis lagopus* (Fig. 5.10a, Table 5.6). Species distinguishing N. Absaroka ridges included *Elymus scribneri*, *Androsace septentrionalis*, *Astragalus kentrophyta* and *Erigeron compositus* (Fig. 5.10b, Table 5.6) Species distinguishing the Beartooth Plateau included *Artemisia scopulorum Bupleurum americanum Geum rossii*, *Silene acaulis* and *Trifolium nanum* (Fig. 5.10c, Table 5.6). Species distinguishing Beartooth Butte included *Oxytropis sericea, Potentilla diversifolia,* and the calcicole *Eritrichium nanum* (Fig. 5.10d, Table 5.6).

Environment Washburn ridges were predicted to be much warmer than other regions (TI = 0.61 versus 0.33-0.48) and drier (WI = 0.16 versus 0.33-0.36) due to lower altitudes and unimpeded southwestern winds (Ch 3). These characteristics explain the lack of desiccation-prone species on Washburn ridges. In contrast, hydric species like *Artemisia scopulorum* (cf. Komárková 1978) and *Erigeron simplex* (Ch. 2) were frequently recorded on ridgetops in the Beartooths.

The environmental variables most strongly associated with ordination scatter on ridgetops were rockiness, soil development (e.g. %N) and conductivity ($r^2 = 0.60$, $r^2 = 0.59$, $r^2 = 0.63$, respectively, $p < 0.001$; Table 5.1, Fig. 5.9). The sparse vegetation of N. Absaroka ridges was no doubt associated with its rocky (rock cover = 24% versus 46-68% in other regions, Table 5.3), poorly developed soils (0.1 %N versus 0.4-0.9 %N in other regions). In contrast, the relatively high productivity of Beartooth Plateau ridges was facilitated by gradual slopes (2.3° versus 9.5° to 12.3° in other regions) which allowed uninterrupted sunlight (90 MJ cm^{-2} yr^{-1} versus 85-89 90 MJ cm^{-2} yr^{-1}) and soil accumulation (68% soil cover versus 24-68% in other regions). As in most other topographic types Beartooth Butte ridge soils had much higher clay content (24%) and pH (8.2) compared to other regions (clay content = 3-6%; pH = 6.7-6.9) due to the weathering of lime substrates (Table 5.3, Fig. 5.9).



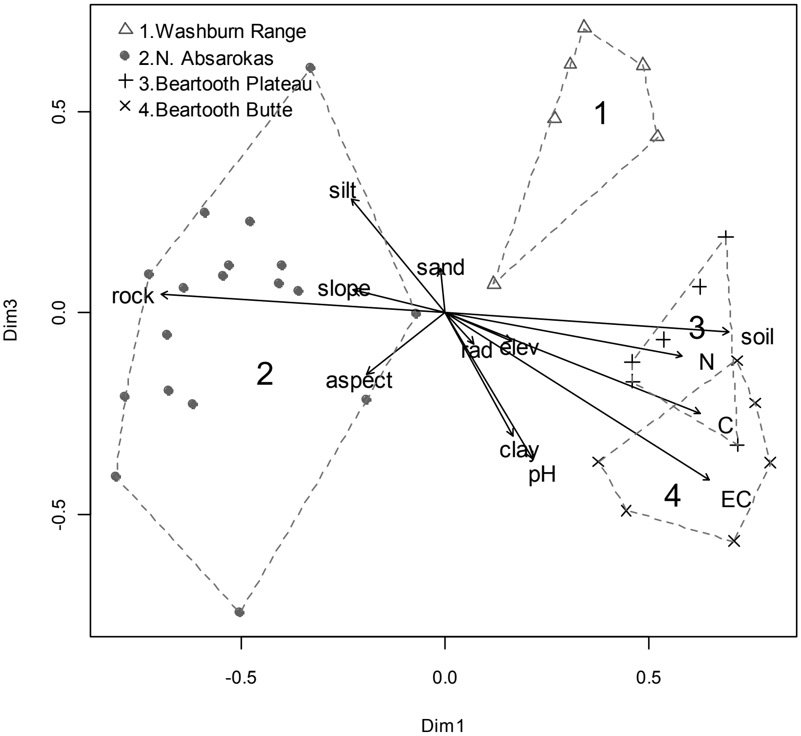
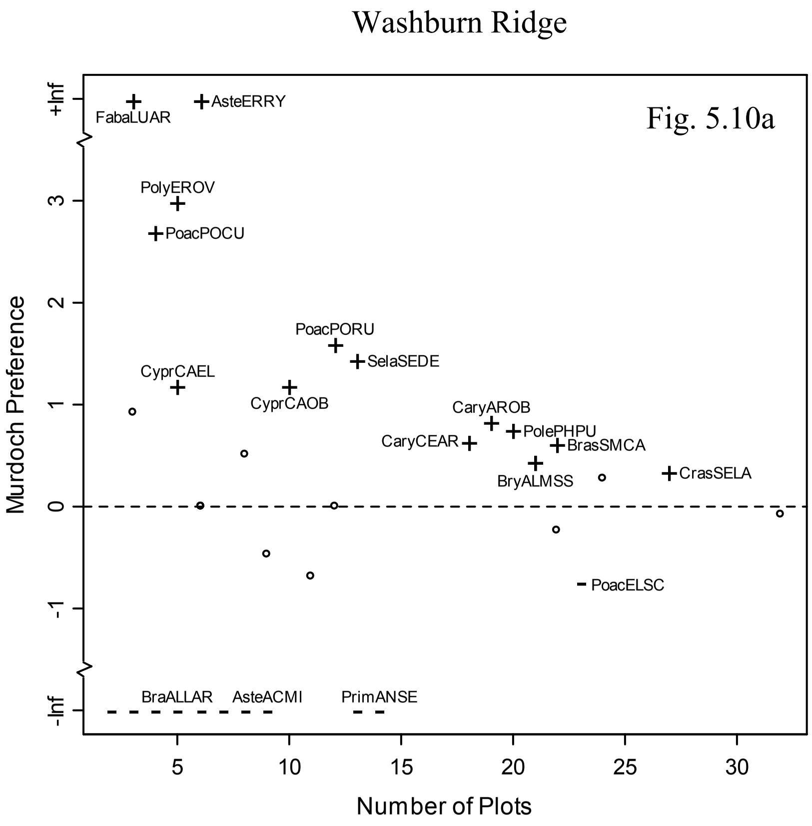
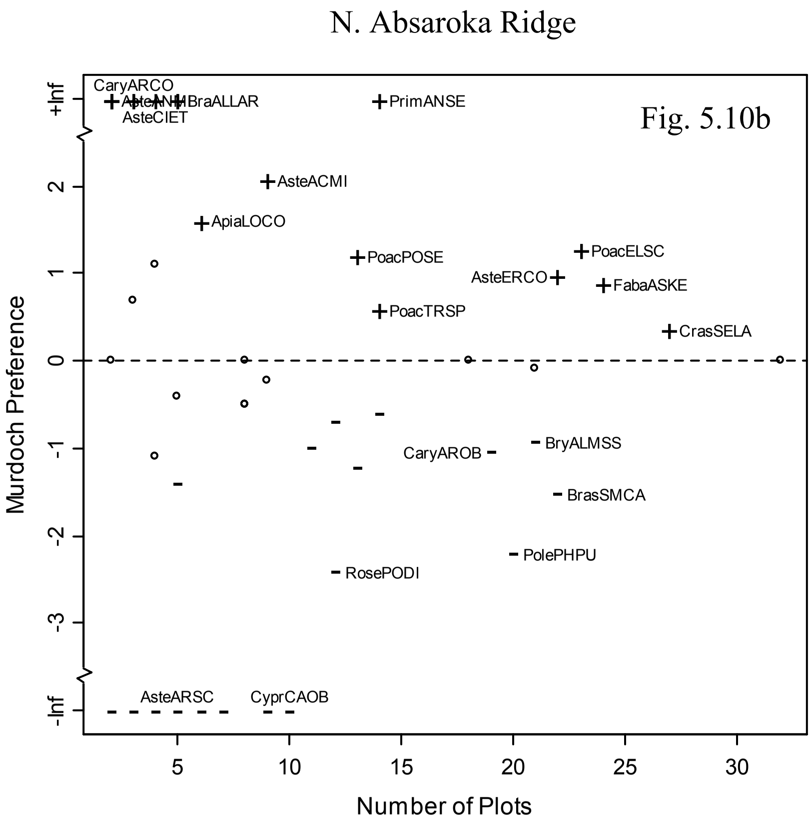


Figure 5.9. Three dimensional NMDS solution for ridge plots, stress = 11.05. Environmental vectors are overlaid, and the four alpine areas are separated by symbols and dashed lines. For exact relationship of vectors to configurations see Table 5.1. For explanation of vector annotations see Fig. 5.3.





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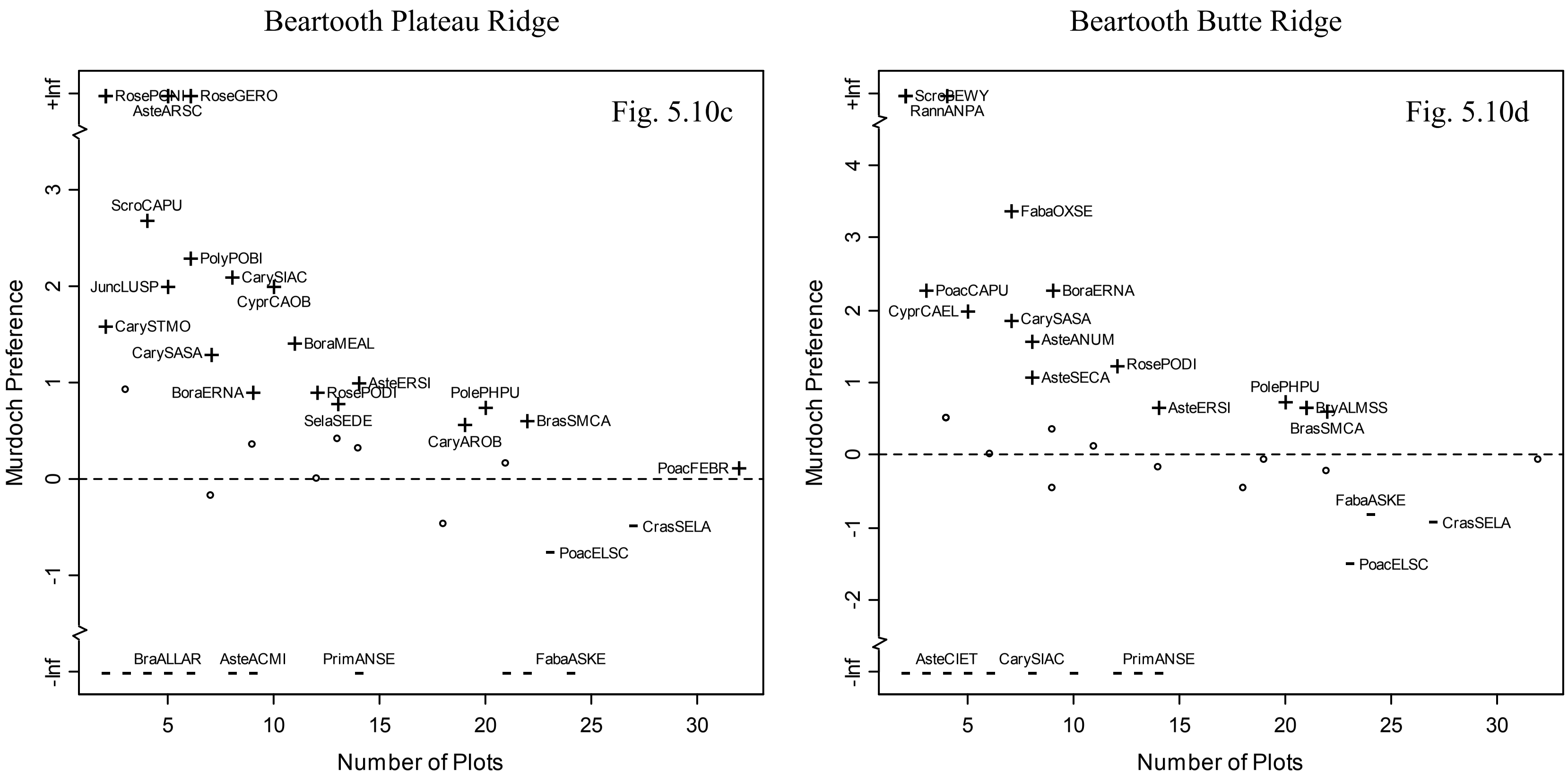

Figure 5.10. Murdoch analysis results for ridgetop sites across alpine regions: (a) Washburn Range, (b) N. Absarokas, (c) Beartooth Plateau, (d) Beartooth Butte. Sixty-seven species (those which occurred in at least 5% of the 36 ridge plots sampled in the 4 alpine regions) were analyzed. Significant positive and negative species are identified where space on the graph allows, "+" indicates a positively significant Murdoch species, "-" indicates a negatively significant Murdoch species, "0" indicates neither significantly positive nor negative. Due to overlaying species not all species can be identified in graphs. For species codes see Appendix D.1. For complete summary of Murdoch analysis for ridge areas see Appendix D.2.4.

South Slope Variation Across Regions

Vegetation Highest south-facing cover and richness occurred on the Beartooth Plateau (71.8% cover, 23.3 spp. plot^{-1}) and Beartooth Butte (81.8% cover, 23.2 spp. plot^{-1}). These responses were lower on the Washburn Range (61.6% cover, 17.8 spp. plot^{-1}) and the N. Absarokas (55.1% cover, 18.7 spp. plot^{-1}). South slope productivity (indexed by soil organic matter) paralleled cover and richness increasing from the N. Absarokas (C = 2.4%, N = 0.2%) to the Washburn Range (4.9%, 0.4%), to Beartooth Butte (8.7%, 0.8%), to the Beartooth Plateau (12.4%, 1.0%).

Ubiquitous indicators of south facing slopes across all alpine regions included *Antennaria umbrinella, Phlox multiflora, Senecio canus,* and *Solidago multiradiata* (Table 5.1, Fig. 5.4c). While not as well clustered as ridgetops, south facing sites within the four alpine areas were significantly different from each other in NMDS ordination space ($r^2 = 0.56$; $p < 0.001$, Table 5.1, Fig. 5.11). Species which distinguished Washburn south slopes from those in other areas included *Oxytropis borealis, Poa cusickii,* and *Polemonium viscosum* (Fig. 5.12a, Table 5.6). Species distinguishing N. Absaroka south faces included *Arabis* spp., *Cirsium eatonii*, and *Phacelia hastata* (Fig. 5.12b, Table 5.6). Species distinguishing the Beartooth Plateau included *Bupleurum americanum, Geum rossi Senecio fuscatus* and *Trifolium nanum* (Fig. 5.12c, Table 5.6). Species distinguishing the Beartooth Butte included *Dodecatheon pulchellum, Draba cana,* and *Elymus trachycaulus* along with calcicoles *Carex rupicola* and *Eritrichium nanum* (Fig. 5.12d, Table 5.6).

Environment The environmental variables most strongly associated with vegetation composition on south slopes were soil carbon and pH (Fig. 5.11, Table 5.1). Soil carbon increased from the N. Absarokas (2.4%), to the Washburn Range (4.9%), to Beartooth Butte (8.7%), to the Beartooth Plateau (12.4%). As in other topographic types high soil pH distinguished the calcareous Beartooth Butte (7.6) from other regions (6.2-6.8). Beartooth Butte south slope soils were also predicted to be much wetter than other regions (WI = 0.64, versus 0.25 to 0.56). The Beartooth Plateau and Beartooth Butte had gradual southern slopes (11.3 and 12.7° respectively) with relatively high levels of soil accumulation (soil cover = 82 and 97% respectively) compared to the steep, rocky Northern Absarokas (slope = 23.4°, rock cover = 51%) and Washburn Range (slope = 20.3°, rock cover = 44%; Fig. 5.11). These characteristics help explain the much higher vegetation cover and richness of Beartooth southern slopes compared to Washburn and the N. Absarokas.

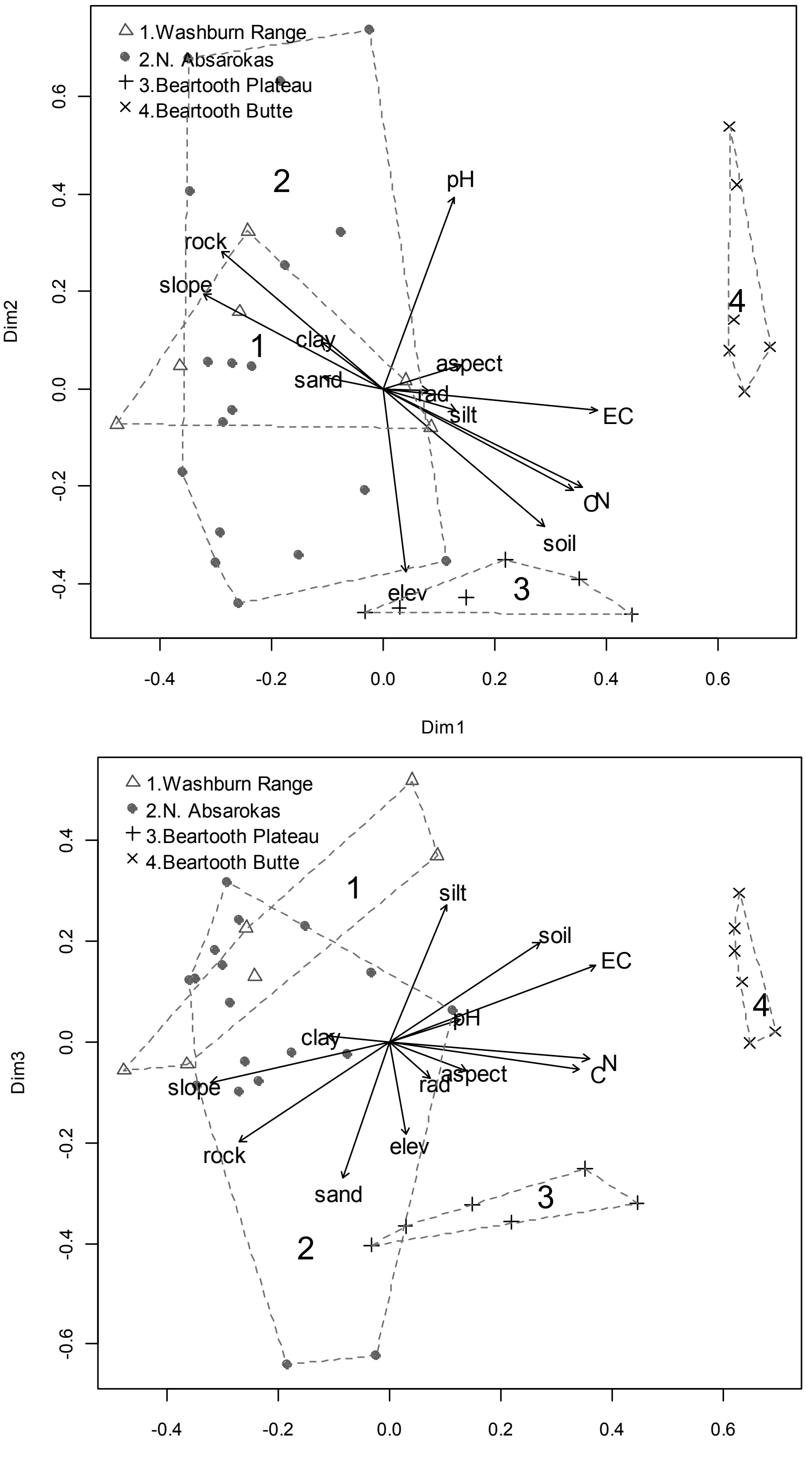

Figure 5.11. Three dimensional NMDS solution for south-facing plots, stress =13.35. Environmental vectors are overlaid, and the four alpine areas are separated by symbols and dashed lines. For exact relationship of vectors to configurations see Table 5.1. For explanation of vector annotations see Fig. 5.3.

Washburn S. Face

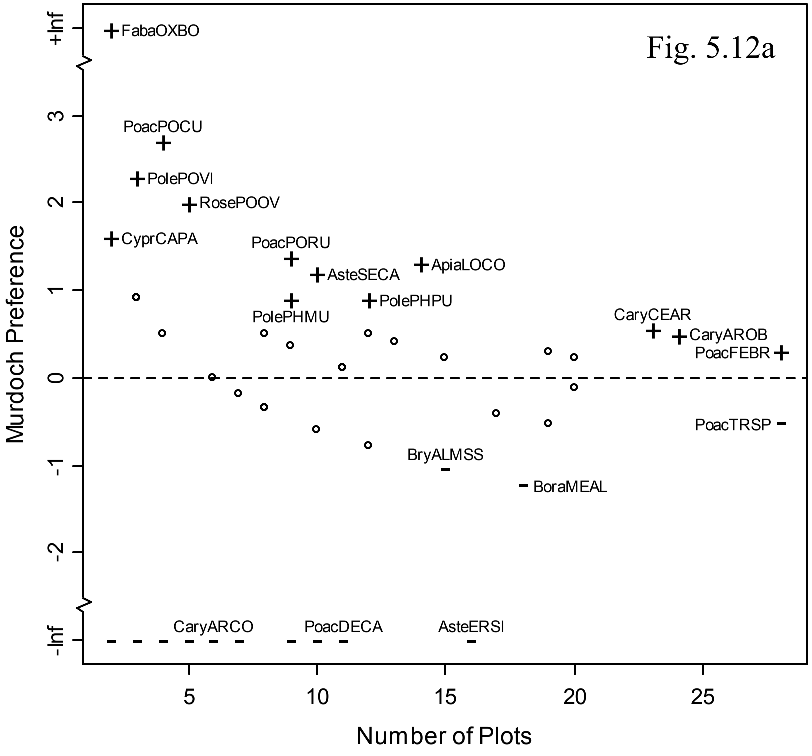
Fig. 5.12a

N. Absaroka S. Face

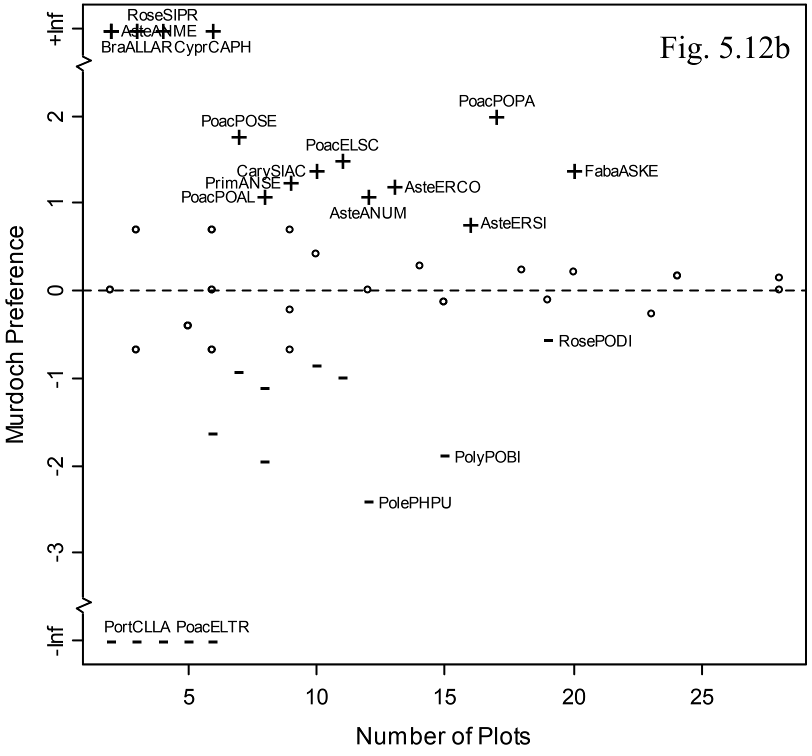
Fig. 5.12b

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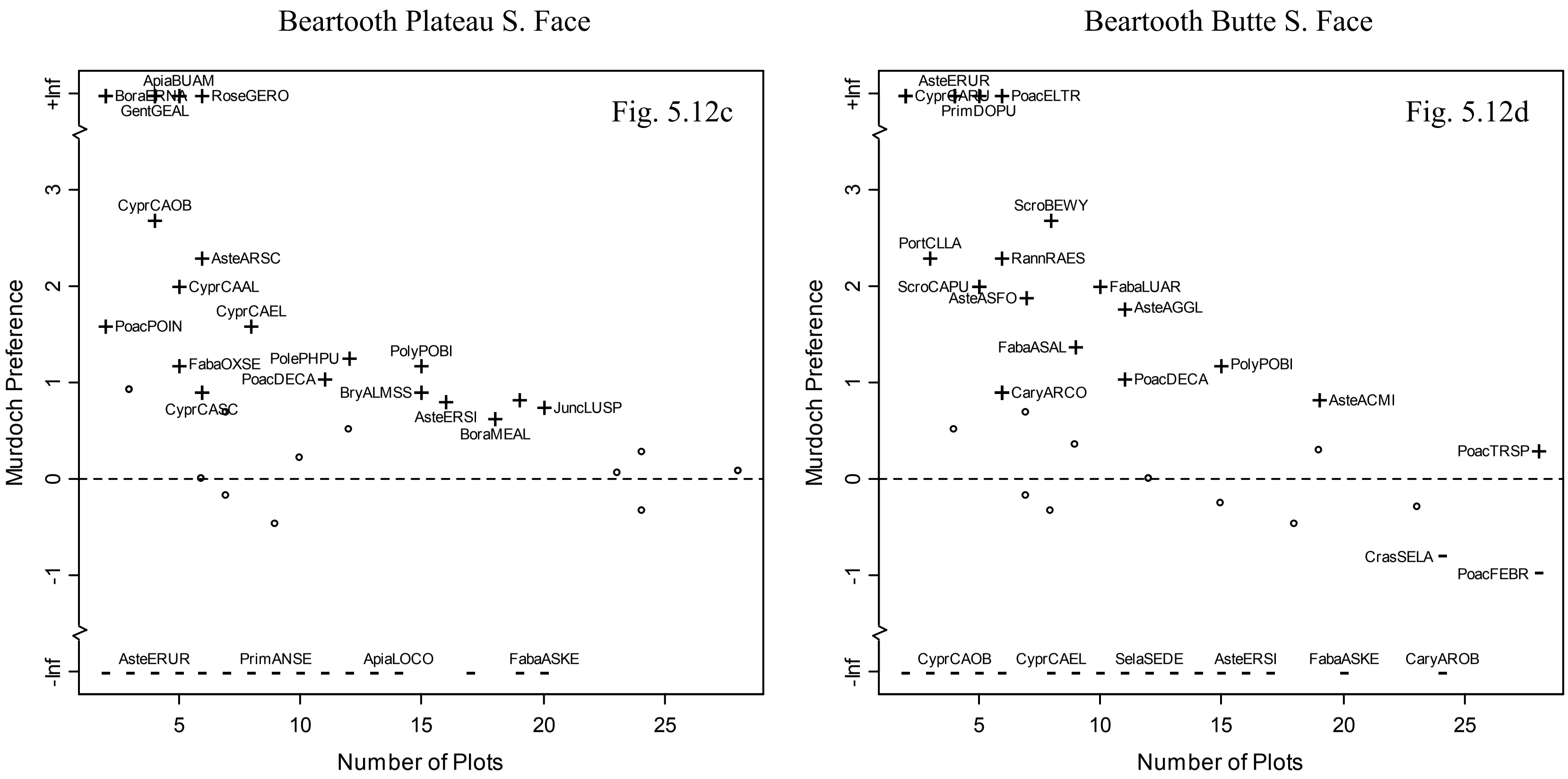

Figure 5.12. Murdoch analysis results for south-facing sites across alpine regions: (a) Washburn Range, (b) N. Absarokas, (c) Beartooth Plateau, (d) Beartooth Butte. Eighty-five species which occurred in at least 5% of the 36 south-facing plots across in the 4 alpine regions were analyzed. Significant positive and negative species are identified where space on the graph allows, “+” indicates a positively significant Murdoch species, “-“ indicates a negatively significant Murdoch species, “0” indicates neither significantly positive nor negative. Due to overlaying species not all species can be identified in graphs. For species codes see Appendix D.1 for complete summary of Murdoch analysis for south facing areas see Appendix D.2, Table D.2.5.

North Slope Variation Across Regions

Vegetation North slope cover and richness were relatively low in the Northern Absarokas 27.1% cover, 16.1 spp. plot^{-1}) compared to other regions (63-98% cover, 22-23 spp. plot^{-1}). Productivity (indexed by soil organic matter) increased from the N. Absarokas (C = 2.4%, N = 0.2%) to Beartooth Butte (8.7%, 0.8%), to the Beartooth Plateau (12.4%, 1.0%) to the Washburn Range (4.9%, 0.4%).

Ubiquitous north slope indicators across all regions included *Astragalus alpinus, Besseya wyomingensis, Poa alpina, Saxifraga bronchialis,* and mosses (Table 5.4, Fig. 5.4d). Clusters distinguishing the four regions explained 77% of the variance in ordination dimensions 1 and 2, indicating that species composition of north slopes was very different across the four regions (Fig. 5.13, Table 5.1). Species distinguishing north slopes of the Washburn Range included *Eriogonum ovalifolium, Carex elynoides, Carex obtusata*, and *Erigeron rydbergii* (Fig. 5.14a, Table 5.6). Species distinguishing the N. Absarokas included *Elymus scribneri, Saxifraga bronchialis, Senecio fremontii,* and *Androsace septentrionalis* (Fig. 5.14b, Table 5.6). On the Beartooth Plateau distinguishing species included *Caltha leptosepala, Bupleurum americanum, Geum rossii*, and *Trifolium parryi* (Fig. 5.14c, Table 5.6). Species distinguishing Beartooth Butte north faces included *Bromus inermis* var. *purpurescens*, *Elymus trachycaulus, Agoseris glauca* and *Solidago multiradiata* (Fig. 5.14d, Table 5.6).

Environment Major separation among alpine regions in north slope ordination space were well explained by variation in environmental factors (Fig. 5.13). Environmental variables strongly associated with vegetation community differences included soil accumulation, soil C and N, elevation, slope, solar radiation, and aspect (r^2 = 0.68-0.78, $p < 0.001$; Fig. 5.13, Table 5.1).

North-facing slopes in all four regions were predicted to be cold, particularly on the high altitude Beartooth Plateau (TI = 0.11 versus 0.23-0.25 in other regions; Table 5.3). North slope soils on Washburn were dehydrated by both climatic conditions (Fig. 5.2) and plant competition for water within areas of dense turf (WI = 0.21 Chapters 2, 3; versus WI = 0.63-0.83 in other regions). As a result Washburn north faces were distinguished by a number xeric species including *Carex elynoides*, *Carex obtusata*, and *Selaginella densa* (cf. Komárková 1978).

Glaciers have sculpted steep valleys below the Beartooth Plateau and Beartooth Butte, but have left the plateau itself relatively flat or rolling (slope = 11° and 19° respectively). Washburn also lacks extremely steep north slopes in its alpine regions (21°). As a result Beartooth Plateau, Beartooth Butte, and Washburn north faces had relatively high levels of soil accumulation (94, 99 and 85% soil cover respectively) and soil development (0.9, 0.5 and 0.6% N respectively). In contrast, north slopes in the N. Absarokas were heavily sculpted by glacial activity most recently during the Pinedale epoch 25,000 BP (Keefer 1976); resulting in rocky (75% rock cover), steep faces (29°) with resultant low levels of incident radiation (0.56 MJ cm^{-2} yr^{-1} versus 0.72-78 MJ cm^{-2} yr^{-1} in other regions). These characteristics explain the low cover and richness of N. Absaroka north faces, and the frequent occurrence of species which prefer steep rocky conditions including *Elymus scribneri, Saxifraga bronchialis,* and *Androsace septentrionalis* (cf. Dorn 1992).

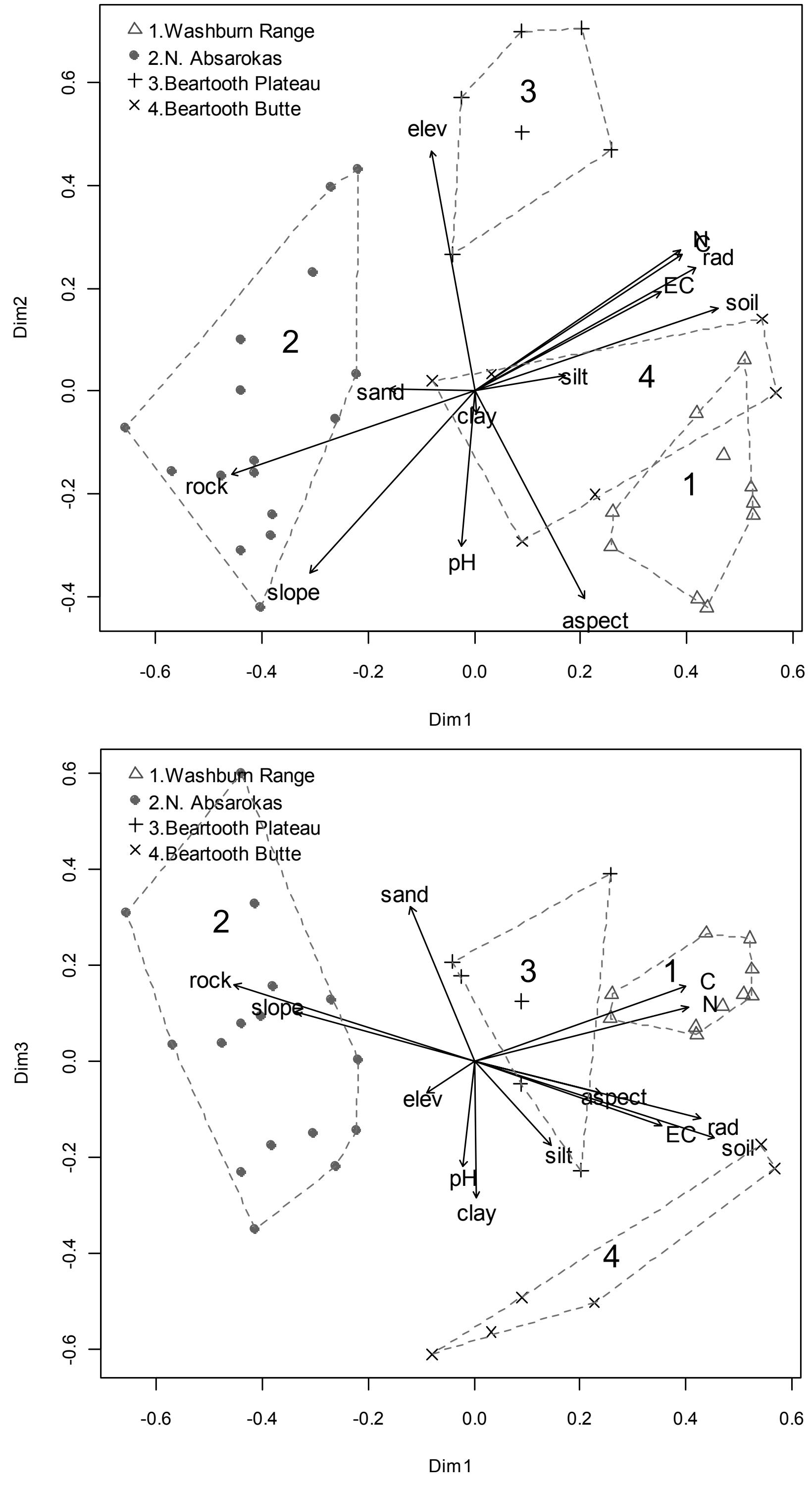

Figure 5.13. Three dimensional NMDS solution for north-facing plots, stress = 11.28. Environmental vectors are overlaid, and the four alpine areas are separated by symbols and dashed lines. For exact relationship of vectors to configurations see Table 5.1. For explanation of vector annotations see Fig. 5.3.

Washburn N. Face

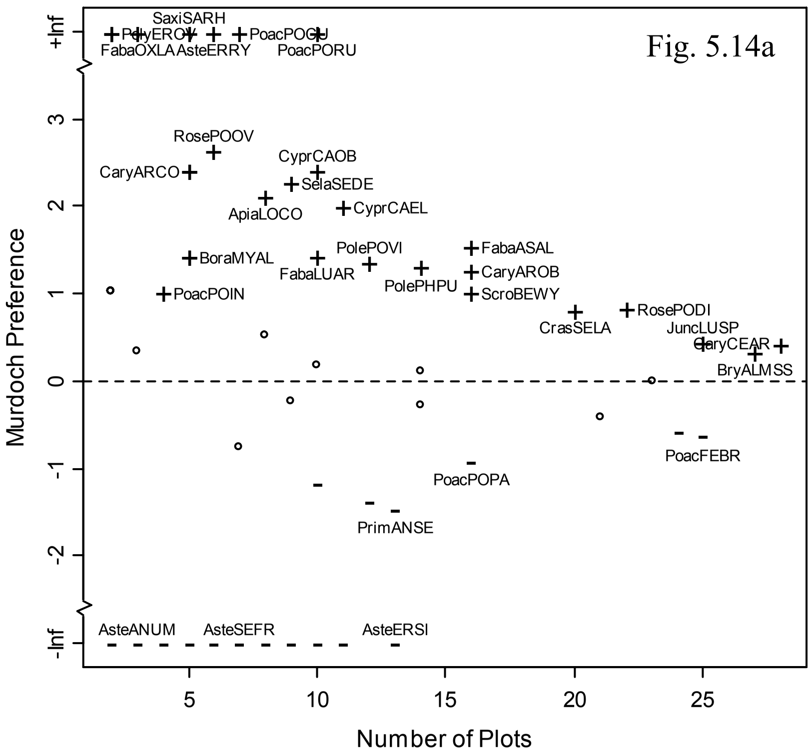

Fig. 5.14a

N. Absaroka N. face

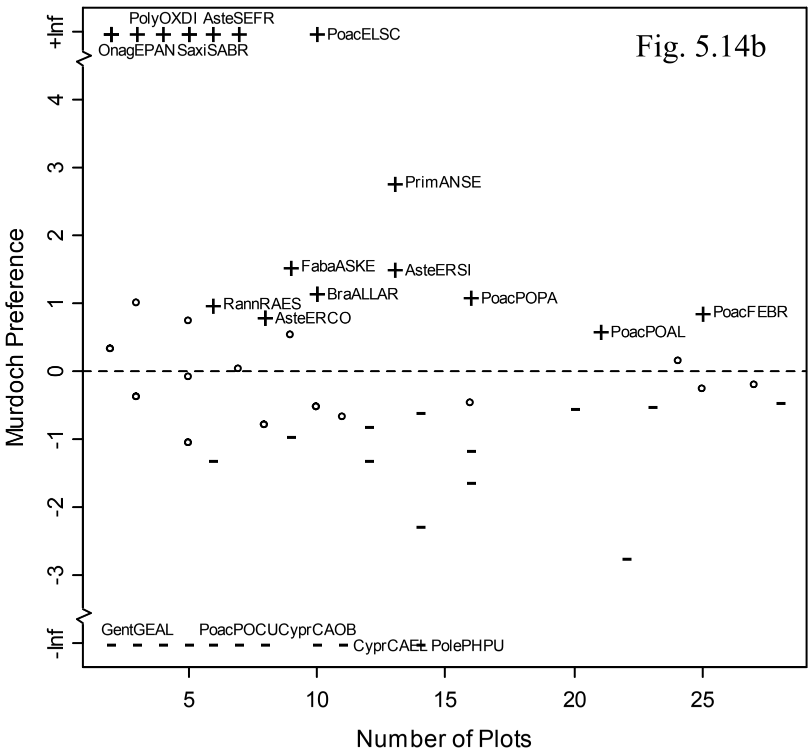

Fig. 5.14b

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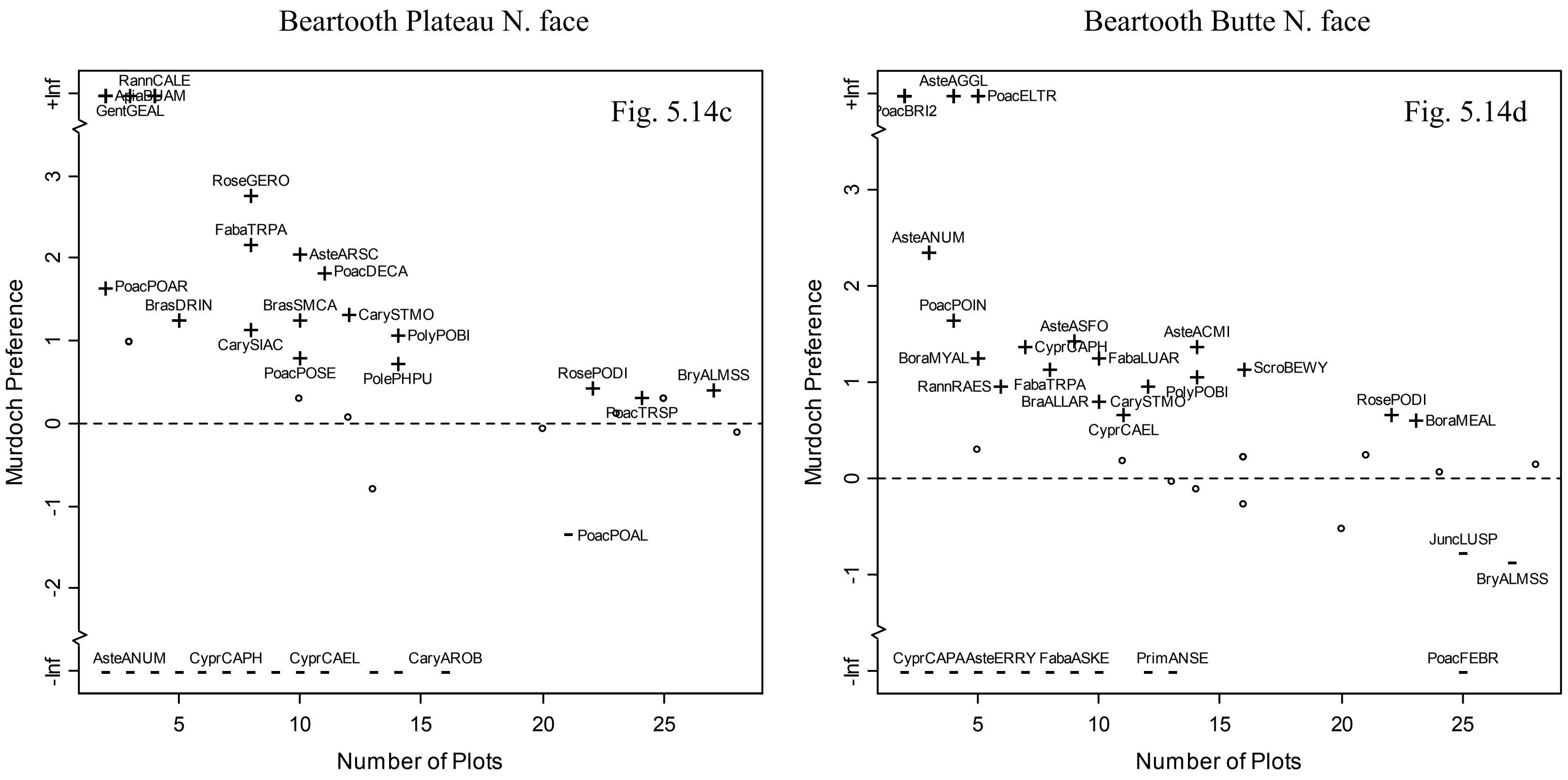

Figure 5.14. Murdoch analysis results for north-facing sites across alpine regions: (a) Washburn Range, (b) N. Absarokas, (c) Beartooth Plateau, (d) Beartooth Butte. Ninety-five species which occurred in at least 5% of the 38 north-facing plots across in the 4 alpine regions were analyzed. Significant positive and negative species are identified where space on the graph allows, "+" indicates a positively significant Murdoch species, "-" indicates a negatively significant Murdoch species, "0" indicates neither significantly positive nor negative. Due to overlaying species not all species can be identified in graphs. For species codes see Appendix D.1. For complete summary of Murdoch analysis for north facing areas see Appendix D.2, Table D.2.6.

Snowbank Variation Across Regions

Vegetation Snow accumulation sites had the highest cover and richness across all topographic types. Vegetation cover was particularly high on the Beartooth Plateau (137% versus 88-111% in other regions). Washburn had the highest levels of snowbank richness (26 spp. plot^{-1} versus 17-22 spp. plot^{-1} in other regions). Productivity (indexed by soil organic matter) increased from the N. Absarokas (C = 4.1%, N = 0.3%) to Beartooth Butte (5.7%, 0.5%), to the Washburn Range (6.0%, 0.5%) to the Beartooth Plateau (8.7%, 0.7%).

Though they were often dominated by similar key species e.g. *Veronica wormskjoldii, Carex paysonis, Salix arctica*, and *Sibbaldia procumbens* (Table 5.3), snowbank sites communities varied greatly across the four regions. This is demonstrated by regional clusters which were well separated (very different) from each other in ordination species space ($r^2 = 0.73$, $p < 0.001$ for the best two NMDS dimensions). Distinguishing species of Washburn late melt sites included *Besseya wyomingensis, Phlox multiflora,* and *Penstemon procerus* (Fig. 5.16a Table 5.6). Species which distinguished the N. Absarokas included *Agrostis variabilis, Lloydia serotina,* and *Silene acaulis* (Fig. 5.16b Table 5.6). Species distinguishing the Beartooth Plateau included *Carex pyrenaica, Antennaria lanata, Caltha leptosepala, Geum rossii* and *Pedicularis groenlandica* (Fig. 5.16c, Table 5.6). Species which distinguish Beartooth Butte included *Phleum alpinum, Dodecatheon pulchellum, Senecio crassulus* and *Trollius laxus* (Fig. 5.16d, Table 5.6).

Environment The most important environmental gradients for late melt sites were soil texture and pH (Table 5.1, Fig. 5.15). Snowbank soils of the granitic Beartooth Plateau were sandy (67% sand versus 47-61%) while limestone Beartooth Butte soils were particularly clayey (23% clay versus 2-4%). Snowbank sites were the most acidic of all topographic types due to leaching of bases by melt water (Fig. 5.3, Table 5.3, Chs. 3, 4). Washburn, N. Absaroka, and Beartooth Plateau snowbank soils were particularly acidic (pH = 5.5-5.6), while those on Beartooth Butte were alkaline-neutral (pH = 7.1).

While all snowmelt sites were wet and cold, those of the Beartooth Plateau, were particularly boggy (WI = 0.97 versus 0.79-0.83 at other regions) and frigid (TI = 0.06 versus 0.08-0.16). This is undoubtedly due to its wet climate and high altitude (3213m versus 3038-3138m in other regions). Consequently Beartooth Plateau snowbank sites had a prominent moss understory allowing high total cover responses, and snowbank species which were highly hydrophilic including *Caltha leptosepala* and *Carex pyrenaica* (cf. Dorn 1992). In contrast snowbanks on the dry Washburn Range were distinguished by a number of less hydrophilic species including *Besseya wyomingensis* and *Phlox multiflora* (cf. Dorn 1992, Ch. 2)

Due to steep north facing slopes, late melt sites in the North Absarokas often appeared as relatively steep (19.2º versus 8.2-18.9º at other regions) ledges near the top of sheer faces. As a result N. Absaroka snowbanks had less incident solar radiation (0.71 MJ cm^{-2} yr^{-1} versus 0.73-0.86 MJ cm^{-2} yr^{-1}) than other regions, were rockier (19% rock cover versus 0-14%), and had poorer developed soils (3% N versus 5-7% N).

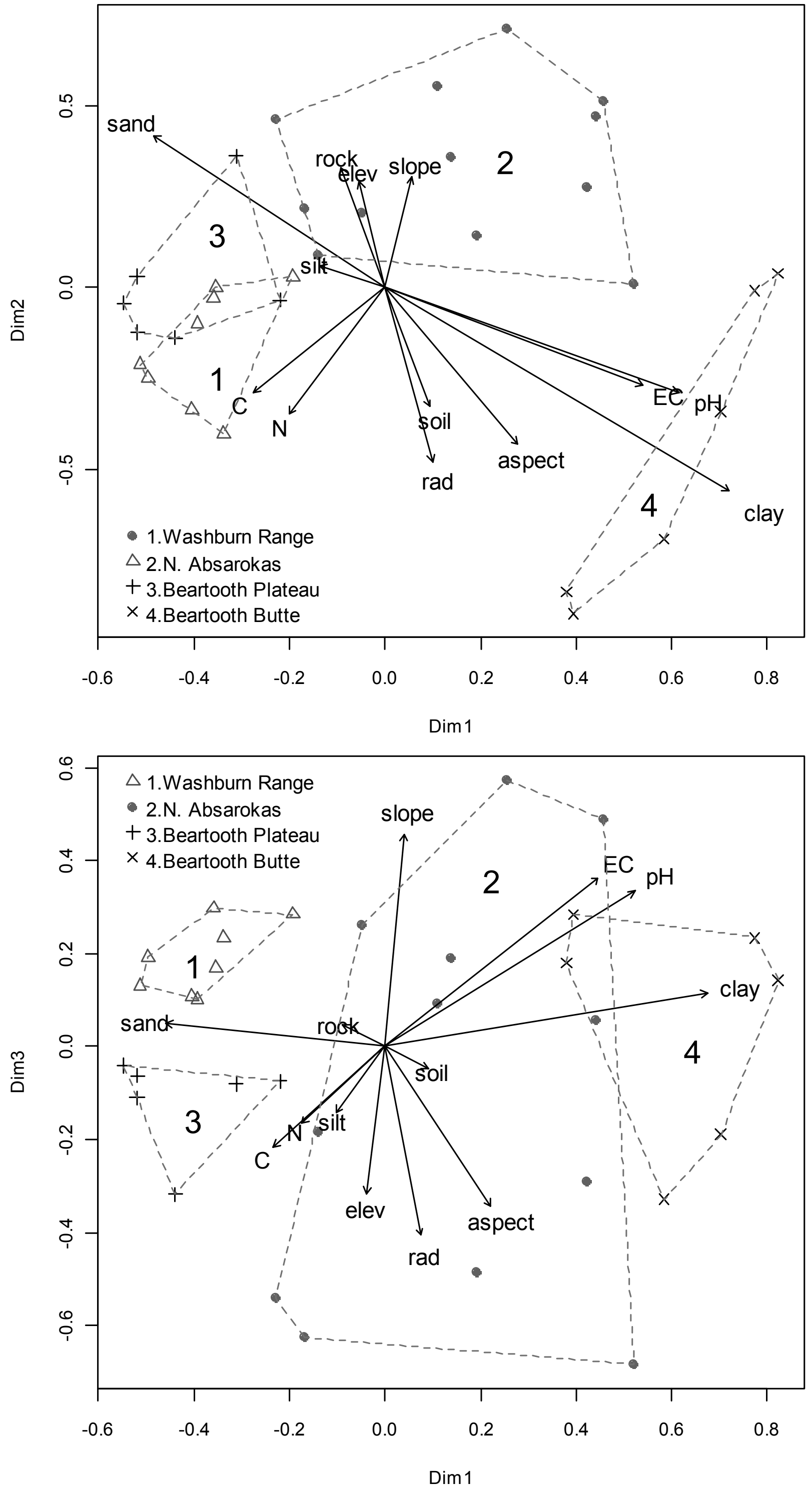

Figure 5.15. Three dimensional NMDS solution for snowbank plots, stress =10.76. Environmental vectors are overlaid, and the four alpine areas are separated by symbols and dashed lines. For exact relationship of vectors to configurations see Table 5.1. For explanations of vector annotations see Fig. 5.3.

Washburn Snowbank

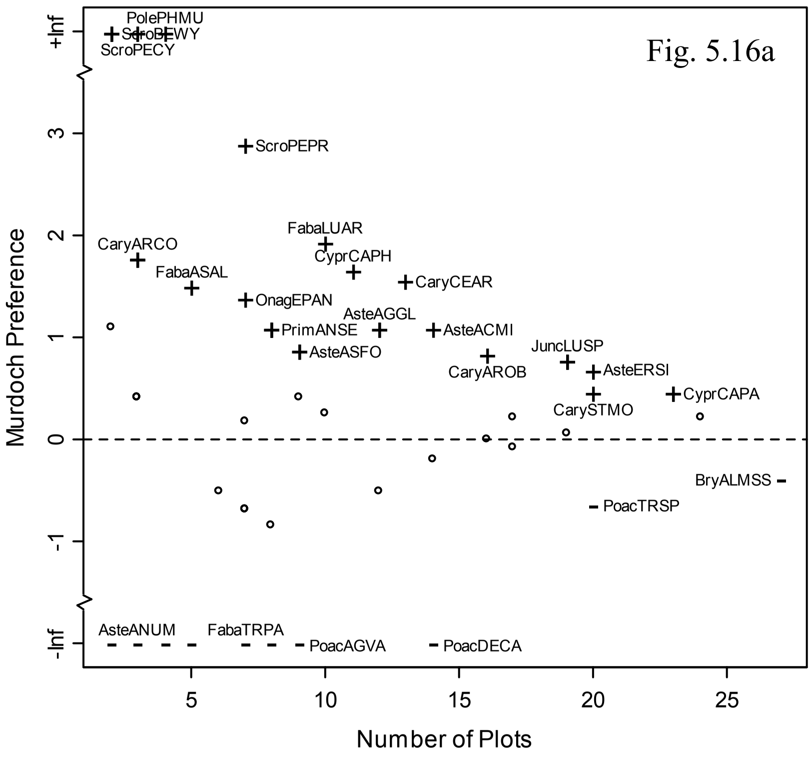
Fig. 5.16a

N. Absaroka Snowbank

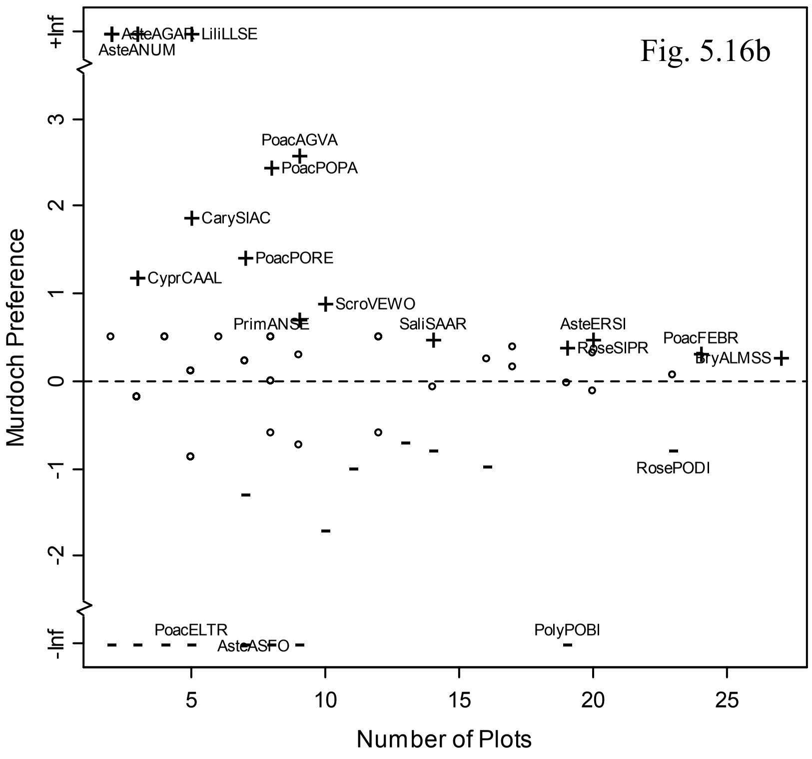
Fig. 5.16b

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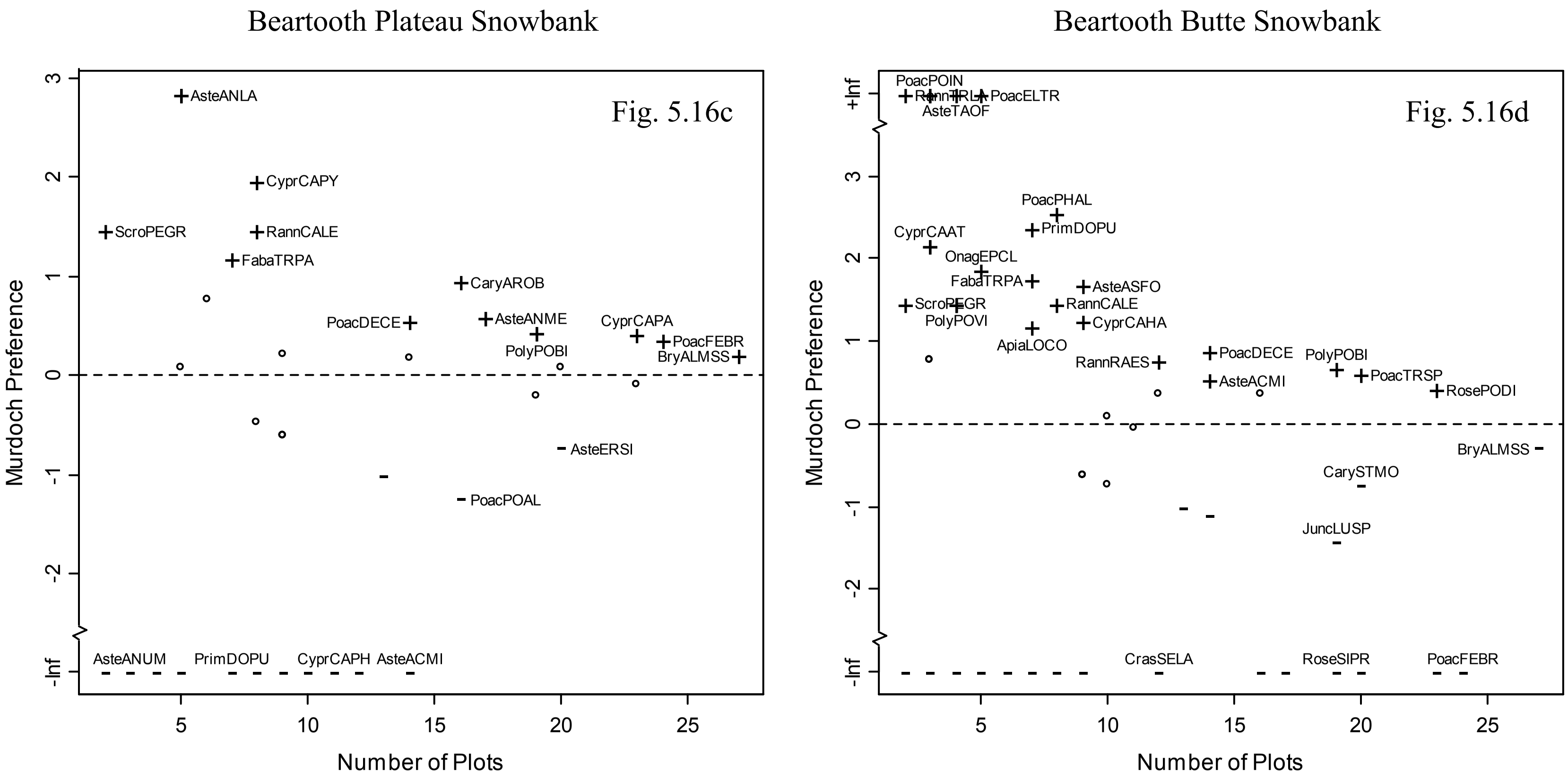

Figure 5.16. Murdoch analysis results for snowbank across alpine regions: (a) Washburn Range, (b) N. Absarokas, (c) Beartooth Plateau, (d) Beartooth Butte. Seven-nine species which occurred in at least 5% of the 32 late-melt plots across in the 4 alpine regions were analyzed. Significant positive and negative species are identified where space on the graph allows, “+” indicates a positively significant Murdoch species, “-“ indicates a negatively significant Murdoch species, “0” indicates neither significantly positive nor negative. Due to overlaying species not all species can be identified in graphs. For species codes see Appendix D.1. For complete summary of Murdoch analysis for late melt areas see Appendix D.2, Table D.2.7.

Species distinguishing N. Absaroka snowbanks have often been associated with rocky sites including *Lloydia serotina* (cf. Dorn 1992) and *Silene acaulis* (cf. Kershaw et al. 1998).

Testing Local and Regional Influence

Ecologists have often commented on the difficultly of demonstrating that environmental heterogeneity is the cause of variability in communities (e.g. Naeem and Colwell 1991). One strategy in identifying important environmental factors is to test community variability against a neutral null model (cf. Wilson 1988). Using this approach we tested the hypothesis that alpine vegetation varies with local and regional factors against null predictions of the unified neutral theory of biodiversity and biogeography (Hubbell 2001).

Unified neutral theory predicts that, in the absence of strong environmental factors and/or niche partitioning by species interactions, community composition will be driven by ecological drift, dispersal (e.g. random immigration and local extinction), and random speciation (Hubbell 2001). Thus, in a purely dispersal-driven system dissimilarity in community composition should be strongly positively associated with spatial distance.

The relationship between vegetation dissimilarity and spatial distance is often effectively modeled by exponential/logarithmic functions (LaRoi and Stringer 1976, Hubbell 2001). While our data weakly follows this general null form (indicated by regression lines in Fig. 5.17) the trend is clearly contradicted in several instances (Fig 5.17). Note in particular the higher than expected community dissimilarities of the adjacent Beartooth Plateau and Beartooth Butte sites across all topographic types. Note also the higher than expected agreement between the alpine areas on volcanic substrates (i.e. Washburn and the N. Absarokas) for talus and south facing slopes (Figs. 5.17a, 5.17c). Such regional patterns may be largely substrate driven.

Patterns of similarity/dissimilarity across regions vary widely for different topographic types. For instance, on snowmelt sites the distant Washburn Range and Beartooth Plateau areas are unexpectedly similar due to the high abundance of *Carex paysonis* and other similar late melt diagnostic species at both areas (Fig. 17e). The reason (environmental or otherwise) for such similar communities is unknown.

Summary/Conclusions

The North-Central Rocky Mountain alpine resembles alpine ecosystems from around the world. Its universal vegetation characteristics include fluctuation from open fellfields and windswept ridges, to forb-graminoid meadows, and wet late-melt meadows and bogs at the base of leeward slopes (cf. Billings 2000, Körner 2003). Typical environmental characteristics include the importance of soil accumulation and soil development to community variability and productivity (cf. Aho et al. 1998, Körner 2003).

Within this general framework, study site ecosystems vary with local and regional factors, and interactions of local and regional factors. Local topographic controls were demonstrated by differences in vegetation composition among five universal topographic types. These include the heterogeneity of talus slopes, the affinity of cushion plants for ridgetops, and the unique community structure of snow collection sites. Local vegetation differences can be largely attributed to topographic environmental differences. These include the exposed aridity of ridges, the low temperatures of north faces, and the short growing season and wet, silty, acidic soils of snowbank sites.

Regional controls were demonstrated by variability in vegetation with respect to substrate and climate. The influence of substrate is confirmed by highly different vegetation on the granitic Beartooth Plateau and the calcareous Beartooth Butte; two areas which are directly adjacent to each other. Beartooth Butte was distinguished by a number of documented calcicoles including *Dryas octopetala, Carex nardina*, and *Carex rupestris*. The influence of climate is demonstrated by the paucity of wet diagnostic species on the dry Washburn range, and dominance of these species in the wet Beartooths.

Local and regional interactions were particularly evident. For instance, on the wet Beartooth Plateau many hydrophilic species including *Artemisia scopulorum*, and *Carex scirpoidea* occur on “dry” ridgetops. On the dry Washburn Range xeric *Carex elynoides* turf communities occur on “wet” northern slopes.

We tested our dataset against a null model that attributes community variability purely to dispersal and ecological drift (Hubbell 2001). A demonstration of the strength of local and regional factors is provided by deviations of study site data from the predictions of this model.

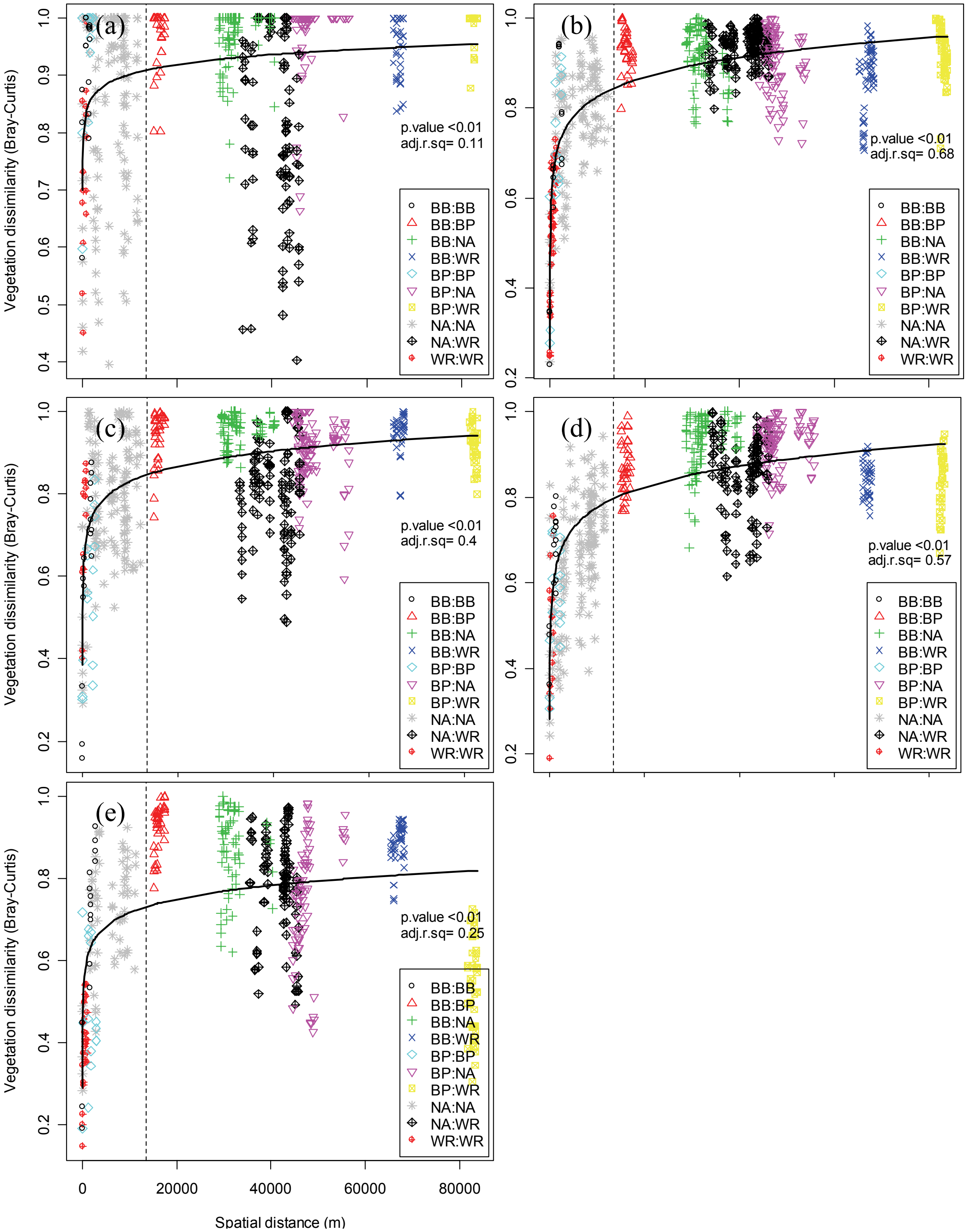

Figure 5.17. Difference in vegetation composition compared to spatial distance for (a) talus, (b) north-facing, (c) south-facing, (d) ridgetop, and (e) snowbank sites. BB=Beartooth Butte, BP=Beartooth Plateau, NA=Northern Absarokas, WA=Washburn range. Left of the dashed line, sites *within* the four areas are compared (spatial distance <1.3 km). Right of the dashed lines, sites *between* the four areas are compared.

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Literature Cited

Aayd, M., and R. Dix. 1964. An analysis of a vegetation-microenvironment on prairie slopes in Saskatchewan. Ecol. Monographs 34: 421-442.

Aho, K., Huntly N., Moen J., and T. Oksanen. 1998. Pikas (*Ochotona princeps*: Lagomorpha) as allogenic engineers in an alpine ecosystem. Oecologia. 114(3): 405-409.

Anderson, B. 1984. Beartooth Country. Montana Magazine Inc. Helena MT.

Anderson, L. et al. 1990. List of North American mosses: The Bryologist 93: 450-499.

Baker, W. L. 1983. Alpine vegetation of Wheeler Peak, New Mexico U.S.A: gradient analysis, classification and biogeography. Arctic and alpine research. 15(2) 223-240.

Bamberg, S. A., and J. Major. 1968. Ecology of the vegetation and soils associated with calcareous parent materials in three alpine areas in Montana. Ecological Monographs. 38: 127-167.

Begon, M., Harper, J. L., and C. R. Townsend. 1996. Ecology: individuals, populations and communities, 3rd edition. Blackwell Science. Oxford, UK.

Billings, W. D. 2000. Alpine Vegetation of North America. pp. 537- 572. *In* North American Terrestrial Vegetation 2nd edition, Barbour, M. D. and Billings, W. D. eds. Cambridge Univ. Press, Cambridge.

Bray J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities in southern Wisconsin. Ecological Monographs. 27: 325-349.

Bridges, E. M. 1978. World soils. Cambridge University Press. London, UK.

Cooper, S. V., Lessica, P., and D. Page-Dumroese. 1997. Plant community classification for alpine vegetation on the Beaverhead National Forest, Montana. Gen. Tech. Rep. INT-GTR -362. Ogden UT: U.S. Department of Agriculture, Forest Service Intermountain Research Station. 61 pgs.

Daubenmire, R. 1959. A canopy coverage method of vegetation analysis. Northwest Science. 33: 43-64.

Daubenmire, R. 1968. Plan communities: A textbook of plant synecology. Harper and Row, New York, USA.

Dorn, R. D. 1992. Vascular Plants of Wyoming. Mountain West Publishing. Cheyenne WY.

Esslinger, T. L. 2006. A cumulative checklist for the lichen-forming, lichenicolous and allied fungi of the continental United States and Canada. North Dakota State University: http://www.ndsu.nodak.edu/instruct/esslinge/chcklst/chcklst7.htm (First Posted 1 December 1997, Most Recent Update 10 April 2006), Fargo, North Dakota.

Faith, D. P., Minchin, P. R. & Belbin L. 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio. 69: 57-68.

Frank, D., Inouye, R. S., Huntley, N., Minshall, G. W., Anderson, J. A. 1994. The biogeochemistry of a North-temperate grassland with native ungulates: nitrogen dynamics in Yellowstone National Park. Biogeochemistry. 26: 163-188.

Gauslaa, Y. 1984. Heat resistance and energy budget in different Scandinavian plants. Holarctic ecology 7: 1-78.

Gardner, W. H. 1986. Soil water content. pgs 493-541. In A. Klute ed. 1986. Methods of soil analysis, part 1-physical and mineralogical methods, second edition. American Society of Agronomy, inc. Soil Science Society of America. Madison WI.

Gee, G., and J. Bauder. 1986. Particle size analysis, pgs. 383-412, *in* Klute, A. (ed.), 1996. Methods of soil analysis I: physical and mineralogical methods. Soil. Sci. Soc. America. Madison, WI. 1188 pgs.

USGS. 1999. Digital Atlas of the Greater Yellowstone Area. Contact information: Greater Yellowstone Area Data Clearinghouse. Montana State University, 59717.

Gjaerevoll, O. 1953. Problems of plant distribution in the White Mountains in Central Alaska. Sci. in Alaska, Proc. 4th Alaska Sci. Conf., 159-162.

Hadley, K. S. 1987. Vascular alpine distributions within the central and southern Rocky Mountains, U.S.A. Arctic and Alpine research. 19(3): 242-251.

Hanson, H. C. and E. D. Churchill. 1961. The plant community. Reinhold Publishing, New York, USA.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press. Seattle WA.

Holdridge, L. R. 1947. Determination of the world plant formations from simple climatic data. Science. 105: 367-368.

Hrapko, J. O., LaRoi, G. H. 1978. The alpine tundra vegetation of Signal Mountain, Jasper National Park. Canadian Journal of Botany. 56: 309-332.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton and Oxford, UK.

Hunter, K. B., and R. E. Johnson. 1983. Alpine flora of the Sweetwater Mountains, Mono County, California. Madrono. 30: 89-105.

Jacobs, J. 1974. Quantitative measurement of food selection. Oecologia. 14: 412-417.

Jenny, H. 1941. Factors of soil formation; a system of quantitative pedology. McGraw-Hill, Columbus, OH. USA.

Johnson, P. L., and W. D. Billings. 1962. The alpine vegetation of the Beartooth Plateau in relation to cryptogenic processes and patterns. Ecolog. Monogr. 32: 105-135.

Jones, M. G. 1933. Grassland management and its influence on the sward. Empire Journal of Experimental Agriculture. 1: 43-367.

Keefer, W. R. 1976. The geologic story of Yellowstone National Park. Geological Survey Bulletin 1347 USGS. 92 pgs.

Kershaw, L., MacKinnon, A., and Pojar, J. 1998. Plants of the Rocky Mountains. Lone Pine Publishing, Edmonton Alberta. Pg. 203

Komárková, V. 1979. Alpine vegetation of the Indian Peaks area, Front Range Colorado Rocky Mountains. PhD dissertation University of Colorado, Boulder. 591 pgs.

Körner, C. 2003. Alpine plant life: Functional plant ecology of high mountain Ecosystems, 2nd edition. Springer-Verlag, Berlin. 338 pgs.

Körner, C., and De Moraes, J. A. P. V. 1979. Water potential and diffusion resistance in alpine cushion plants on clear summer days. Oecol. Plant. 14: 109-120.

Kruskal, J. B. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychmetrika. 29: 1-27.

Küchler, A. W. 1975. Potential natural vegetation of the conterminous United States. American Geographical Society special publication 36. New York, USA.

Lackschewitz, K. H. 1994. Beartooth alpine flora, pgs. 105-113. *in*: Anderson B. (ed). Beartooth Country: Montana's Absaroka and Beartooth Mountains. Unicorn Publishing, Helena MT.

Laroi, G. H., and M. H. Stringer. 1976. Ecological studies on the boreal spruce-fir forests of the North American taiga. I. Analysis of vascular flora. Ecological Monographs. 37: 239-253.

Lawton, E. 1971. Moss flora of the Pacific Northwest. Hattori botanical library, Nichinan, Miyazaki, Japan.

MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. Ecology. 42: 594-598.

Mellman-Brown, S. 2002. The regeneration of whitebark pine in the timberline ecotone of the Beartooth Plateau, Montana and Wyoming. Doctoral Dissertation. University of Münster, Germany. 157 pgs.

Milton, W. E. J. 1940. The effect of manuring, grazing, and limiting on the yield, botanical and chemical composition of natural hill pastures. Journal of Ecology. 28: 326-356.

Milton, W. E. J. 1947. The composition of natural hill pasture, under controlled and free grazing, cutting and manuring. Welsh Journal of Agriculture. 14: 182-195.

Naeem, S., and W. K. Colwell. 1991. Ecological consequences of heterogeneity in consumable resources. Pp. 224-255. In J. Kolasa and S.T.A. Picket, eds. Ecological Heterogeneity. Ecological Studies no 86. Springer-Verlag, NY. USA.

Nelson, D. W., and L. E. Sommers. 1996. Total carbon, organic carbon, and organic matter, pgs 961-1010, *in* D. L. Sparks (ed.). Methods of soil analysis, Part 3. Chemical methods. Soil Science Society of America book series number 5. American Society of Agronomy, Madison WI

Okasnen, J. 2005. Community ecology package, vegan ver. 1.6-6. http://www.cran.r-project.org

Pemble, R. H. 1965. A survey of distribution patterns in the Montana alpine flora. Masters Thesis, University of Montana, Missoula. 146 pages.

Roberts, D. 2005. Vegetation classification in R, for labdsv ver. 1.1-1, vegetation ecology package. http://www.cran.r-project.org.

Rorison, I. H. 1969. Ecological aspects of the mineral nutrition of plants, a symposium of the British Ecological society. Blackwell Scientific Publications, Oxford, UK.

Rottman, M. L., Hartman E. L. 1985. Tundra vegetation of three cirque basins in the northern San Juan Mountains, Colorado. Great Basin Naturalist. 45: 87-93.

Seagrist, R. V., and K. J. Taylor. 1998. Alpine vascular flora of Buffalo Peaks, Mosquito Range, Colorado USA. Madrono. 45(4) 319-325.

Simpson, E. H. 1949. Measurement of diversity. Nature. 163: 688.

Smedes, H. W., and Protska, H. J. 1972. Stratigraphic framework of the Absaroka Volcanic Supergroup in the Yellowstone National Park region: U.S.G.S. Prof. Pap. 720-C, US Gov. Print. Office, Wash. DC, 33 pgs.

Sørenson, T. 1933. The vascular plants of East Greenland from 71˚00' to 73˚30' N. Lat. Medd øm Gronl. 101 (3) : 1-177.

Spence, J. R. and R. J. Shaw. 1981. A checklist of the alpine vascular flora of the Teton Range, Wyoming, with notes on biology and habitat preferences. Great Basin Naturalist. 41(2): 232-241.

Taylor, S. T., and R. D. Jackson. 1986. Temperature. *In*, pp. 927-941. A. Klute ed. Methods of soil analysis, part 1, physical and mineralogical methods, 2nd edition. Soil Science Society of America Inc. Madison, WI.

Thilenius, K. F., and D. R. Smith. 1985. Vegetation and Soils of an Alpine Range In the Absaroka Mountains, Wyoming. USDA Forest Service General Technical Report RM-121, 18 pgs. Rocky Mountain Forest and Range Experiment Station, Fort Collins Colo.

Thomas, G. 19996. Soil pH and acidity. Pgs 475-490, *in*: Klute, A. (ed.). 1996, Methods of soil analysis I: Physical and mineralogical methods. Soil Sci. Soc. America. Madison WI. 1188 pgs.

Tilman, D. 1988. Dynamics and structure of plant communities. Princeton University Press, New Jersey, USA.

Venables S., and B. Ripley. 2004. MASS ver. 7.2-1. http://cran.r-project.org

Walter, H.,and H. Leith. 1967. Klimadiargramm-Weltaltas. Gustav Fisher, Jena.

Western Regional Climate Center (WRCC). 2006. Reno NV. 89512.

Whittaker, R. H. 1960. Vegetation of the Sisikyou Mountains, Oregon and California. Ecological Monographs. 30: 279-338.

Willard, B. E. 1979. Plant Sociology of alpine tundra, Trail Ridge, Rocky Mountain

National Park, Colorado. Quarterly of the Colorado school of mines. 74: 4.

Wilson, J.B. 1988. Community structure in the flora of islands in Lake Manapouri, New Zealand. Journal of Ecology. 76: 1030-1042.

CHAPTER 6

WATER AND SUBSTRATE CONTROL OF CLIFF COMMUNITIES (NORTH-CENTRAL ROCKY MOUNTAINS)

Introduction

While cliff communities are much studied in Europe (Escudero 1996, Pentecost 1980, Bunce 1968, Hora 1947 many others) and considered on eastern North American sea cliffs (Good and Good 1970) and low altitude escarpments (Bartlett et al. 1991, Wiser 1998, Graham and Knight 2004), the ecology of cliff communities in the Rocky Mountains is largely unknown. This deficiency is of concern for at least three reasons.

First, cliff areas often support rare endemic species (Ursic et al. 1997, Graham and Knight 2004) and specialized communities (Okusanya 1979) vulnerable to extinction. This factor is particularly relevant in the Rocky Mountains where rock climbing (cf. Nuzzo 1996, Farris 1998), introduced mountain goats (cf. Houston et al. 1994), pollution (cf. Larson et al 2000), and other human disturbance may threaten undocumented cliff vegetation.

Second, because cliffs have a relatively low degree of community complexity, vascular plant, lichen, and moss interactions are simplified, allowing these general groups to be studied with greater ease (cf. Farrar 1998). Insights from these studies may be extrapolated to more complex communities occupying a wider geographic range.

Finally, recognition of widespread species which have specific abiotic requirements will provide indicator species useful in characterizing conditions at unstudied cliffs elsewhere (cf. Ellenberg 1979). Indeed, since terrestrial vegetation often varies with latitudinal changes in climate (Holdridge 1947) the communities of subalpine cliffs in the Rocky Mountains are likely to be comparable to other cliff sites in the circumboreal spruce-fir zone (cf. Larson et al. 2000). This zone occupies the Rockies, the North American Coastal Cordillera, the Alps, Siberia and Kamchatka (Weaver 1990).

Within a climatically uniform region (e.g. the Rocky Mountain spruce-fir zone) cliff vegetation varies with the heterogeneous microenvironments of cliff faces (Escudero 1996, Nuzzo 1996, Farrar 1998). For instance, vascular plants in cliff areas often require ledges, cracks, and crevices which provide soil/nutrient accumulations, rooting sites, and potential water sources (Farris 1998, Ursic et al. 1997). In contrast lichens often favor dry sheer faces which are free of crevices (Larson et al. 2000, Coates and Kirkpatrick 1992). Two environmental factors which greatly influence cliff community composition are substrate (Larson 2000, Pentecost 1980), and water availability (Foote 1966).

Objectives

In this chapter we attempt to describe the range of cliff communities common to timberlines of the Northern Rocky Mountains across water and substrate gradients. We manage this by systematically sampling sites occupying cardinal positions of the water gradient (i.e. dry, mesic, and wet) and those occupying substrate extremes (i.e. andesitic/volcanic and calcareous/limestone). We have three objectives:

1. Describe variation in communities with respect to life-form (e.g. moss, lichen, vascular plant) and species composition across water and substrate gradients.

2. Quantitatively compare the physical character of andesitic and calcareous substrates.

3. Determine which species are strongly associated with water, substrate, and water/substrate nodes as indicator species useful in characterizing the environments of other sites.

Study area

Mountains in the Northern Absarokas (North-Central Rockies) provide an outstanding setting for studying the effects of substrate and water on high altitude cliff communities. At sub-alpine elevations andesitic cliff faces overlay limestone cliff bands. A large number of waterfalls simultaneously fall over both substrates simultaneously and provide replicates of wet, dry and intermediate treatments for both substrates.

Large cliffs in the Northern Absarokas consist of Paleozoic sediments unconformably overlain by andesitic Eocene volcanic layers. Prominent Paleozoic layers consist mostly of Pilgrim Limestones deposited 500-570 MYA (Metesh et al. 1999). The Pilgrim Formation produces a consistent stratum of 30-55m limestone and limestone conglomerate cliffs on the lower slopes (2200-2300m) of the Northern Absarokas (Metesh et al. 1999).

Broken volcanic cliffs 200-300m high overlay limestone layers. These volcanic outcrops are deposits from the Lamar River Formation (47-49 MYA) a subunit of the Absaroka Volcanic supergroup (Smedes and Prostka 1972). The Lamar River Formation consists mostly of light colored andesitic lava flows and alluvial volcaniclastics.

The mountains chosen for the study, Barronette and Abiathar Peak, lie along the North Eastern Absaroka Range and are located within Yellowstone National Park (Fig.

6.1). The two mountains lie directly east-west of each other, and are separated by the Soda Butte Creek, and the upper Lamar River drainage system (Figs. 6.1-6.2). A large number of waterfalls drain the east/west faces of Abiathar and Barronette and fall simultaneously across both andesite and limestone cliffs before emptying into Soda Butte Creek, and the Yellowstone River (Figs. 6.1-6.2).

The general vegetation of the study area is *Abies lasiocarpa/Vaccinium scoparium* or *Pinus albicaulis/ V. scoparium* at higher altitudes (Weaver 1990). The general climate of *A. lasiocarpa/V. scoparium* is relatively consistent across circumboreal regions in the Rockies, the Alps, Siberia, and mountains of eastern China (Weaver 1990). A more specific description of the climate is provided by the nearby (< 10 km) northeast entrance weather station (see Chapter 4, Fig. 4.2b).

The study site has generally been protected from domestic grazing and other human impacts by its location in Yellowstone National Park (YNP). However introduced mountain goat populations (*Oreomnos americanus*) are expanding on both mountains (Lemke 2004) and may impact cliff vegetation (cf. Houston et al. 1994). Pollution from automobiles and coal fired generators to the northeast may also have increasing impacts.

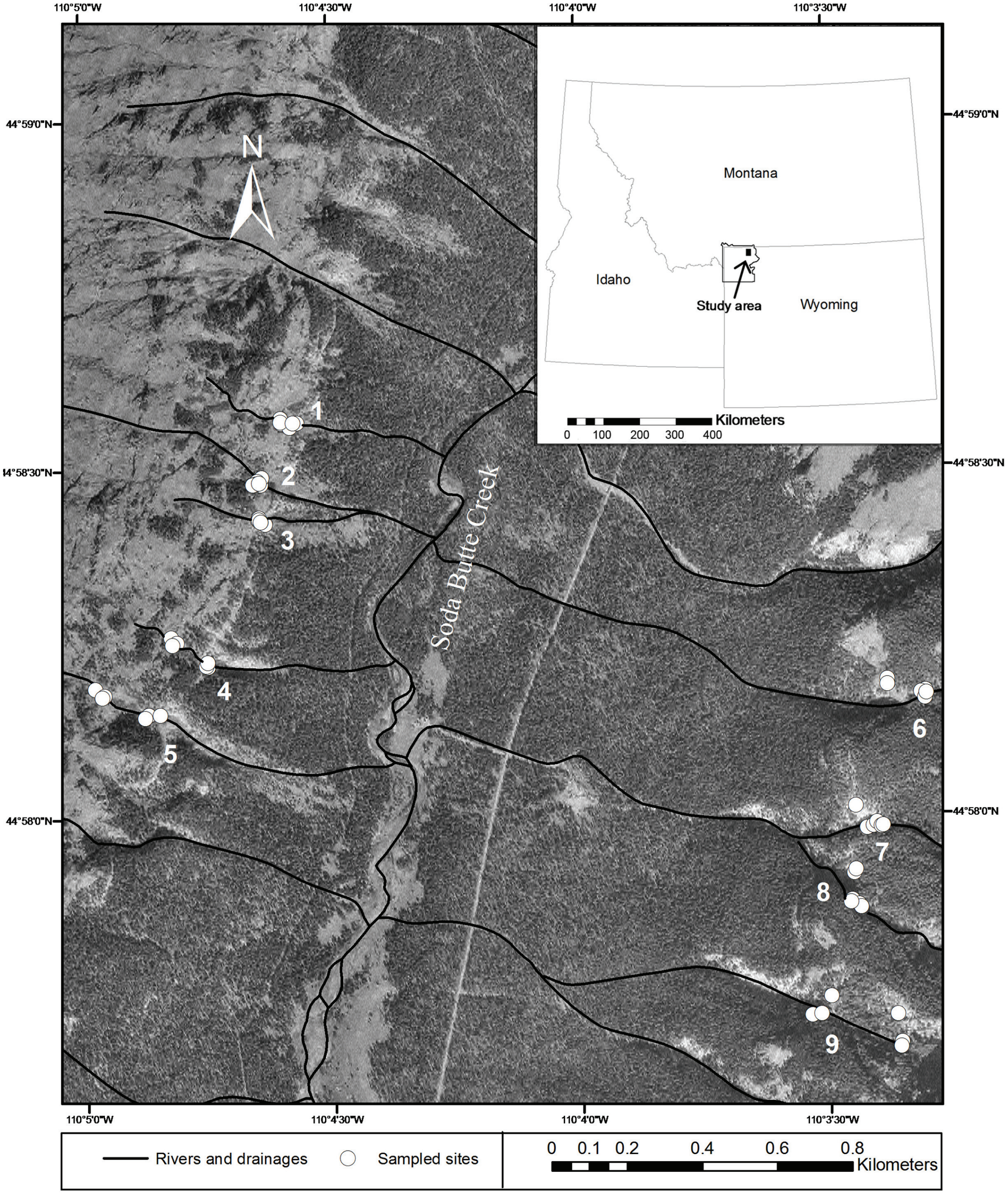

Figure 6.1. Location of the study area and the sites sampled. The inset map locates the area in YNP and the Northern Rocky Mountains. Replicate sites are located at waterfalls on Barronette (1-5) and Abiathar (6-9). The park highway lies east of Soda Butte Creek near the center of the orthophoto.

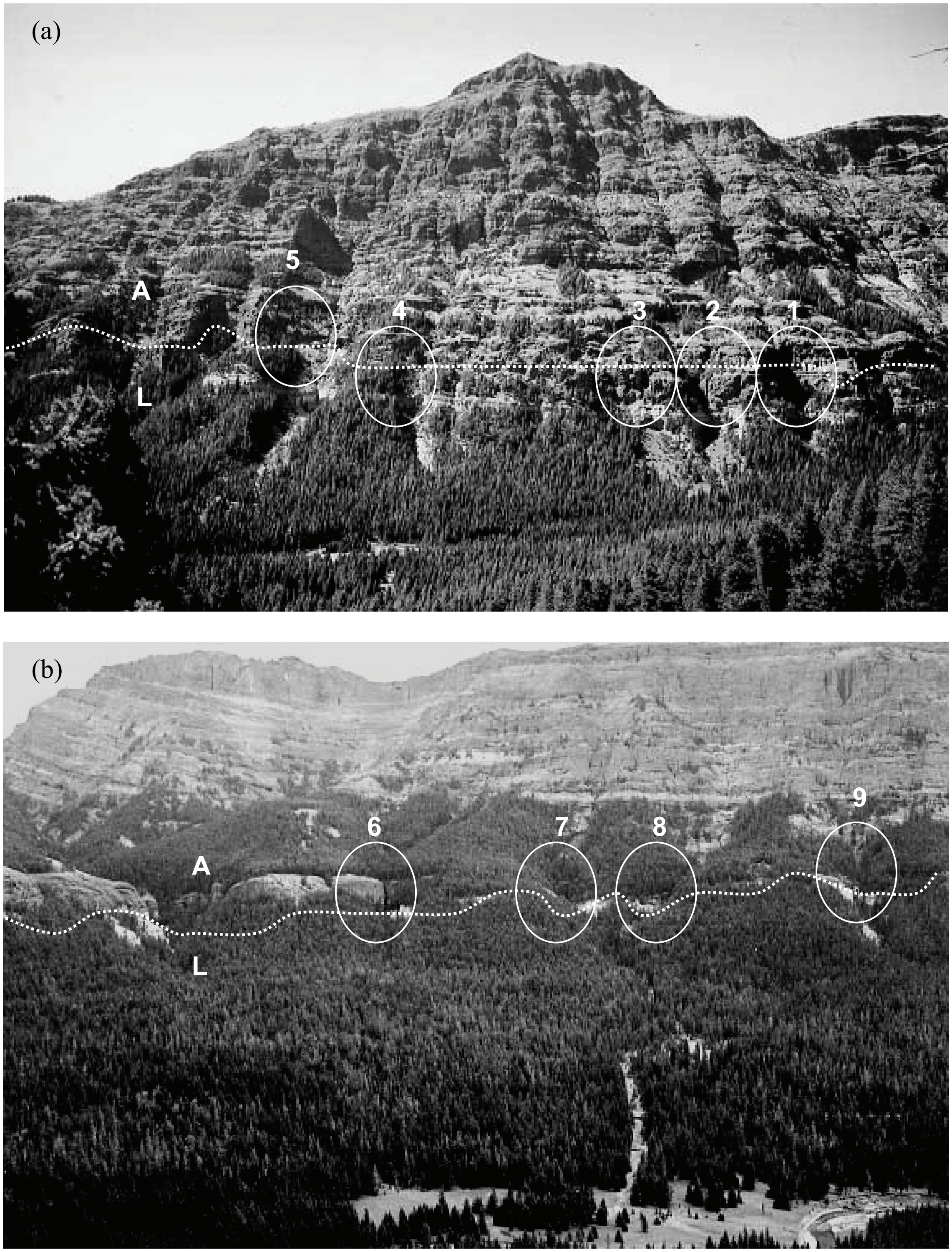

Figure 6.2. Horizontal views of the study sites (circles) at waterfalls descending from andesite (A) above, to limestone (L) below the dotted line. (a) Barronette looking west from Abiathar. (b) Abiathar looking east from Barronette.

Methods

Field sampling

We sampled the vegetation of cliffs in the subalpine elevation zones (2250-2500m) of Abiathar and Barronette Peaks. To contrast the effects of andesite and limestone strata we chose sites at the junction of the two substrates. We selected nine waterfalls, five on the east face of Barronette (Fig. 6.2a), and four on the west face of Abiathar (Fig. 6.2b). Both substrates were sampled at each waterfall in the following areas: wet (areas within the constant spray zone of waterfalls), intermediate (areas 10-30m from the spray area), and dry (areas 30-100m from the waterfall spray zone). Hence six combination substrate/moisture treatments were sampled at each waterfall: 1. andesite-dry 2. andesite-intermediate, 3. andesite-wet, 4. limestone-dry, 5. limestone-intermediate, and 6. limestone wet.

Two 1 m^2 quadrats were sampled for species presence/absence for each treatment at each site. Each quadrat was a 100 point grid. The grid was created by moving a 1 meter rod perforated with 10 evenly spaced nails horizontally along the cliff face ten times at 10cm intervals. Quadrat locations were randomly located whenever possible.

Access to the sites was gained by rock climbing equipment and techniques. Trees were used as climbing anchors. Sampling of cliff faces was generally accomplished by rappelling and ascending fixed ropes (e.g. Graydon 1996).

Vascular plants, ferns, liverworts mosses lichens encountered while sampling were identified and vouchers were deposited in the Yellowstone National Park herbarium, Gardiner, MT (YELLO). Nomenclature follows Dorn (1992) for vascular plants and ferns, (Lawton 1971 and Anderson et al. 1990) for mosses, (Stotler and Crandall-Stotler. 1977) for liverworts, and (Esslinger 2006) for lichens.

Analysis-- Major Life Form Distributions

Changes in the cover of major phyla/life-forms [i.e. flowering plants (Anthophyta), ferns (Pterophyta), mosses (Bryophyta), liverworts (Hepatophyta) and lichens] were compared along water and substrate gradients. Differences were statistically quantified with Kruskal-Wallis simultaneous multiple comparisons (cf. Neter et al. 1996, pg. 1097). Dunn's procedure was used to adjust for simultaneous inference (Dunn 1964).

Analysis—Species Distributions

Ordination To examine relationships of cliff communities we ordinated data with Non-Metric Multidimensional Scaling (NMDS, Kruskal 1964). Bray-Curtis dissimilarity (Bray and Curtis 1957, Faith et al. 1987) was used was used to create the NMDS distance matrix. Although random starting points were also tried, the best (lowest stress) solutions resulted from using PCoA (Principal Coordinates Analysis) scores as initial starting points (cf. Roberts 2005). A tolerance of $1 \cdot 10^{-7}$ was used with 200 iterations to create the scatterplot projection. Strength of association between categorical treatments (i.e. moisture level, substrate, moisture-substrate combination) and the ordination solution was quantified with Eq. 6.1 (Oksanen 2005).

$$r^2 = 1 - \mathrm{SSW} / \mathrm{SSTO} \tag{6.1}$$

where *SSW* = within-group sums of squares (scatter with respect to a treatment centroid for two dimensions of interest) and and *SSTO* = total sums of squares (overall scatter with respect to the scatterplot centroid for the same two dimensions of interest).

MRPP Analysis To quantitatively test for differences in community composition patterns between water and substrate nodes we used Multi Response Permutation Procedures (MRPP; Mielke 1984). MRPP provides a multivariate nonparametric test of the hypotheses of no community difference between treatments (e.g. Zimmerman et al. 1985). Results of pairwise tests between treatments were adjusted for simultaneous inference with Holm's sequential procedure (Holm 1979).

Indicator Species Analysis Indicator species analysis (ISA; Dufrêne and Legendre 1997) and tabling were used to find species that were indicative of particular treatments. *P*-values for ISA indicator values were calculated with Monte Carlo permutation techniques using 1000 iterations (e.g. McCune and Mefford 1999).

Data Considerations Data were subset slightly differently for MRPP, ordination and ISA analyses. For MRPP and ordination specimens keyed only to genus were deleted from analyses if other specimens in the genus were successfully keyed to species. Given these procedures, 104 species were retained for quantitative analysis: 45 lichens, 21 mosses, and 38 vascular plants. Conversely, for indicator species analysis and tabling all species and unknowns were used. Indicator species analysis is not greatly affected by additional cases since each "species" is evaluated individually for significant association with categorical treatments (Dufrêne and Legendre 1997). In addition, for ISA and tabling, specimens from genera *Collema, Candelariella* and *Schistidium* not keyed successfully to species were placed into the composite groups *Collema* spp. and *Candelariella* spp and *Schistidium* spp.

Software Pairwise Kruskal-Wallis non-parametric tests were run in MINITAB using a customized macro (Orlich 2004). Ordination analyses were run in R primarily using MASS (Venables and Ripley 2004) and vegan (Oksanen 2004) packages. MRPP tests and indicator species analyses were run using default settings in PC-ORD (McCune and Mefford 1999).

Chemical and Physical Comparison of Substrates

Community differentiation across substrates is likely due to differences in their water, nutrient, and toxin supplying capacities. Andesite and lime water retention was determined by measuring weight change of saturated rock samples over several days. To measure water absorbance a humidity chamber was created using an airtight plastic box and a humidifier, and weight change in rock samples was monitored several days. Acidity/alkalinity of rock surfaces was measured by determining the rate of OH^- change in a solution of 0.1 M KCL using standard electrodes. All measurements were adjusted with respect to surface area of rock samples. The mineralogy of substrates was determined with x-ray diffraction techniques (Moore & Reynolds 1997) using a powder x-ray diffractometer (Syntag Inc.). The presence of $CaCO_3$ on rock surfaces was determined with “fizz tests” by applying 0.5 M HCl to rock surfaces (Brice & Levin 1960). Density was measured by weighing rocks, determining volume displacement in a graduated cylinder and dividing mass by volume (Davis & Reitan 1976). For further methodological details of substrate analyses see Chapter 8.

Results

Community Distribution--Major Life Forms

Life form distribution varied strongly with water availability but did not vary across substrates. Total cover for flowering plants and bryophytes was higher in wet sites for both types of substrates ($p < 0.001$), while lichens were more abundant on dry sites ($p < 0.001$; Fig 6.3a). Although ferns were relatively rare, they were also more abundant on intermediate and wet sites ($p \leq 0.02$; Fig. 6.3a). Cover of life forms did not differ between substrates ($p = 0.21$ to 0.4; Fig. 6.3b). Vascular plants and mosses had significantly higher cover in wet sites on both limestone and andesite, while lichen cover was significantly higher on dry sites on both substrates ($p \leq 0.01$; Fig. 6.3c).

Community Distribution--Species

Species composition of cliff sites was controlled by both water and substrate. This is demonstrated by multivariate analyses i.e. NMDS ordination, MRPP, and indicator species analysis.

Ordination A three dimensional ordination solution resulted in a final stress of 14.26, indicating an effective ordination with little risk of drawing false inferences (McCune and Grace 2002). The first ordination axis separated samples along a water gradient (Figs. 6.4a, 6.5a). Clusters indicating intermediate water treatments were poorly defined and often overlapped with dry replicates (Figs. 6.4a, 6.5a). The second and third axes separated substrates (Fig. 6.4b). Figure 6.5 shows well separated combination treatment clusters particularly in dimensions 1 and 2. When used as explanatory categorical variables water, substrate, and combination treatments all explained significant amounts of variation in ordination scatter (Table 6.1).

MRPP Analysis Multi-Response Blocked Permutation Procedure tests showed that water, substrate, and combination treatments (i.e. water/substrate combinations) significantly affected cliff communities (Table 6.2). All water and substrate comparisons and thirteen of fifteen possible combination comparisons had significantly different community composition (Table 6.2). Wet treatments were very similar between substrates resulting in a high *p*-value for the null hypothesis of no difference between andesite wet and lime wet treatments ($p = 0.77$, Table 6.2).

Indicator Species Analysis (ISA)

Twenty-seven species significantly indicated ($p \leq 0.05$) at least one moisture, substrate or combination treatment (Table 6.3). Most of these species are widespread in the Rocky Mountain and coastal Cordilleras (Table 6.3).

Moisture Indicators Sixteen taxa were significantly associated with either dry or wet conditions (Table 6.3). Dry condition indicators were lichens *Aspicilia caesiocinerea, Caloplaca saxicola, Lecidella stigmatea, Lobothallia alphoplaca, Physcia dubia, Rhizocarpon geographicum, Staurothele drummondii, Xanthoria elegans,* and *Candelariella spp.*, and the bryophyte genus *Schistidium* (Table 6.3). Indicators of wet conditions were the vasculares *Cystopteris fragilis, Mimulus guttatus, Saxifraga cespitosa, Epilobium clavatum, and Saxifraga odontoloma* and bryophytes *Cratoneuron filicinum, and Philonotis fontana* (Table 6.3). No species were significantly indicative of intermediate moisture.

Substrate Indicators Seven taxa were significantly related to either limestone or andesitic substrates at α = 0.05. Significant andesite indicators were lichens *Aspicilia caesiocinerea* and *Lecidea atrobrunnea*. Significant lime indicators were lichens *Staurothele fissa, Toninia candida,* and *Collema* spp., moss *Schistidium* spp., and the vascular plant *Sedum lanceolatum* (Table 6.3).

Combination Substrate-Moisture Indicators Eighteen taxa were significant indicators of combination treatments (Table 6.3). Note that several of these species were also indicators of more general moisture and substrate conditions described above (Table 6.3). Dry andesite indictors were *Aspicilia caesiocinerea, Lecidea atrobrunnea Caloplaca saxicola, Candelariella* spp., *Lecidea stigmatea, Physcia dubia, Rhizocarpon geographicum, Rhizocarpon geminatum,* and *Rhizoplaca melanopthalma* (Table 6.3). Dry limestone indicators were *Collema* spp., *Schistidium* spp., and *Xanthoria elegans* (Table 6.3). Andesite wet indicators were *Saxifraga rivularis,* and *Philonotis fontana* (Table 6.3). Wet limestone indicators were *Epilobium clavatum, Mimulus guttatus,* and *Saxifraga odontoloma* (Table 6.3). No species indicated combination treatments associated with intermediate water (i.e. andesite-intermediate, lime-intermediate).

Substrate Characteristics

Andesitic rocks were more porous, absorbed more water from air and rain, and supplied it longer than limestone (Table 6.4). Porosity was documented by air escaping from submerged rocks and by lower andesite density. Andesite absorption of liquid water was approximately 6 times that of limestone (Table 6.4). Andesite absorption of water from air was approximately 10 times that of limestone at 20%, 75%, and 100% RH (Table 6.4). More than 26 hours after saturation, andesite continued to retain relatively large quantities of water (0.009 mL cm^{-2}), while saturated limestone samples were essentially dry in less than 2 hours in room conditions.

The mineralogy of limestone (calcite and dolomite) and andesite (andesine, augite, and smectite clays) were very different (Table 6.4). All limestone samples tested positively for calcium while no andesite samples did (Table 6.4). Limestone samples were significantly more basic than andestic samples due to the presence of calcite which buffers H^+ (equilibrium pH = 8.6 and 6.6 respectively). Such pH differences may equate with large differences in substrate nutrient and toxin availability (Brodo 1973).

Discussion

Community Distribution--Major Life Forms

While life form composition of cliff vegetation varied strongly with water availability, we saw no evidence of life form variation with substrate (Fig. 6.3). On both substrates lichens were the dominant life form on dry cliff faces where desiccation resistance (Brodo 1973), and lack of requirement for rooting sites (Larson et al. 2000) allowed them to persist without competition. Lichens were generally excluded from wet sites where: 1) a conservative poikilohydric water use physiology was unnecessary, and 2) excess water may disrupt algal/fungal symbioses (S. Eversman, per. communication).

In contrast, vascular plants and mosses generally occupied wet (often densely vegetated) cracks and crevices near waterfalls (cf. Farris 1998, Ursic et al. 1997).

Community Distribution--Species

Unlike the distribution of life forms, species composition varied with respect to water, substrate, and combinations of water/substrate treatments (Tables 6.1-6.3, 6.5, Figs. 6.3-6.5). This result is consistent with the observation that, while general strategies (e.g. life forms) may account for general distributional trends (e.g. lichens on dry cliffs), the success of these strategies will often spur specialization to narrower niches (Begon et al. 1996). The spatially heterogeneous environments of cliffs may be particularly conducive to niche differentiation (cf. Cody 1975, Escudero 1996).

Species Distributions with Respect to Water While ordination diagrams (Figs. 6.3-6.4, Table 6.1) and MRPP analyses (Table 6.2) showed a clear separation between dry and wet transects, large confidence intervals around intermediate treatment centroids (Fig. 6.5) indicate that some sites only 10-30 meters from waterfalls were very dry (since their community responses resembled those of dry sites), and would have been better assigned to the dry moisture category. Note the position of several intermediate transects at the far left (dry) side of dimension 1 in ordination diagrams (Fig. 6.4a and 6.5a). This error in *a priori* designation does not affect determination of dry or wet indicators (since none of these transects were misclassified), but would affect the ability of indicator species analysis to discern significant indicators of intermediate conditions. No species indicating intermediate moisture or intermediate moisture combination treatments (i.e. andesite-intermediate, limestone-intermediate) were found in our analyses.

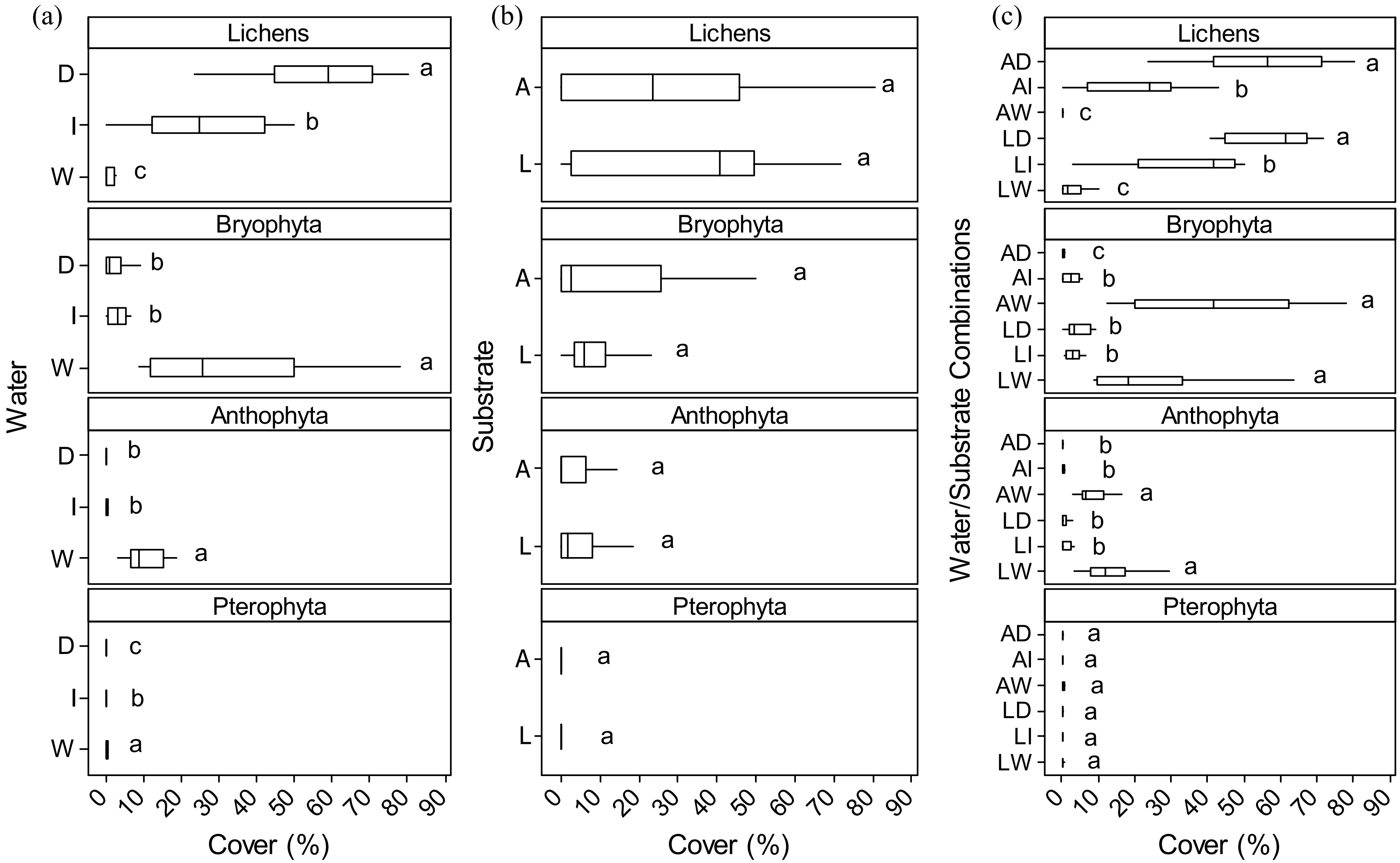

Figure 6.3. Response of life form cover to (a) substrate, (b) water, and (c) and combination treatments. D = Dry, I = Intermediate, W = Wet, A = Andesite, L = Limestone. Interquartile ranges are indicated by clear boxes. Medians given by centerline, Boxes with different letters are significantly (α = 0.05) different using Kruskal-Wallis tests with Dunn’s simultaneous pairwise comparisons.

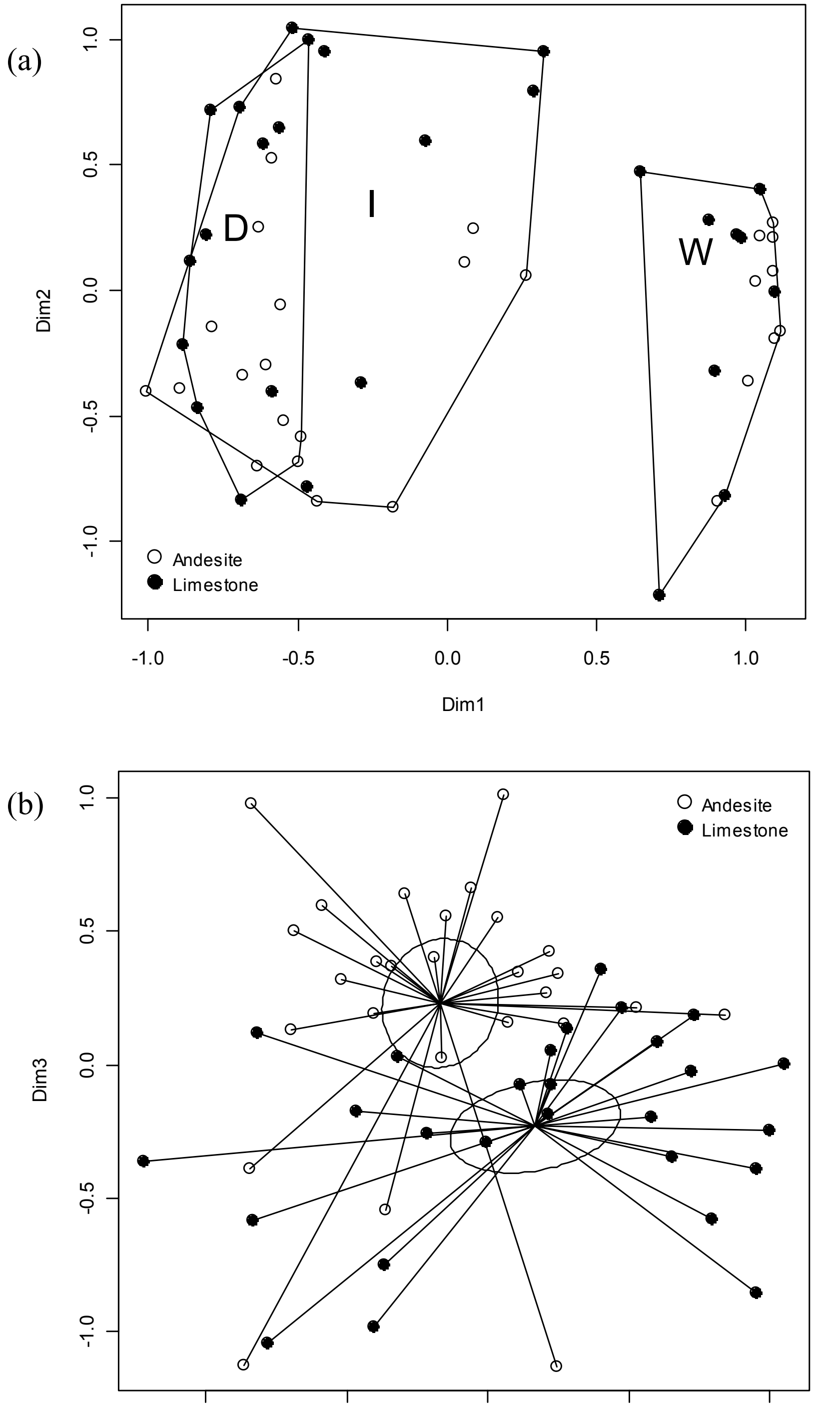

Figure 6.4. NMDS distribution of communities with overlays indicating water and substrate treatments. a) Hulls encircle communities of dry (D), intermediate (I), and wet (W) treatments. b) Spiders diagrams indicate communities of andesite and limestone. Ellipses indicate the 95% confidence intervals around treatment centroids.

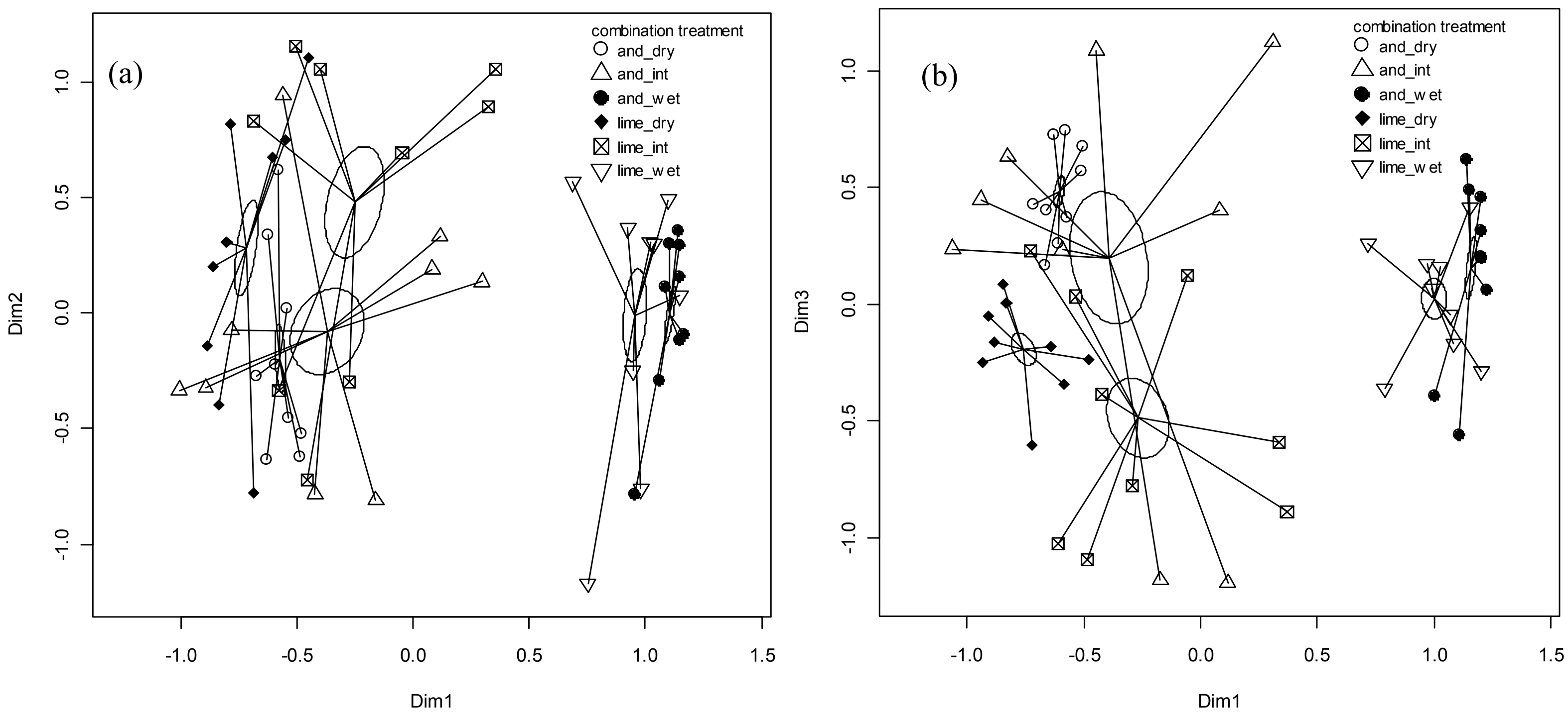

Figure 6.5. Ordination with six water/substrate combination treatments indicated. Spiders connect replicates with the same treatment. Ellipses indicate 95% confidence intervals around treatment centroids.

Table 6.1. Results from factor fitting analysis showing relationship of treatments to NMDS configurations (i.e. Figs. 6.4 and 6.5).

	Dims 1 and 2		Dims 2 and 3		Dims 1 and 3	
	r^2	p-value	r^2	p-value	r^2	p-value
Water	0.57	< 0.001	0.04	0.425	0.63	< 0.001
Substrate	0.03	0.18	0.14	< 0.001	0.067	0.04
Water-substrate combo.	0.63	< 0.001	0.23	< 0.001	0.721	< 0.001

Table 6.2. Multi-Response Permutation Procedure (MRPP) tests comparing communities with respect to water substrate and combination treatments. Asterisks indicate *p*-values were significant ($\alpha = 0.05$) after adjustment for simultaneous inference.

Treatment (pairwise comparisons)	*A*[1]	*T*[2]	*p*-value[3]
Water			
All (54)	0.110	-17.564	0.000000*
wet vs. dry (18)	0.140	-18.086	0.000000*
wet vs. intermediate (18)	0.0917	-13.226	0.000000*
dry vs. intermediate (18)	0.025	-3.601	0.004060*
Substrate			
All (54)	0.016	-3.806	0.003568*
Substrate-Water Combinations			
All (54)	0.139	-13.542	0.000000*
lime-dry vs. lime-intermediate (9)	0.029	-1.466	0.085463
lime-dry vs. lime-wet (9)	0.127	-8.533	0.000004*
lime-dry vs. andesite-dry (9)	0.072	-4.422	0.001455*
lime-dry vs. andesite-intermediate (9)	0.0321	-2.763	0.010252*
lime-dry vs. andesite-wet (9)	0.160	-9.017	0.000010*
lime-intermediate vs. lime-wet (9)	0.099	-6.081	0.000016*
lime-intermediate vs. andesite-dry (9)	0.118	-6.067	0.000056*
lime-intermediate vs. andesite-intermediate (9)	0.033	-1.939	0.044235
lime-intermediate vs. andesite-wet (9)	0.132	-7.056	0.000012*
lime-wet vs. andesite-dry (9)	0.161	-9.307	0.000014*
lime-wet vs. andesite-intermediate (9)	0.072	-6.484	0.000052*
lime-wet vs. andesite-wet (9)	-0.013	0.779	0.771509
andesite-dry vs. andesite-intermediate (9)	0.035	-2.847	0.010079*
andesite-dry vs. andesite-wet (9)	0.191	-9.587	0.000018*
andesite-intermediate vs. andesite-wet (9)	0.098	-7.293	0.000050*

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[1] The *A* statistic is a measure of homogeneity and agreement *within* treatments. When all transects are identical within groups then $A = 1$, the highest possible value for *A*. If heterogeneity within groups equals expectation by chance then $A = 0$. If heterogeneity within groups is greater than expected by chance $A < 0$.

[2] The *T* statistic, describes the separation between treatments. The more negative the *T* statistic the stronger the separation.

[3] p = probability of Type I error for H_0: no difference between treatments.

Table 6.3. Species which indicate water, substrate, and water–substrate combinations at α = 0.05. Indicator values which range from 0 (no indication) to 100 (perfect indication) and their statistical significance are shown for each species.

	Indicators (citations supporting ISA results)	LF^1	Indicator value	*p*-val.	Geog. Range (citation)^2
Moisture	Dry				
	Aspicilia caesiocinerea (1)	L	52.3	0.001	Entire (1)
	Candelariella spp. (1)	L	74.5	0.001	Entire (1)
	Lecidea stigmatea (1)	L	35.6	0.003	Entire (1)
	Lobothallia alphoplaca (1)	L	22.2	0.038	Disjunct, mostly southern (1)
	Physcia dubia (1)	L	22.2	0.022	Entire (1)
	Rhizocarpon geographicum (1)	L	22.2	0.022	Entire (1)
	Staurothele drummondii (1)	L	62.8	0.001	Entire (1)
	Xanthoria elegans (1)	L	67.1	0.001	Entire (1)
	Schistidium spp. (2)	M	46.9	0.008	Entire (2)
	Wet				
	Cratoneuron filicinum	M	22.2	0.030	
	Cystopteris fragilis (2,12)	F	25.0	0.023	Entire (6)
	Philonotis fontana (9)	M	85.0	0.001	Entire (9)
	Epilobium clavatum (12)	P	77.8	0.001	Entire (8)
	Mimulus guttatus (2,12)	P	66.3	0.001	Entire (1)
	Saxifraga cespitosa (2,12)	P	22.2	0.028	Entire (5)
	Saxifraga odontoloma (2,12)	P	50.0	0.001	Southern (8)
Substrate	Andesite				
	Aspicilia caesiocineria (13-16)	L	46.6	0.001	Entire (1)
	Lecidea atrobrunnea (13-16)	L	18.5	0.042	Entire (1)
	Limestone				
	Collema spp. (1)	L	35.2	0.047	Entire (1)
	Staurothele fissa (1)	L	29.6	0.005	Mostly southern (1)
	Toninia candida (16)	L	18.5	0.041	Southern* (1)
	Schistidium spp. (2)	M	51.6	0.002	Entire (2)
	Sedum lanceolatum	P	18.5	0.046	Entire (3)
Moisture-substrate	Andesite-Dry				
	Aspicilia caesiocinerea (13-16)	L	73.2	0.001	Entire (1)
	Candelariella spp.	L	53	0.001	Entire (1)
	Caloplaca saxicola	L	33.3	0.024	Southern (1)
	Lecidea atrobrunnea (13-16)	L	43.1	0.006	Entire (1)
	Lecidea stigmatea (14,16)	L	31.2	0.030	Entire (1)
	Physcia dubia	L	31.5	0.040	Entire (1)
	Rhizocarpon geographicum (1)	L	30.6	0.024	Entire (1)
	Rhizocarpon geminatum (1)	L	28.7	0.040	Entire (1)
	Rhizoplaca melanopthalma (14-16)	L	30.6	0.025	Entire (1)
	Limestone-Dry				
	Collema spp.	L	31.6	0.039	Entire (1)
	Xanthoria elegans	L	57.2	0.001	Entire (1)
	Schistidium spp.	M	65.1	0.002	Entire (2)
	Andesite-Wet				
	Philonotis Fontana	M	55	0.001	Northern (4,7)
	Saxifraga rivularis	P	33.3	0.022	Entire (9)
	Limestone-Wet				
	Epilobium clavatum	P	58.4	0.001	Southern (3)
	Mimulus guttatus	P	34.8	0.044	Mostly southern (3)
	Saxifraga odontoloma	P	37	0.005	Entire (3)

Table 6.3 cont.

[1]LF = life form (L = lichen, M= moss, F = fern, P = Vascular plant).

[2]Refers to approximate North American latitude range: Southern = 30°-50°N, Northern = 40°-70°N, Entire = 30°-70°N, *Rocky Mountains only.

Citation numbers refer to both columns 2 and 6. 1=Brodo et al. 2001, 2=Kershaw et al. 1998, 3=Hitchcock and Cronquist 1973, 4=Aiken et al. 1999, 5=Hitchcock et al. 1961, 6=Haufler et al. 1993, 7=Rydberg 1921, 8=NatureServe 2005, 9=Lawton 1971, 10=Crum 2001, 11=Schofield 2002, 12=Dorn 1992, 13=DeBolt and McCune 1993, 14=Eversman 1995, 15=Eversman 1998, 16=Eversman et al. 2002.

Table 6.4. Surface characteristics of andesite and limestone rocks. *P*-values are for hypotheses of no difference between substrates. *N* = number of rock samples compared with Kruskal-Wallis nonparametric tests. Significance levels were adjusted for simultaneous inference using Dunn's (1964) procedure.

	Andesite		Limestone		
	Median	N	Median	N	*P*-val.
Rock character					
Mineralogy	andesine, augite, smectite clay		calcite, dolomite		
Density (g cm^{-3})	2.26	27	2.72	27	<0.001
Liquid H_2O absorption					
H_2O content (mL cm^{-2}) of saturated rocks	0.06	22	0.01	20	<0.001
Absorption of atmospheric H_2O (mL cm^{-2})					
H_2O abs. at 20% RH after 10 mins.	0.0003	18	<0.0001	27	<0.001
after 22 hours	0.005	12	0.0001	18	<0.001
H_2O abs. at 75% RH after 10 mins.	0.001	6	0.0001	9	0.001
after 23 hours	0.02	6	0.0008	8	0.002
H_2O abs. at 100% RH after 15 mins.	0.002	7	0.0001	6	0.003
after 22 hours	0.029	22	0.0004	19	<0.001
H_2O retention/storage (mL cm^{-2})					
H_2O content after drying 26.5 hours	0.009	15	0.0001	13	<0.001
pH—acidity/alkalinity					
Ca presence ("fizz test" with 0.5 M HCl)	100% Ca-	27	100% Ca+	27	
Log(mol OH^- increase) cm^{-2} after 15 mins.	-8.63	19	-7.23	19	<0.005
Equilibrium pH – initial (KCl) pH = ***ΔpH***	6.6-6.1=**0.5**	26	8.7-6.1=**2.6**	26	<0.001

Substrate specialists (i.e. species which persist solely on andesite or limestone) were generally not significant indicators of moisture conditions. This is true since they occurred in only half the potential replicates for a particular moisture treatment in ISA analyses. As a result ISA significant indicators of general moisture conditions should be considered particularly robust. Most significant dry lichen indicators including *A. caesiocinerea, L. stigmatea, P. dubia, X. elegans* are potential substrate generalists (Brodo et al. 2001). *Candellariella* spp. is a predictable dry condition indicator since it is largely a combination of *C. vitellina*, which is exclusive to dry non-calcareous substrates, and *C. aurella* which favors dry limestone (Brodo et al. 2001).

Our indicator species results for moisture are well supported by qualitative surveys and floristic keys (Table 6.3). The fern *Cystopteris fragilis,* and vascular plants *Mimulus guttatus, Saxifraga cespitosa, Epilobium clavatum, and Saxifraga odontoloma* are all well documented indicators of rocky, wet sites (Hitchcock et al. 1961, Hitchcock and Cronquist 1973, Kershaw et al. 1998). The bryophyte *Philonotis fontana* is a wide-spread hydrophile and substrate generalist (Lawton 1971). While not statistically significant, two foliose lichens from the genus *Dermatocarpon* (*D. intestiniforme* and *D. miniatum*) mostly occurred near waterfalls and appear to be hydrophilic in an ordered table of the data (Appendix E.3).

<u>Species Distributions with Respect to Substrate</u> While total cover of major life forms did not differ between the substrates (Fig. 6.3), species composition differences were illustrated by NMDS scatterplots and factor analyses (Figs. 6.4-6.5, Table 6.1), MRPP tests (Table 6.2), and indicator species analysis (Table 6.3).

Five lichens, one moss and one plant taxa significantly indicated ($p \leq 0.05$) andesite or limestone regardless of moisture (Table 6.3). As with the general moisture treatments indicators above, significant substrate indicators should be considered particularly robust since species responses to the substrates were consistent across all three moisture treatments.

Although *A. caesiocinerea and L. atrobrunnea* occurred occasionally on lime, both were very abundant on andesite. Locally both species have been found to indicate non-calcareous substrates in Glacier National Park (DeBolt and McCune 1993), the Beartooth Plateau (Eversman 1995), Grand Teton National Park (Eversman 1998), and other volcanic sites in Yellowstone National Park (Eversman 2002). Similarly, both species are abundant across a range of moisture conditions on non-calcareous/siliceous rock in the Niwot Range in Colorado (Flock 1978). Globally *A. caesiocinerea* is an important species on siliceous watercourses in England (Gilbert and Giavarini 1993, Gilbert and Giavarini 1997)

Lime indicators were more numerous and dependable. Significant lime indicators included five lichens *Staurothele fissa, Toninia candida, Collema spp.,* moss *Schistidium spp.* and the vascular plant *Sedum lanceolatum*. *S. fissa* and *T. candida* were two of seven species found only on calcareous rock in a comprehensive lichen inventory of Yellowstone National Park (Eversman et al. 2002) *T. candida* is acknowledged as a calciophile throughout North America (Brodo et al. 2002). *S. fissa* is an important component of calcareous lichen communities in Europe (Gilbert and Giavarini 1993, Gilbert 1996). Despite this it is often reported from non-calcareous substrates in North

America (Brodo et al. 2002, DeBolt and McCune 1993). Along with unidentified specimens from the same genus, *C. polycarpon, C. tenax,* and *C. undulatum* were combined to create the composite *Collema* spp. Because *C. polycarpon, C. tenax,* and *C. undulatum* are recognized calciophiles (Brodo et al. 2002) the genus *Collema* was also a significant indicator of limestone. *Protoblastenia calva*, a common regional lichen and calciophile (Eversman et al. 2002), was found only on lime substrates in the study area, although it did not occur in any transects. A list documenting all species that occurred in or near transects is included in Appendix E.

Species Distributions With respect to Moisture-Substrate Combinations Simultaneous use of substrate and moisture often explained community variability better than using either variable alone (Tables 6.1-6.2, Figs. 6.3- 6.4). In MRPP tests particularly high '*A'* and low '*T'* statistics indicate high levels of homogeneity within groups and high levels of heterogeneity between groups respectively (Table 6.2). Greater heterogeneity existed among dry sites (Table 6.2). Although andesite and limestone wet groups were similar, andesite and limestone dry groups were significantly different (Table 6.2). The difference of community composition among the six treatments is also illustrated by the non-overlapping confidence intervals of treatment clusters in the NMDS ordination (Figure 6.5, Table 6.1). These results are strongly reinforced by a qualitative examination of the relevé table (Appendix E.3). In particular a block of seven lichen species indicating andesitic dry conditions is evident (Appendix E.3).

A number of lichen species were dry andesite indicators. *A. caesiocinerea and L. atrobrunnea* were discussed above as strong indicators of andesitic substrate regardless of moisture. Along with these species, eight other lichen taxa were indicators of dry andesite. These were *Candelariella* spp., *Caloplaca saxicola, Lecidella stigmatea, Lobothallia alphoplaca, Physcia dubia, Rhizocarpon geographicum, Rhizocarpon geminatum* and *Rhizoplaca melanopthalma*. Locally *L. stigmatea, R. geographicum,* and *R. melanopthalma* are found on primarily on non-calcareous rock on the Beartooth Plateau (Eversman 1995), and in other areas of Yellowstone National Park (Eversman et al. 2002). *R. geographicum and R. geminatum* grow almost solely on siliceous non-calcareous substrates throughout North America (Brodo et al. 2002), and Europe (Gilbert and Giavarini 1993). *Candelariella* spp. should be disregarded as an andesite-dry indicator since it includes the calciophile *C. aurella*. Its high indicator value for andesitic dry conditions is probably due to because a number of unidentified individuals in *Candelariella* spp. were the siliceous lichen *C. vitellina.*

Lichens *Xanthoria elegans*, *Collema* spp., and the moss *Schistidium* spp. were significant indicators of dry limestone conditions. *Schistidium* spp. has been mentioned independently as a general indicator of both dry conditions and limestone substrates (Table 6.3). Several species from the genus *Schistidium* are recognized as indicators of dry limestone sites particularly *S. apocarpum* (Kershaw et al. 1998). While the genus *Collema* should be considered a strong indicator of limestone substrates, it should be regarded cautiously as an indicator dry-limestone since its constituents, *C. polycarpon, C. tenax,* and *C. undulatum* may occupy different segments of the water gradient (S. Eversman per. obs.).

Species requiring both wet conditions *and* a specific substrate include vascular plants and mosses. *Saxifraga rivalis,* and *Philonotis fontana* indicated andesitic wet conditions, While *Epilobium clavatum, Mimulus guttatus,* and *Saxifraga odontoloma* indicated wet limestone conditions. Although these species are documented hydrophiles (Kershaw 1998), substrate preferences have not been previously noted.

Factors Driving Community Variability

Water Largest changes in cliff community composition are surely due to differences in available water (Figs. 6.4a, 6.5a; Tables 6.1 and 6.2; cf. Larson 2001, Foote 1966). Hydric species (mosses, ferns, and vascular plants) disappear with distance from waterfalls because they control transpiration poorly and/or rely on water for reproductive purposes. In contrast, species including the moss *Schistidium* spp., and lichens tolerate dry sites with a poikilohydric strategy, i.e. functioning when wet and aestivating when dry.

Substrate Less dramatic differences in community composition are due to substrate differences. Andesite and limestone rocks differed with respect to water retention, water absorption, and mineralogy (e.g. acidity/alkalinity).

Porous surfaces and hydrophilic smectite clays allowed andesite rocks to retain more water when saturated, retain water for longer periods of time, and absorb more atmospheric water than limestone (Table 6.4). Substrate water supply affects cryptogam community composition on both bark (e.g., Hale 1955) and rock-surfaces (Larson et al. 2000; Pentecost 1980). The interaction of substrate with distance from waterfalls, and its effect on community distribution is notable in ordinations (Figs. 6.4 and 6.5). Note that within both wet and dry treatments limestone communities lie further to the left (were drier) on the water gradient (dimension 1) than sites occupying andesite (Figs. 6.4a, 6.5a).

Mineralogy further distinguishes andesite and lime substrates and their communities (ordination dimensions 2 and 3, Fig. 6.3b). (Table 6.4). Variability in pH across substrates causes certain minerals and toxins (e.g. P, Fe, Ca) to vary in availability (Brodo 1973). Cryptogam communities growing on calcite rocks have been previously found to differ from those on lime-free rocks, particularly among lichen species (Armstrong 1990, Brodo 1973).

Conclusions

Major life forms (flowering plants, ferns, mosses, and lichens) varied with available water, but not with substrate. Both vascular and non vascular plant cover declined with increasing drought, while lichen cover increased due to desiccation tolerance.

Unlike major life forms, species composition differed with respect to water, substrate and water substrate combinations This reinforces our expectation that members of major life forms are strongly driven to occupy different segments of environmental (e.g. water or substrate) gradients (i.e. evolutionary divergence, Begon et al. 1996) . We speculate that community differences between andesite and limestone substrates are due to differences in resource (water/nutrient) or toxin availability.

Identification of indicator species may be useful to field practitioners who are characterizing environmental conditions of particular sites or for tracking community responses to environmental changes (e.g. acid rain or invasive herbivores). Comparison of species morphology and physiology along water and substrate gradients will help physiologists more precisely identify causal factors and plant adaptations to them.

To summarize, our analyses suggest regulation of community composition by three environmental forces. First, major life-forms vary on the water gradient due to differential inputs of liquid water. Second, species composition varies on the water gradient due to substrate water relations differences (e.g. the superior water absorption/retention capacity of andesite compared to limestone). Third, species composition varies on a substrate gradient associated mineralogy (e.g. pH and the availability of nutrients or toxins).

Previously Undocumented species

In accordance with other cliff studies, a large number of species previously undocumented for the region were collected and identified on Abiathar and Barronette cliffs (cf. Okusanya 1979, Ursic et al. 1997, Farrar 1998). Of special note are the lichens *Gyalidea hyalinescens, Rinodina* cf. *calcigena*, and *Rinodina* cf. *oleaca* which are rare throughout the Northern Rocky Mountains (S. Eversman pers. obs.). A complete list of all species including new reports for YNP is included as Appendix E.

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Literature cited

Aiken, S. G., Dallwitz, M. J., Consaul, L. L., McJannet, C. L., Gillespie, L. J., Boles, R. L., Argus, G. W., Gillett, J. M., Scott, P. J., Elven, R., LeBlanc, M. C., Brysting A. K., and H. Solstad. 1999. Flora of the Canadian Arctic Archipelago: Descriptions, Illustrations, Identification, and Information Retrieval. Version: 29th April 2003. http://www.mun.ca/biology/delta/arcticf/.

Anderson, L. et al. 1990. List of North American Mosses: The Bryologist 93: 450-499.

Armstrong, R. A. 1990. The influence of calcium and magnesium on the growth of the lichen *Parmelia saxitalis* and *Xanthoria Parietina* on slate substrates. Environemntal and experimental biology 30(1): 51-57.

Bartlett, R. M., Reader, R. J., and D. W. Larson. 1991. Multiple controls of cliff edge distribution of patterns of *Thuja occidentalis* and *Acer saccharum* at the stage of seedling recruitment. Journal of Ecology. 79: 183-197.

Begon, M., Harper, J. L., and C. R. Townsend. 1996. Ecology: individuals, populations and communities, 3rd edition. Blackwell Science. Oxford, UK.

Bray J. R., and J. T. Curtis. 1957. An ordination of the upland forest communties in southern Wisconsin. Ecological Monographs. 27: 325-349.

Brice, J. C. & H. L. Levin 1960. Laboratory Studies in Earth History. Wm. C. Brown Co., Dubuque, Iowa, U.S.A.

Brodo, I. M. 1973. Substrate ecology. Pages 401-441 in V. Ahmadjihan and M. E. Hale, eds. The lichens. Academic Press, London.

Brodo, I. M., Sharnoff, S. D., and S. Sharnoff. 2001. Lichens of North America. Yale University Press, New Haven.

Bunce, R. G. H. 1968. An ecological study of Ysgolion Duon, a mountain cliff in Snowdonia. Journal of Ecology. 56 (1): 59–75.

Coates, F., and J. B. Fitzpatrick. 1992. Environmental relations and ecological responses of some higher plants on rock cliffs in Northern Tasmania. Australian Journal of Ecology.

Cody, M. L. 1975. Towards a theory of continental species diversities. In: Ecology and Evolution of Communties, M. L. Cody, and J. M. diamond, eds., pp. 214-257. Belknap, Cambridge, MA., USA.

Crum, H. A. 2001. Conardia, In Bryophyte Flora of North America, Provisional Publication, Buffalo Museum of Science. www.buffalomuseumofscience.org/BFNA/bfnamenu.htm

Davis, S. & P. Reitan. 1976. Geology, Our Physical Environment. McGraw-Hill, Boston, MA, U.S.A.

DeBolt, A., and B. McCune. 1993. Lichens of Glacier National park. The Bryologist. 96: 192-204.

Dorn, R. D. 1992. Vascular Plants of Wyoming. Mountain West Publishing. Cheyenne WY.

Dufrêne and Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetric approach. Ecological Monographs. 67(3): 345-367.

Dunn, O. J. 1964. Multiple comparisons using rank sums. Technometrics 6: 241-252.

Ellenberg, H. 1979. Ziegerwerte der Gefässpflanzen Mittleeuropas. Scripta Geobotanica 9, Göttingen, 121 pgs.

Escudero, A. 1996. Community patterns on exposed cliffs in a Mediterranean calcareous mountain. Vegetatio. 125: 99-110.

Esslinger, T. L. 2006. A cumulative checklist for the lichen-forming, lichenicolous and allied fungi of the continental United States and Canada. North Dakota State University: http://www.ndsu.nodak.edu/instruct/esslinge/chcklst/chcklst7.htm (First Posted 1 December 1997, Most Recent Update 10 April 2006), Fargo, North Dakota.

Eversman, S. 1995. Lichens of alpine meadows on the Beartooth Plateau, Montana and Wyoming, U.S.A. 27 (4): 400-406.

Eversman, S. 1998. Lichens of Grand Teton National Park, Wyoming, in Eds. Glenn, M. G., Harris, R. C., Dirig, R., and S. Cole, Lichenographia Thomsoniana: North American Lichenology in honor of John W. Thompson. Mycotoxon ltd. Ithaca NY. 295-307.

Eversman, S., Wetmore, C. M., Glew, K., Bennet, J. P. 2002. Patterns of lichen diversity in Yellowstone National Park. The Bryologist. 105(1): 27-42.

Faith, D. P., Minchin, P. R. & Belbin, L. 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio. 69: 57-68.

Farrar, D. R. 1998. The tropical flora of rockhouse cliff formations in the Eastern United States. Journal of the Torrey Botanical Society. 1258(2): 91-108.

Farris, M. A. 1998. The effect of rock-climbing on the vegetation of three Minnesota cliff systems. Canadian Journal of Botany. 76: 1981-1990.

Flock, J. W. 1978. Lichen-bryophyte distribution along a snow-cover-snow-moisture-gradient, Niwot range, Colorado. Arctic and Alpine research. 10 (1): 31-47.

Foote, K. G. 1966. The vegetation of lichens and bryophytes on limestone outcrops in the Driftless Area of Wisconsin. Bryologist. 69: 265-292.

Gilbert O. L. and J. L. Giavarini. 1993. The lichens of high ground in the English lake district. Lichenologist 25(2): 147-164.

Gilbert, O. L., and J. L. Giavarini. 1997. The lichen vegetation of acidic watercourses in England. Lichenologist. 29 (4): 347-367.

Gilbert, O. L. 1996. The lichen vegetation of chalk and limestone streams in Britain. Lichenologist 28(2): 145-149.

Good, R. E., and N. F. Good. 1970. Vegetation of the sea cliffs and adjacent uplands on the north shore of Long Island, New York. Bulletin of the Torrey botanical club. 97(4): 204-208.

Graham, L., and R. L. Knight. 2004. Multi-scale comparisons of cliff vegetation in Colorado. Plant Ecology. 170: 223-234.

Graydon, M. 1996. Mountaineering, Freedom of the hills (5th edition). The Mountaineers. Seattle, WA. 350pp

Haufler, C. H., Moran, R. C., and M. D. Windham. 1993. Cystopteris. In: Flora of North America. Eds. Flora of North America editorial committee. Oxford University press

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press. Seattle WA.

Hitchcock, C. L., Cronquist, A., Ownbey, M., and J. W. Thompson. 1961. Vascular plants of the Pacific Northwest. University of Washington Press.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scandinavian journal of statistics. 6: 65-70.

Holdridge, L. R. 1947. Determination of the world plant formations from simple climatic data. Science. 105: 367-368.

Hora, F. B. 1947. The pH range of some cliff plants on rocks of different geological origin in the Cader Idris area of North Wales. Journal of Ecology. 35(1/2): 158-165.

Houston, D. B., Schriener E. G., and B. B. Moorhead. 1994. Mountain goats in Olympic National Park: biology and management of an introduced species. Scientific Monographs. NPS/NROLYM/NRSM-94125.

Kershaw, L., MacKinnon, A., and J. Pojar. 1998. Plants of the Rocky Mountains. Lone Pine press, Edmonton, AB, Canada.

Kruskal, J. B., and M. Wish. 1978. Multidimensional scaling. Sage Publications. Beverly Hills, CA. 93 pp.

Larson, D., U. Mattes & P. E. Kelly. 2000. Cliff Ecology. Cambridge University Press, Cambridge, U.K.

Lawton, E. 1971. Moss flora of the Pacific Northwest. Hattori botanical library, Nichinan, Miyazaki, Japan.

Lemke, T. O. 2004. Origin, expansion, and status of mountain goats in Yellowstone national Park. Wildlife Society Bulletin. 32(2): 532-541.

McCune, B., and M. J. Mefford. 1999. PC-ORD ver. 4 multivariate analysis of ecological communities. MjM Software design. Gelenden Beach OR. 237 pp.

McCune, B., and J.B. Grace. 2002. Analysis of ecological communities. MjM Software design. Gelenden Beach OR. 300 pp.

Metesh, J., English, A., Lonn, J., Kendy, E., and C. Parret. 1999. Hydrogeology of the Upper Soda Butte Creek Basin, Montana. Montana Bureau of Mines and Geology. 62 pp.

Mielke, P. W. Jr. 1984. Meteorological applications of permutation techniques based on distance functions. pp. 813-830. In P. R. Krishnaiah & P. K. Sens eds., handbook of Statistics, VOl. 4. Elsevier Science Publications.

Moore, D. M. & R. C. Reynolds. 1997. X-ray Diffraction and the Identification and Analysis of Clay Minerals. Oxford University Press, Oxford, U.K.

NatureServe. 2005. NatureServe Explorer: An online encyclopedia of life [web application]. Version 4.5. NatureServe, Arlington, Virginia. Available http://www.natureserve.org/explorer. (Accessed: September 25, 2005).

Neter, J., Kutner, M. H., Nachtsheom C. J., and W. Wasserman. 1996. Applied linear statistical models, 4th edition. Boston, MA., USA.

Nuzzo, V. A. 1996. Sructure of vegetation on exposed cliffs and the effects of rock climbing. Canadian Journal of Botany. 74: 607-617.

Oksanen, J. 2004. vegan ver. 1.6-2, a community ecology package. http://cran.r- project.org

Okusanya, O. T. 1979. An experimental investigation into the ecology of some maritime cliff species: II. Germination studies. Journal of Ecology. 67(1): 293-304.

Orlich, S. 2004. Kruskal-Wallis multiple comparisons with a MINITAB macro Dunn's test. Minitab Inc. 14 pgs.

Pentecost, A. 1980. The lichens and bryophytes of rhyolite and pumice-tuff rock outcrops in Snowdonia, and some factors affecting their distribution. Journal of Ecology 68: 251–267

Roberts, D. 2005. Vegetation classification in R, for labdsv ver. 1.1-1, vegetation ecology package. http://www.cran.r- project.org. unpubl.

Rydberg, P. A. 1921. Flora of the Rocky Mountains and the adjacent Great Plains. Intelligence printing, Lancaster PA.

Schmidt, J., Kricke, R., and G. B. Feige. Measurement of bark pH with a modified flathead electrode. The lichenologist. 33: 456-460.

Schofield, W. B. 2002. Field guide to the liverwort genera of Pacific North America. University of Washington Press, Seattle WA., U.S.A.

Smedes, H. W., and Protska, H. J. 1972. Stratigraphic framework of the Absaroka Volcanic Supergroup in the Yellowstone National Park region: U.S.G.S. Prof. Pap. 720-C, US Gov. Print. Office, Wash. DC, 33 pgs
.

Stotler, R. and B. Crandall-Stotler. 1977. A checklist of the liverworts and hornworts of North America. The Bryologist 80: 407-428.

Ursic, K. A., Kenkel, N. C., and D. W. Larson. 1997. Revegetation of cliff faces in abandoned limestone quarries. Journal of Applied Ecology. 34: 289-303.

Venables S., and B. Ripley. 2004. MASS ver. 7.2-1. http://cran.r-project.org

Weaver, T. 1990. Climates of subalpine pine woodlands. p 72-79 *in* W Schmidt and K McDonald ed 1990 Proceedings-- Symposium on whitebark pine ecosystems: ecology and management of a high mountain resource. USDA Forest Service General Tech Report INT-270. Ogden UT.

Wiser, S. K. 1998. Comparison of Southern Appalachian high-elevation outcrop plant communities with their Northern Appalachian counterparts. Journal of Biogeography. 25: 501-513.

Zimmerman, G. M., Goetz, H., and P. W. Kielke, Jr. 1985. An improved statistical method for group comparisons to study the effects of prairie fire. Ecology. 66: 606-611.

CHAPTER 7

USING GEOMETRIC AND NON-GEOMETRIC INTERNAL EVALUATORS TO COMPARE EIGHT VEGETATION CLASSIFICATION METHODS[*]

Introduction

Given the large number of classification methods available, ecologists need criteria to choose among them, i.e. measures of classification effectiveness. Classification solutions can be evaluated with external or internal tests (Gauch and Whittaker 1981). External tests compare the results of a classification with a previously established standard. Examples include recovery of clusters embedded within simulated datasets (Milligan and Cooper 1985; Belbin and McDonald 1993; Hirano et al. 2002), or recovery of subjectively assigned *a priori* clusters from ecological data (Cao et al. 1997; Gauch and Whittaker 1981). In contrast, internal tests use the characteristics of the clusters themselves to gauge effectiveness. Examples include cophenetic correlation (Sneath and Sokal 1973), and maximization of between cluster variance (Orloci 1967).

Geometric and Non-Geometric Evaluators

Internal evaluators can be separated into two classes, those which use geometric criteria and those which use non-geometric criteria. Consider a typical vegetation data matrix with plant species as columns and samples as rows. In most situations ecologists are interested in clustering samples based on their compositional similarity/dissimilarity.

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After distances or dissimilarities between samples have been calculated, and a classification has been imposed on a dataset, most internal evaluators index classification effectiveness based on cluster compactness (e.g. average silhouette width, Kauffman and Rousseeuw 1990), or the similarity/dissimilarity of samples between or within clusters (e.g. C-index, Hubert and Levin 1975, Goodman-Kruskal index, Goodman and Kruskal 1954). These algorithms are geometric evaluators, i.e. methods which evaluate classification effectiveness based on the relationship/geometry of samples within and between clusters (cf. Dale 1991). In contrast, non-geometric evaluators measure classification effectiveness with respect to species distributions. For instance, a clustering solution in which a species occurs predominantly in one cluster while being absent from others indicates a “real” cluster structure from the perspective of that species. To oversimplify: geometric evaluators determine classification effectiveness based on samples (rows) while non-geometric evaluators determine classification effectiveness based on species (columns).

Dale (1995) criticized internal tests which evaluate classifications using purely geometric criteria since they ignore what many phytosociologists are interested in--characterization with indicator species—and emphasized the lack of non-geometric strategies for evaluating classification solutions. A recently developed non-geometric (flexible-asymmetric) evaluator is indicator species analysis (ISA, Dufrêne and Legendre 1997), which indexes species abundance and fidelity to treatments and allows evaluation of classification solutions. Although not previously considered for this purpose, a number of standard ecological indices can also be adapted as non-geometric evaluators, e.g.

Morisita's index of niche overlap (Horn 1966), Murdoch's index of prey preference (Jacobs 1974), and Hurlbert's Index (Hurlbert 1978). Another unreviewed non-geometric evaluator is Indicator Species Analysis Minimizing Intermediate Constancies (ISAMIC, Roberts 2005), which measures the degree to which species are either always present or always absent within clusters or types.

Using Internal Evaluators to Compare Classification Methods

In most cases classification methods have been compared using only external evaluations while internal evaluators (both geometric and non-geometric) have been ignored (Belbin and McDonald 1993, Cao et al. 1997, Gauch and Whittaker 1981, Hartigan 1975, many others). Furthermore, while many internal evaluation strategies exist (Dale 1991), most have been used solely as stopping rules in classification solutions (i.e. determining the optimal number of clusters between 1 and n clusters, where n = number of classified objects). Comparisons of classification method efficacy using internal evaluators are rare though studies which have used a single criterion include Sokal and Rohlf (1962) who compared four methods using cophenetic correlation, Dufrêne and Legendre (1997) who compared two methods using ISA indicator values, and Milligan (1980) who compared fifteen methods using point biserial correlation. Only one paper we know of (Bolshakova and Azuaje, in press) has compared classification methods using multiple internal evaluators.

Classification comparisons using multiple internal evaluators are important for at least three reasons. First, multivariate techniques may go in and out of favor without sufficient testing (Beals 1984, McCune and Grace 2002). Inadequate assessments include comparisons of classification methods using biased criteria which always make one method appear superior to others (Kauffman and Rousseeuw 1990, pg. 239). Internal evaluators may provide important additional criteria since external tests have often contradicted each other. Compare the results of Belbin and McDonald (1993), Gauch and Whittaker (1981), and Cao et al. (1997), or the results of Kuiper and Fisher (1975) to Everitt (1977). These external evaluations using synthetic data with "real" clusters differed in what they perceived as the best classification method. Second, external evaluation of classification solutions may be difficult with non-simulated datasets. Thus, scientists working with ecological (non-synthetic) data must rely largely on internal strategies for objective assessment of classifications. Indeed, by choosing evaluators with appropriate optimality criteria, one can verify that a classification has the characteristics one is interested in (e.g. compact clusters, high fidelity of species to clusters). Finally, and perhaps most importantly, many authors agree that there is no correct classification method for all datasets (Dubes and Jain 1976; Kaufman and Rousseeuw 1990), suggesting that the relationship between classification methods and data should be examined preceding a definitive classification of data. For example, variance minimization linkage (i.e. Ward's Method) recovers clusters effectively from spherical multivariate-normal distributions but may perform poorly when clusters in a dataset are ellipsoidal (Everitt 1977). Internal evaluation allows examination of the suitability of ecological data to particular classification methods.

Objectives

In this paper we will compare and evaluate the classification solutions of two distinct vegetation datasets produced by eight commonly used classification methods. Agreement among classifiers will be determined, and classification solutions will be assessed with five geometric and four non-geometric internal evaluators. We have three objectives.

1. Determine how different/similar classifications solutions of different methods are for ecological datasets. We expect greatest incongruity between methods which implicitly seek and those which do not seek spherical clusters in data.
2. Identify which classification methods are deemed particularly effective or ineffective by internal evaluators, i.e. recognize methods with consistent classification characteristics as identified by internal evaluators (e.g. compact clusters, or high fidelity of species to clusters).
3. Recognize how classification evaluators agree/differ in their interpretation of classification solutions. Of particular interest is the extent of agreement between geometric and non-geometric evaluators.

Methods

Datasets

Two vegetation datasets were analyzed. The first described alpine vegetation from three high altitude ranges in the Northern Rocky Mountains (the Washburn, Absaroka and Beartooth Ranges). This dataset contained 178 plots and 180 species and was taken from author Aho's dissertation work. A second dataset described a prairie steppe ecosystem from Southeast Montana. It contained 113 plots and 173 species, and was generated from sampling intended to guide mine reclamation/revegetation. (Weaver and Aho 2006). Quantitative responses for both datasets were ocular estimates of species cover within sampled plots.

Classification Methods

The eight evaluated classification methods consisted of five hierarchical agglomerative methods: [flexible-β linkage (Lance and Williams 1967), Ward's method (Ward 1963), complete linkage (McQuitty 1966), average linkage (Sokal and Michener 1958), and single linkage (Sokal and Sneath 1963)]; a hierarchical divisive method: [TWINSPAN (Hill 1979)]; and two non-hierarchical methods: [partitioning around medoids (PAM, Kauffman and Rousseeuw 1990), and k-means analysis (Hartigan and Wong 1979)]. The value $\beta = -0.25$ was used for flexible-β linkage as recommended by McCune and Grace (2002). TWINSPAN was run using default parameters from PC-ORD (McCune and Mefford 1999). Random starting points were used as initial cluster centers for k-means analysis. For six of the eight classification methods inter-stand dissimilarity was calculated with Bray-Curtis dissimilarity (Bray and Curtis 1957), an index often preferred by vegetation ecologists (Beals 1984). Euclidean distance was used for k-means analysis, and chi-squared distance was used for TWINSPAN since these two measures are integral to their respective algorithms. While Ward's linkage was originally designed for and restricted to Euclidean distance (Orloci 1978; Pielou 1984), we used Bray-Curtis dissimilarity. We made the substitution to be as be consistent as possible with other methods, and based on the demonstration that Ward’s method is often highly successful when used with non-Euclidean (dis)similarity measures (Cao et al. 1997; McCune and Grace 2002).

Classification Evaluators

The eight classification methods were compared with nine internal classification evaluators, most of which have been well tested and reviewed in the literature. The nine evaluators, consisting of five geometric and four non-geometric measures, are summarized in Table 7.1. Among geometric evaluators we introduce partition analysis (PARTANA) which measures the ratio of within-cluster similarity to between-cluster similarity. PARTANA is related to the W/B algorithm of McClain and Rao (1975), but uses similarities rather than dissimilarities or distances. Because similarity and dissimilarity are complements rather than opposites, PARTANA and W/B are generally not reciprocals except in the trivial case of no cluster structure (i.e. PARTANA = W/B = 1). Among non-geometric evaluators we introduce two previously unreviewed measures: an adapted form of Morisita’s index of niche overlap (Horn 1966), and Indicator Species Analysis Minimizing Intermediate Constancies (ISAMIC, Roberts 2005). Detailed descriptions and equations for all evaluators are included in Appendix F.

Procedure

Both datasets were classified with each of the 8 classification methods (i.e. 16 classifications). Classifications were pruned to find their 20 simplest solutions (i.e. 2 to 21 clusters). Within each dataset, each of the twenty solutions was 1) compared to the other seven solutions with the same numbers of clusters to find percent agreement among methods, and 2) was evaluated by each of the nine classification evaluators to compare solution efficacy/character.

Average percent agreement between methods (i.e. number of samples assigned by each method to the same cluster at a particular clustering level $\div$ total number of samples) was calculated for all possible pairwise combinations within each dataset ((8^2-8)/2 = 28 pairwise combinations). Average percent agreement for each of the pairwise combinations (e.g. average vs. single linkage) was calculated across the 20 clustering solutions. Thus, average percent agreement for an entire dataset (i.e. alpine or prairie) was calculated using $28 \cdot 20 = 560$ pairwise percent agreements. Pairwise agreement at each clustering level was tested for significance with Monte Carlo procedures by permutating categorical assignments of one of the two classification vectors being compared 1000 times and rechecking percent agreement at each permutation. Superimposing classification solutions onto the same 2-dimentsional NMDS ordination scatterplots (Kruskal and Wish 1978) allowed qualitative visual comparisons of classification agreement.

For both datasets, and each evaluator's assessment of each method, median values, confidence intervals for medians, and maximum values (best solution) across the 20 solutions were determined. Medians rather than means were used as estimates of evaluator central tendency since distributions of evaluator responses were generally non-normal. Confidence intervals for medians were calculated from the interquartile range, and are based on the asymptotic normality of the median for roughly equal sample sizes for two medians being compared (McGill et al. 1978, p. 16).

Table 7.1. Summary of classification evaluators used in this paper.

Evaluator	Optimality criteria*	Comments [reference]**
GEOMETRIC EVALUATORS		
Average Silhouette Width (ASW, Rousseeuw 1987)	Low within-cluster dissimilarity and high dissimilarity of samples to nearest neighbor cluster (Appendix F, Eq. 7.1).	Use of nearest neighbor cluster provides "local" criterion. Useful for seeking compact, widely separated clusters [1]
C-Index (Hubert and Levin 1975)	Low within-cluster dissimilarity, with respect to d_{min} and d_{max} coefficients (Appendix F, Eq. 7.2).	Effective for cluster recovery, and as a stopping criterion [2,3]. Minimum response = optimal solution.
Gamma (Goodman and Kruskal 1954)	High number of concordant compared to non-concordant quadruples (Appendix F, Eq. 7.3).	An adaptation of this algorithm [4] was found to be effective for cluster recovery, and as a stopping criterion [2,3].
PARTANA ratio (Roberts 2005)	Low within-cluster dissimilarity and high dissimilarity of samples within clusters to samples outside of clusters (Appendix F, Eq. 7.7).	Not previously reviewed. "W/B" [5], a similar algorithm, was found effective for cluster recovery [2], but ineffective as a stopping criterion [3].
Point Biserial Correlation (PBC; Brogden 1949)	Low within cluster dissimilarity (Appendix F, Eq. 7.8).	Effective for cluster recovery [2,6], May underestimate number of clusters as a stopping criterion [3].
NON-GEOMETRIC EVALUATORS		
ISA (Average *p*-value) (Dufrêne and Legendre 1997)	High fidelity and abundance of species within particular clusters. ISA-values are tested for significance with Monte-Carlo procedures to calculate *p*-values (Appendix F, Eq. 7.4).	Useful as a stopping criterion [7,8]. Proposed as a procedure for comparing classification methods [8]. Minimum response = optimal solution.
ISA (Number of significant indicators α = 0.05) (Dufrêne and Legendre 1997, McCune and Grace 2002)	See explanation above (Appendix F, Eq. 7.4).	Useful as a stopping criterion [7].
ISAMIC (Roberts 2005)	Consistent presence or absence of species within single clusters (Appendix F, Eq. 7.5).	Not previously reviewed
Morisita's index of niche overlap (adapted from Horn 1966)	High proportional occurrence of species within single clusters (Appendix F, Eq. 7.6).	While found to be an unbiased estimator of niche overlap [9], This algorithm has not been reviewed as a classification evaluator. Minimum response = optimal solution.

*Equations and descriptions for all evaluators are included in Appendix F.

**1 = Kaufman and Rousseeuw (1990), 2 = Milligan (1981), 3 = Milligan and Cooper (1985), 4 = Baker and Hubert (1975), 5 = McClain and Rao (1975), 6 = Milligan (1980), 7 = McCune and Grace (2002), 8 = Dufrêne and Legendre (1997), 9 = Smith and Zaret (1984).

Differences in median evaluator responses among methods were tested for significance with Kruskal-Wallis non-parametric pairwise tests. Significance levels were adjusted for simultaneous inference using Dunn's (1964) procedure. Standardized values were presented in the results to allow comparability among evaluators. Responses were standardized using $(x_i - \bar{X})/S$.

All classifications were run in PC-ORD (McCune and Mefford 1999), except for k-means analysis and PAM which were run in R (R Development Core Team 2005). All evaluator algorithms and all other functions used to compare classifications were coded using the R language.

Results

Classification Agreement

Clustering solutions within a dataset (alpine or prairie) were similar among classification methods. Agreement among methods in assignment of samples to clusters was significantly ($\alpha = 0.05$) better than random for 77% percent of alpine, and 93% of prairie clustering solutions with the same number of clusters (Tables 7.2, 7.3, Fig. 7.1). Single linkage classification solutions were least similar to those of other methods. Its agreement with other methods was significantly better than random for only 43% of alpine comparisons, and 80% of prairie comparisons (Table 7.3, Fig 7.1). Agreement between single linkage and k-means analysis was especially poor, being significantly better than random for only 10% (2/20) of prairie, and 0% of alpine classification solutions (Table 7.3).

Predictably, agreement among methods decreased for both datasets as numbers of clusters increased and solutions became more complex. The significance of the trend was determined by Spearman's rank correlation tests (r_s= -0.39, $p < 0.01$ alpine data, r_s = -0.23, $p < 0.01$ prairie data; Fig. 7.2). The only exception was k-means analysis vs. single linkage solutions which increased in agreement with number of clusters (alpine data) or agreed most at an intermediate number of clusters (prairie data). *P*-values for the hypothesis of no agreement between methods also decreased as statistical power increased with cluster number (r_s = -0.39, $p < 0.01$ alpine data, r_s = -0.31, $p < 0.01$ prairie data; Fig. 7.2).

Median Evaluator Response

Average linkage, flexible-β = -0.25 and Wards linkage were found to be the best classification methods in essentially all ten Kruskal-Wallis pairwise tests comparing median geometric evaluator responses (i.e. 5 evaluators · 2 datasets = 10 tests; Table 7.4a). These three classifiers had the highest median response in 10/10, 9/10, and 8/10 tests respectively (Table 7.4a). Note that several methods may "tie" for best when their median evaluator scores do not differ significantly. PAM, complete linkage, and single linkage performed at an intermediate level with respect to median geometric evaluator response while TWINSPAN and k-means analysis performed poorly. These five methods had the highest median response in 4/10 3/10, 3/10, 1/10, and 0/10 tests respectively (Table 7.4a).

Table 7.2. Average agreement (%) for pairs of classifiers (i.e. number of samples assigned to the same cluster at a particular clustering level ÷ total number of samples) across 20 clustering solutions (2-21 clusters). Average agreement is reported separately for alpine (A) and prairie (P) datasets.

	Average	Complete	Flexible	K-means	PAM	Single	TWINSPAN	Wards
	A ▪ P	A ▪ P	A ▪ P	A ▪ P	A ▪ P	A ▪ P	A ▪ P	A ▪ P
Average		67 ▪ 62	41 ▪ 71	50 ▪ 53	38 ▪ 60	63 ▪ 54	45 ▪ 60	41 ▪ 64
Complete	67 ▪ 62		54 ▪ 69	48 ▪ 54	43 ▪ 57	48 ▪ 34	44 ▪ 51	52 ▪ 74
Flexible	41 ▪ 71	54 ▪ 69		47 ▪ 59	61 ▪ 61	25 ▪ 39	55 ▪ 55	89 ▪ 84
K-means	50 ▪ 53	48 ▪ 54	47 ▪ 59		46 ▪ 55	46 ▪ 29	48 ▪ 47	47 ▪ 57
PAM	38 ▪ 60	43 ▪ 57	61 ▪ 61	46 ▪ 55		21 ▪ 32	50 ▪ 51	62 ▪ 67
Single	63 ▪ 54	48 ▪ 34	25 ▪ 39	46 ▪ 29	21 ▪ 32		30 ▪ 43	24 ▪ 35
TWINSPAN	45 ▪ 60	44 ▪ 51	55 ▪ 55	48 ▪ 47	50 ▪ 51	30 ▪ 43		53 ▪ 53
Wards	41 ▪ 64	52 ▪ 74	89 ▪ 84	47 ▪ 57	62 ▪ 67	24 ▪ 35	53 ▪ 53	
Overall	49 ▪ 61	51 ▪ 49	53 ▪ 63	47 ▪ 51	46 ▪ 55	37 ▪ 38	46 ▪ 52	52 ▪ 62
								48 ▪ 54

Table 7.3. The percentage (%) of levels (i.e. 2-21 clusters) for which agreement between classification solutions was statistically significant[1,2]. Comparisons made for both alpine (A) and prairie (P) datasets.

	Average	Complete	Flexible	K-means	PAM	Single	TWINSPAN	Wards
	A ▪ P	A ▪ P	A ▪ P	A ▪ P	A ▪ P	A ▪ P	A ▪ P	A ▪ P
Average		85 ▪ 95	75 ▪ 100	60 ▪ 95	90 ▪ 95	100 ▪ 95	75 ▪ 95	75 ▪ 95
Complete	85 ▪ 95		85 ▪ 95	85 ▪ 95	85 ▪ 100	95 ▪ 85	85 ▪ 100	85 ▪ 100
Flexible	75 ▪ 100	85 ▪ 95		90 ▪ 100	100 ▪ 95	30 ▪ 90	100 ▪ 95	100 ▪ 95
K-means	60 ▪ 95	85 ▪ 95	90 ▪ 100		100 ▪ 95	0 ▪ 10	100 ▪ 95	90 ▪ 95
PAM	90 ▪ 95	85 ▪ 100	100 ▪ 95	100 ▪ 95		30 ▪ 90	100 ▪ 100	100 ▪ 100
Single	100 ▪ 95	95 ▪ 85	30 ▪ 90	0 ▪ 10	30 ▪ 90		25 ▪ 100	20 ▪ 90
TWINSPAN	75 ▪ 95	85 ▪ 100	100 ▪ 95	100 ▪ 95	100 ▪ 100	25 ▪ 100		100 ▪ 100
Wards	75 ▪ 95	85 ▪ 100	100 ▪ 95	90 ▪ 95	100 ▪ 100	20 ▪ 90	100 ▪ 100	
Overall	80 ▪ 96	86 ▪ 96	83 ▪ 96	75 ▪ 84	86 ▪ 96	43 ▪ 80	84 ▪ 98	81 ▪ 96
								77 ▪ 93

[1] H_0: there is no agreement between methods, i.e. agreement between methods is not greater than expected by chance. See methods for testing procedures.

[2] *P*-values were not adjusted for simultaneous inference.

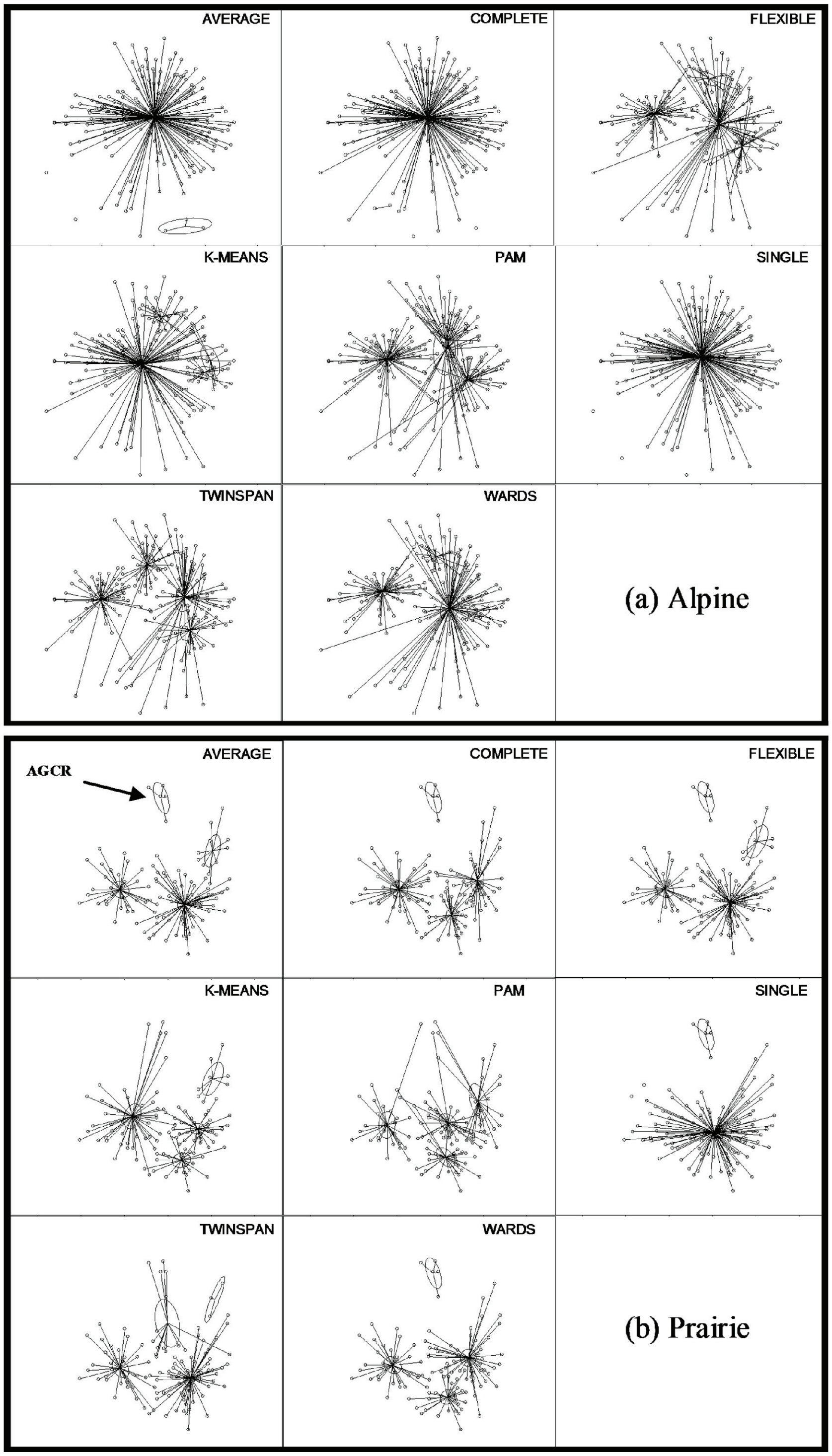
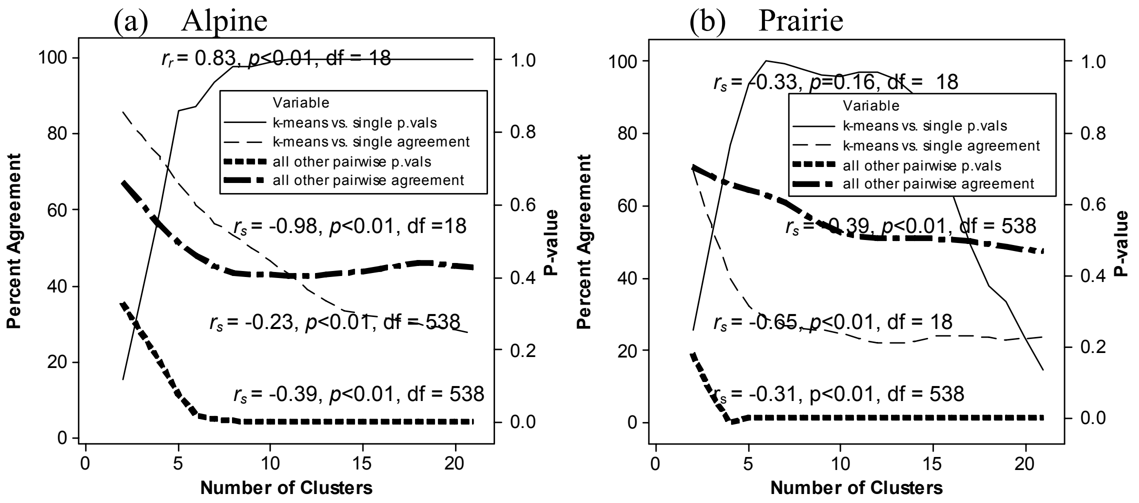


Figure 7.1. Four cluster solutions from the (a) alpine and (b) prairie datasets overlaid on a 2D NMDS ordination solution (Kruskal and Wish 1978). Final stress for 2D configurations = 25.97 for the alpine and 20.68 for the prairie dataset. Ellipses are 95% confidence intervals around cluster centroids. A disturbed *Agropyron cristatum* (AGCR) group in the prairie dataset recognized by most methods is also indicated in (b).


(a) Alpine

(b) Prairie

Figure 7.2. Variation in classification agreement (and associated *p*-values from tests of agreement) and number of clusters for (a) alpine data, and (b) prairie data. Correlations and *p*-values are from Spearman's rank tests. Lines are lowess smoothers.
P-values on the second Y-axis are from tests of the H_0: there is no agreement between methods.

Non-geometric evaluators were more divided in their preference of methods. At least one of the four non-geometric evaluators found flexible-β = -0.25, PAM, TWINSPAN, single linkage and/or Ward's linkage to be effective methods across the two datasets (Table 7.4b). For non-geometric evaluators k-means analysis was again the poorest method.

Optimal Level Evaluation: Maximum Evaluator Response

With respect to maximum evaluator response, geometric evaluators preferred flexible-β = -0.25, single linkage and particularly average linkage, and found k-means analysis and TWINSPAN to be inferior (Table 7.5a). Among non-geometric evaluators, the two non-ISA evaluators (Morisita's index and ISAMIC) preferred single and average linkage solutions, while ISA evaluators found several methods including flexible-β = -0.25, PAM, TWINSPAN and Ward's method to be effective (Table 7.5b).

Comparing Evaluators

Evaluators were generally either significantly positively or negatively correlated with each other (Fig. 7.3). Across both datasets geometric evaluators were significantly positively correlated ($\alpha = 0.05$) in 19 of 20 possible pairwise comparisons using Spearman's rank tests (Fig. 7.3). The exception, C-index vs. PBC in the alpine dataset, was significant at $\alpha = 0.07$ ($r_s = 0.14$, $p = 0.07$; Fig. 7.3a). In particular, C-index, Gamma, and PARTANA were strongly correlated for both datasets ($\overline{r_s} = 0.86$, $p < 0.01$; Fig. 7.3). Among non-geometric evaluators, ISA evaluators were strongly negatively correlated to non-ISA evaluators, i.e. Morisita's index and ISAMIC ($\overline{r_s} = -0.65$, $p < 0.01$; Fig. 7.3). ISA evaluators were strongly positively correlated ($\overline{r_s} = 0.81$, $p < 0.01$; Fig. 7.3), as were Morisita's index and ISAMIC ($\overline{r_s} = 0.91$, $p < 0.01$; Fig. 7.3). Geometric and non-geometric evaluators were poorly correlated (Fig. 7.3). Thirty-three percent of comparisons (13/40) between geometric and non-geometric evaluators showed a lack of any statistical association at $\alpha = 0.05$ (Fig. 7.3).

Table 7.4. Standardized median evaluator responses ± 95% CI for standardized (a) geometric and (b) non-geometric evaluators. Medians were calculated across 20 different clustering solutions (2-21 clusters) for each method. Assessments for method responses followed by the same letter are not significantly different at $\alpha = 0.05$ using Kruskal-Wallis multiple comparisons. Simultaneous inference adjusted using Dunn's (1964) procedure. The best responses in each column are bolded.

(a)

	GEOMETRIC EVALUATORS										High Scores	
	ASW		1-C index		Gamma		PARTANA		PBC			
	Alpine	Prairie	Alpine	Prairie	Alpine	Prairie	Alpine	Prairie	Alpine	Prairie	A	P
Classifiers												
Average	**0.5 ± 0.7AB**	**1.0 ± 0.5 A**	**0.6 ± 0.3 AB**	**0.9 ± 0.3 A**	**0.7 ± 0.2 A**	**0.6 ± 0.3 A**	**-0.2 ±0.1 AB**	**0.3 ± 0.1 A**	**0.7 ± 0.7 A**	**1.5 ± 0.3 A**	**5**	**5**
Complete	-0.6 ± 0.8 BC	0.1 ± 0.2 CD	0.0 ± 0.3 C	0.1 ± 0.4 BC	**0.5 ± 0.4 AB**	**0.4 ± 0.4 A**	-0.2 ± 0.1 BC	-0.1 ± 0.3 BC	**0.4 ± 0.8 A**	0.0 ± 0.1 B	2	1
Flexible	**1.1 ± 0.3A**	**0.8 ± 0.1 A**	0.2 ± 0.3 BC	**1.1 ± 0.3 A**	**0.7 ± 0.6 AB**	**1.0 ± 0.4 A**	**-0.2± .1ABC**	**0.5 ± 0.1 A**	**1.1 ± 0.4 A**	**0.8 ± 0.4 AB**	4	**5**
K-means	-0.6 ± 0.2 C	-0.4 ±0.2 CD	-1.7 ± 0.3 D	-1.3 ± 0.2 C	-1.9 ± 0.1 C	-0.6 ± 0.4 C	-0.4 ± 0 D	-0.8 ± 0.2 C	-1 ± 0.2 B	-1 ± 0.2 C	0	0
PAM	**0.2 ± 0.2 AB**	0.2 ± 0.1 BC	-0.2 ± 0.1 C	0.2 ± 0.3 BC	**0.5 ± 0.2 AB**	**0.6 ± 0.3 AB**	**-0.2 ± 0ABC**	0.1 ± 0.2 BC	**0.6 ± 0 A**	-0.4 ± 0.2 C	4	1
Single	-0.8 ± 0.4 C	-1.6 ± 0.3 D	**1.6 ± 0.2 A**	-0.5 ± 0.1 C	**0.6 ± 0.3 A**	-1.3 ± 0.1 C	**0.2 ± 0.7 A**	-0.1 ± 0.3 BC	-1 ± 0.1 B	-1 ± 0.3 C	3	0
TWINSPAN	-0.9 ± 0.1 C	-1.6 ±0.7 CD	-0.7 ± 0.0 D	-0.5 ± 0.2 C	0.1 ± 0.1 BC	0.0 ± 0.1 BC	-0.3 ± 0 C	-0.3 ± 0.1 C	**0.3 ± 0 A**	0.0 ± 0.6 BC	1	0
Ward	**1.0 ± 0.2 AB**	**0.7 ± 0.1 AB**	0.1 ± 0.2 D	**0.7 ± 0.4 AB**	**0.7 ± 0.5 AB**	**0.8 ± 0.4 A**	**-0.2 ±0 ABC**	**0.3 ± 0.3 AB**	**0.8 ± 0.3 A**	0.1 ± 0.3 BC	4	4

(b)

	NON – GEOMETRIC EVALUATORS								High scores	
	1-ISA *p*-val.		ISA sig. indicators		ISAMIC		1 – Mor.index			
	Alpine	Prairie	Alpine	Prairie	Alpine	Prairie	Alpine	Prairie	A	P
Classifiers										
Average	-0.7 ± 0.3 CD	0.0 ± 0.1 B	-1.3 ± 0.0 D	-0.9 ± 0.2 C	**1.1 ± 0.1 A**	0.2 ± 0.4 CD	**1.2 ± 0.1 A**	**0.7 ± 0.2 A**	**2**	1
Complete	-0.1 ± 0.3 CD	0.2 ± 0.1 B	-1.1 ± 0.1 D	0.1 ± 0.2 B	**0.4 ± 0 A**	-0.4 ± 0.2 D	**0.8 ± 0.1 A**	-0.2 ± 0.3 C	**2**	0
Flexible	**0.8 ± 0.1 A**	**0.4 ± 0.1 AB**	**1.2 ± 0.2 A**	**0.5 ± 0.2 A**	-0.5 ± 0.2 B	-0.5 ± 0.2 D	-0.7 ± 0.2 B	-0.4 ± 0.2 C	**2**	**2**
K-means	0.3 ± 0.1 BC	0.1 ± 0.2 B	0.0 ± 0.1 C	**0.3 ± 0.1 A**	-0.8 ± 0.3 B	-0.1 ± 0.2 D	-0.9 ± 0.2 B	-0.6 ± 0.3 C	0	1
PAM	**0.8 ± 0 A**	**0.5 ± 0.2 A**	**1.1 ± 0.1 AB**	**0.7 ± 0.3 A**	-0.7 ± 0.2 B	-0.4 ± 0.2 D	-0.8 ± 0.1 B	-0.3 ± 0.3 C	**2**	**2**
Single	-1.9 ± 0.1 D	-2.1 ± 0.2 C	-1.1 ± 0.1 B	-2.1 ± 0.3 D	**1.9 ± 0.1 A**	**2.6 ± 0.4 A**	**1.4 ± 0.1 A**	**1.7 ± 0.1 A**	**2**	**2**
TWINSPAN	**0.6 ± 0 AB**	**0.5 ± 0.1 A**	0.0 ± 0.3 BC	-0.2 ± 0.3 BC	-0.6 ± 0.3 B	0.0 ± 0.2 BC	-0.2 ± 0.3 B	0.5 ± 0.3 B	1	1
Ward	**0.9 ± 0.1 A**	**0.6 ± 0.1 AB**	**1.2 ± 0.1 A**	**0.6 ± 0.2 A**	-0.5 ± 0.2 B	-0.5 ± 0.1 D	-0.7 ± 0.2 B	-0.5 ± 0.2 C	**2**	**2**

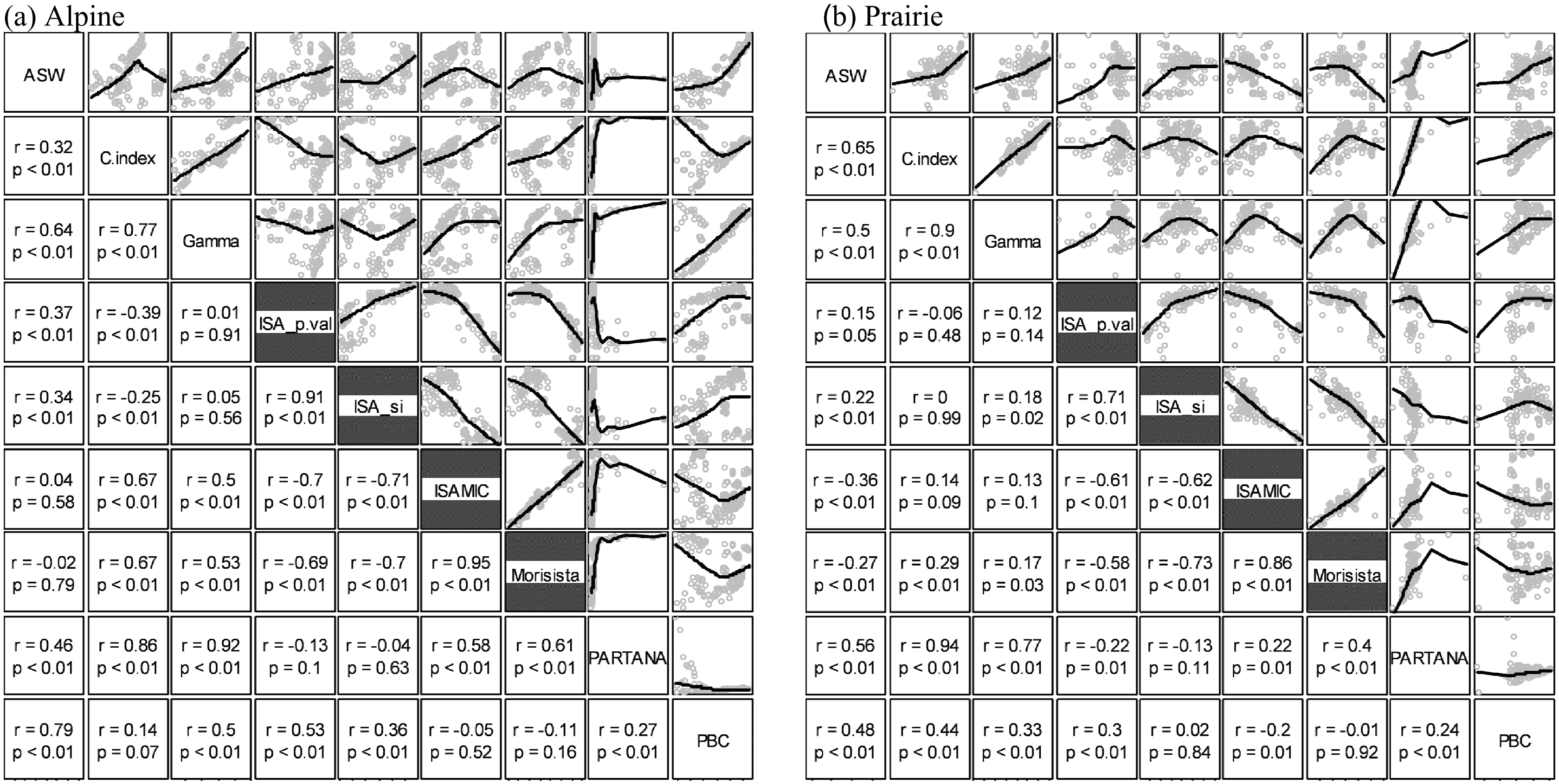
Table 7.5. Maximum standardized responses for (a) geometric, and (b) non-geometric evaluators. In each cell maximum response is listed to the left of the dot, and the number of clusters associated with that response is listed to its right. Notably high responses in each column are indicated in bold font.

(a)

	GEOMETRIC EVALUATORS										High scores	
	ASW		1-C index		Gamma		PARTANA		PBC			
	Alpine	Prairie	Alpine	Prairie	Alpine	Prairie	Alpine	Prairie	Alpine	Prairie	A	P
Classifier												
Average	**2.2 ▪ 20**	**2.4 ▪ 2**	**1.9 ▪ 2**	**1.7 ▪ 2**	**1.6 ▪ 2**	**1.2 ▪ 21**	**6.6 ▪ 2**	**7.8 ▪ 2**	**1.5 ▪ 21**	**1.7 ▪ 7**	**5**	**4**
Complete	**1.7 ▪ 21**	0.5 ▪ 2	**1.8 ▪ 4**	1.2 ▪ 21	1.1 ▪ 21	**1.3 ▪ 21**	0.6 ▪ 4	0.7 ▪ 21	1.1 ▪ 21	0.8 ▪ 8	0	0
Flexible	**1.7 ▪ 21**	**1.5 ▪ 4**	0.8 ▪ 21	**1.4 ▪ 21**	**1.3 ▪ 21**	**1.5 ▪ 21**	-0.1 ▪ 21	0.9 ▪ 2	**1.3 ▪ 21**	**1.7 ▪ 4**	0	**2**
K-means	0.0 ▪ 20	0.8 ▪ 6	-0.2 ▪ 2	-0.2 ▪ 6	-1.5 ▪ 12	0.2 ▪ 20	-0.4 ▪ 12	-0.2 ▪ 20	-0.7 ▪ 12	0.7 ▪ 6	0	0
PAM	1.0 ▪ 21	0.7 ▪ 2	0.1 ▪ 21	1.0 ▪ 21	0.9 ▪ 21	1.2 ▪ 21	-0.2 ▪ 21	0.6 ▪ 21	0.9 ▪ 9	0.6 ▪ 7	0	0
Single	0.1 ▪ 7	1.0 ▪ 4	**1.9 ▪ 2**	**1.3 ▪ 4**	**1.6 ▪ 2**	0.2 ▪ 4	**6.6 ▪ 2**	5.1 ▪ 4	-0.7 ▪ 16	0.3 ▪ 21	**3**	0
TWINSPAN	-0.6 ▪ 11	0.7 ▪ 6	-0.1 ▪ 2	0.3 ▪ 7	0.4 ▪ 21	0.4 ▪ 20	-0.2 ▪ 21	0.0 ▪ 6	0.4 ▪ 12	1.5 ▪ 6	0	0
Ward	1.3 ▪ 19	1.1 ▪ 8	0.4 ▪ 19	1.3 ▪ 21	1.0 ▪ 19	1.4 ▪ 21	-0.1 ▪ 21	0.8 ▪ 21	1.1 ▪ 11	1.1 ▪ 8	0	0

(b)

	NON - GEOMETRIC EVALUATORS								High scores	
	1-ISA p-val.		ISA sig indicators		ISAMIC		1 – Mor.index			
	Alpine	Prairie	Alpine	Prairie	Alpine	Prairie	Alpine	Prairie	A	P
Classifier										
Average	-0.5 ▪ 21	0.5 ▪ 6	-0.6 ▪ 3	0.1 ▪ 4	1.5 ▪ 8	1.0 ▪ 20	**1.7 ▪ 2**	1.1 ▪ 14	**1**	0
Complete	0.1 ▪ 14	1.1 ▪ 3	-0.1 ▪ 2	**2.3 ▪ 2**	1.3 ▪ 4	-0.1 ▪ 21	**1.5 ▪ 4**	0.2 ▪ 18	0	0
Flexible	**1.0 ▪ 9**	1.1 ▪ 3	**1.4 ▪ 9**	1.2 ▪ 10	0.1 ▪ 21	-0.1 ▪ 20	0.1 ▪ 20	0.1 ▪ 15	0	0
k-means	0.5 ▪ 10	1.1 ▪ 3	0.6 ▪ 7	1.0 ▪ 20	0.0 ▪ 20	0.4 ▪ 21	-0.4 ▪ 21	0.0 ▪ 19	0	0
PAM	**0.9 ▪ 11**	**1.4 ▪ 4**	**1.3 ▪ 8**	**2.5 ▪ 4**	-0.1 ▪ 21	0.0 ▪ 21	-0.3 ▪ 21	0.1 ▪ 21	**1**	**1**
Single	-1.3 ▪ 4	-1.5 ▪ 7	-0.2 ▪ 3	-1.0 ▪ 2	**2.1 ▪ 15**	**2.8 ▪ 17**	**1.7 ▪ 2**	**2.4 ▪ 4**	**2**	**2**
TWINSPAN	**1.1 ▪ 6**	**1.4 ▪ 2**	1.1 ▪ (4 ,7)	**2.0 ▪ 2**	-0.1 ▪ 19	0.7 ▪ 21	0.1 ▪ 19	1.1 ▪ 18	**1**	**1**
Ward	**1.1 ▪ 10**	0.9 ▪ 12	**1.5 ▪ 10**	1.5 ▪ 3	-0.1 ▪ 21	-0.1 ▪ 21	-0.2 ▪ 21	0.1 ▪ 18	**2**	0


(a) Alpine

(b) Prairie

Figure 7.3. Correlation matrices showing pairwise correlation comparisons of evaluator responses for alpine and prairie datasets (a and b respectively). Evaluator comparisons in each cell are across all 20 clustering solutions (2-21 clusters) within each of the eight classification methods. Thus each cell compares 20 · 8 = 160 responses, df = 158. Correlations (r_s) and *p*-values are from Spearman's rank tests. Lines are lowess smoothers. Shaded cells are non-geometric evaluators.

Discussion

Classification Agreement

Clustering solutions from seven of the eight methods (i.e. all but single linkage) showed a high degree of similarity, particularly for classifications of the prairie dataset (Tables 7.2, 7.3, Fig. 7.1). Such strong correspondence among methods is surprising given their completely different approaches. K-means analysis assigns sample units to *p*-dimensional cluster centroids, PAM assigns sample units to *p*-dimensional cluster medoids, TWINSPAN is a hierarchical divisive clustering based on eigenanalysis of chi-squared distances, while the hierarchical agglomerative methods tested (average, complete, single, and Wards linkage) represent the entire range of Lance and Williams (1967) flexible-β continuum. Since highly different methods repeatedly detect the same clusters in noise-free artificial data (Milligan 1980), our results suggest the presence of a valid underlying cluster structure in the two datasets which is detectable from a variety of perspectives. A cluster structure appears to be particularly strong/recognizable in the prairie dataset where method agreement is exceptionally high (Tables 7.2, 7.3, Fig. 7.1).

The incongruity of the single linkage solutions is due to this method's classification strategy. While single linkage is space contracting and seeks long-shaped (non-compact) clusters, other tested methods do not seek this structure. The only method in frequent agreement with single linkage was average linkage; this method is more similar to single linkage within the flexible-β continuum than the other tested methods (Lance and Williams 1967). A high degree of similarity between flexible $\beta = -0.25$ and Ward's linkage appears in both datasets (Tables 7.2, 7.3, Fig. 7.1). This correspondence been noted by other authors (Lance and Williams 1967; McCune and Grace 2002), though even these methods significantly disagree for their simplest (2 cluster) solution in the prairie dataset (Table 7.3).

Median Evaluator Response--Geometric Evaluators

Since each classification method was evaluated at twenty cluster levels, a measure of overall effectiveness is median evaluator response (cf. Dufrêne and Legendre 1997). Geometric evaluator medians were highest for flexible-β = -0.25, average linkage, and Ward's method (Table 7.4a). Flexible β = -0.25 has been recommended by several authors (Lance and Williams 1967; McCune and Grace 2002). Average linkage has been widely recommended as an effective method for detecting clusters with spherical or ellipsoidal shapes (Cunningham and Ogilvie 1972; Milligan and Isaac 1980; Milligan 1980; Kaufman and Rousseeuw 1990), although it may produce more chaining than other space conserving methods (McCune and Grace 2002). Ward's method is generally effective with spherical multivariate distributions (Kaufman and Rousseeuw 1990; Hirano et al. 2002), though it may perform poorly if cluster populations are unequal in size or have unequal cluster diameters (Kuiper and Fisher 1975; Kaufman and Rousseeuw 1990; Milligan 1980). In addition, although Ward's method may perform well with non-Euclidean distance measures (like Bray-Curtis dissimilarity used in this paper), this may not be entirely appropriate since Ward's method calculates internal dendrogram distances with the Euclidean method (Pielou 1984).

Geometric evaluators found TWINSPAN solutions to be poor (Table 7.4). TWINSPAN may suffer from a number of problems in its parent method, correspondence analysis (CA), which may fail to find patterns in multi-gradient datasets (McCune and Grace 2002), and implicitly uses chi-squared distance, a measure which gives high weight to species with low total abundance (Faith et. al 1987). It should be noted that Dale (1995) argued TWINSPAN should not be compared to other classification methods on the basis of cluster geometry since its primary goal is characterization through indicator species, rather than creating a cluster structure.

K-means analysis performed poorly with respect to both geometric and non-geometric evaluators. This is due to at least three factors. First, Euclidean distance, the measure used by k-means analysis, is generally a poor choice for vegetation data since (like all metric distances) it loses sensitivity and introduces spurious values at higher distances, and has no fixed upper bound for sample units that have nothing in common (McCune and Grace 2002). Dufrêne and Legendre (1997) used Principal Coordinates Analysis (PCoA) species and site scores from an ordination of a Stienhaus similarity matrix instead of Euclidean distances to avoid this problem. Secondly, random starting points (our method) may result in poor cluster recovery for k-means analysis (Milligan 1980). Much better recovery characteristics can be achieved when using valid seed points, e.g. average linkage centroids (Milligan 1980). Finally, the use of means may be disadvantageous to k-means analysis, since this statistic is often a poor indicator of centrality in ecological data (Kaufman and Rousseeuw 1990). The much better performance of PAM, a non-hierarchical method which addresses these deficiencies, is evident in Tables 7.4-7.5.

It should be emphasized that geometric evaluators will, by definition, tend to favor compact spherical solutions more than long linear-shaped solutions. Thus, single-linkage, flexible-β > 0 solutions, or for that matter TWINSPAN (which does not implicitly seek spherical clusters), may be unduly penalized by geometric evaluators.

Median Evaluator Response: Non-Geometric Evaluators

Among non-geometric evaluators very different conclusions were drawn by the ISA evaluators which penalize species with low within-group constancy and Morisita's index of niche overlap and ISAMIC which penalize species with intermediate within-group constancy (Table 7.4b). Morsisita's index and ISAMIC prefer single linkage since this method continually isolates individual outlier clusters with relatively distinctive taxa (thus lacking species with intermediate constancy) as it chains together the rest of the data. In contrast, while ISA evaluators found several non-space-contracting methods to be valid (i.e. flexible β = -0.25, PAM, TWINSPAN, and Wards method), they found single linkage solutions to be exceptionally poor (Table 7.4b).

Optimal Level Evaluation: Maximum Evaluator Response

The best (maximum) internal evaluator response across cluster levels is often used as a pruning criterion (i.e. the correct number of clusters) in a classification. Thus, while the median evaluator response may describe the overall performance of a classification method it also penalizes methods which may have a single desirable optimum. We addressed this discrepancy by comparing maximum evaluator responses among the 20 clustering solutions (Tables 7.5a and 7.5b).

While single linkage and particularly average linkage performed well with respect to the maximum evaluator criterion, in most cases the maximum response was a two cluster solution in which a well defined outlier group was isolated from the rest of the dataset (Table 7.5a). For the prairie dataset this outlier group consisted of five "disturbed" plots, i.e. agricultural range sites dominated by an exotic wheat-grass (*Agropyron cristatum*). While most other methods also recognized the *A. cristatum* group in three to four cluster solutions (Fig. 7.1b), they did not recognize this separation as the simplest solution. For the alpine dataset the outlier "group" consisted of a single talus transect. Only two other methods (complete linkage and TWINSPAN) recognized the individual alpine transect as a viable group, and only average and single linkage recognized this partition as the simplest solution (Fig. 7.1a, Table 7.5a). While the identification of multivariate outliers may be a useful by-product of cluster analysis (Kaufman and Rousseeuw 1990), continual chaining of classification solutions generally resulted in lower overall (median) evaluator responses for single linkage (Tables 7.4a, 7.4b).

Geometric evaluators which are sensitive to the difference of within cluster and between cluster distances may find the separation of a single well defined outlier or outlier group to be a particularly good solution regardless of heterogeneity in the non-outlier group (Kaufman and Rousseeuw 1990). C-index, Gamma, and particularly PARTANA appeared to be sensitive to outliers in both datasets (Table 7.5a). It should be emphasized that the isolation of an outlier or outlier group does not mean that a valid clustering structure has been found (Kaufman and Rousseeuw 1990). Thus, when using optimal solutions as validity or pruning criteria, it is important to verify that high evaluator responses are not merely the product of outlier recognition.

For maximum non-geometric responses the best non-ISA respondents were average and single linkage. In contrast, ISA evaluators found flexible-$\beta = -0.25$, PAM, Ward's method and TWINSPAN to be effective, and single linkage to be exceptionally poor (Table 7.5b). Although TWINSPAN has come under heavy criticism for its poor performance in complex multiple-gradient datasets (McCune and Grace 2002), and though most geometric evaluators found its solutions to be inferior (Table 7.4a), it outperformed most other methods with respect to ISA evaluators (Tables 7.4b, 7.5b). Furthermore, for our datasets, TWINSPAN clustering solutions generally did not differ greatly from other methods often considered to be more robust (i.e. average linkage, flexible-β = -0.25, Ward's methods; Table 7.3).

Classifier Performance Across Datasets

The performance of several classification methods varied between datasets. While flexible- β = -0.25, average, and Wards linkage had high median responses in both datasets, single linkage and PAM had much higher median evaluator responses for their classifications of the alpine dataset than classifications of the prairie dataset (Fig. 7.4a). Flexible-β = -0.25 had several high maximum non-geometric responses in the alpine dataset, but several particularly low maximum responses in the prairie dataset (Table 7.5b).

The between-dataset variability of classifier performance seems to indicate a general difference in underlying cluster structure/shapes in the two datasets. The incongruity between single linkage and other methods indicates that single linkage solutions are unrelated to those of other methods particularly in the alpine dataset (Tables 7.1, 7.2, Fig. 7.1). This in conjunction with better single linkage evaluator scores in the alpine dataset (Table 7.4a) indicates the validity of an independent long-cluster (non-spherical) interpretation of the alpine data. PAM, a spherical cluster method, also does much better in the alpine dataset (Table 7.4a) although it creates solutions completely unlike those of single linkage (Table 7.2, 7.3, Fig. 7.1). Valid non-spherical and spherical interpretations may both be possible for the alpine dataset, and final choice for best method should be based on a thorough examination of results from both general strategies.

It is worth noting that a number of different classification methods have recently been proposed to recover clusters regardless of their shape in data (e.g. spherical or linear). These include maximum certainty data partitioning which attempts to reduce partition entropy while eliminating model-based shape assumptions (Roberts et al. 2000), and iterative partitioning of a relative neighborhood graph without cluster shape assumptions (Bandyopadhyay 2004).

Comparing Evaluator Criteria

Similarities and dissimilarities of evaluator criteria underlie correlations of evaluator responses (Fig. 7.3). The two ISA evaluators interpret classification solutions similarly because they are derived from the same algorithm (Appendix F, Equation 4). The agreement between geometric evaluators (ASW, C-index, Gamma, PARTANA ratio, and PBC) is also due to similarity in their criteria. At least in part, all geometric evaluators sought solutions with high within-cluster cohesion, i.e. low within-cluster dissimilarity (Table 7.1). In particular, C-index and Gamma and PARTANA give very similar evaluations of clustering solutions (Fig. 7.3). All three methods use the global dissimilarity/similarity of samples between and within clusters as criteria. Perhaps most interesting is the contrast, noted earlier, between the two non-geometric evaluators that heavily penalize intermediate constancy species, Morisita's index of niche overlap and ISAMIC, and the ISA methods which penalize low constancy species (Fig. 7.3). These two strategies tend to give opposite interpretations of the efficacy of classification solutions (Fig. 7.3).

Geometric and non-geometric evaluators appear to provide highly independent perspectives of classification efficacy. While the non-geometric evaluators differed from each other, their assessments were generally completely unrelated to those of geometric evaluators (Fig. 7.3). As noted earlier thirty-three percent of comparisons (13/40) between geometric and non-geometric evaluators showed a lack of any statistical association (Fig. 7.3).

Conclusions

1) Classifications made by different methods were remarkably similar, suggesting a strong underlying cluster structure, particularly in the prairie dataset (cf. Milligan 1980). Greatest differences in classification solutions were between methods which sought spherical clusters in data (6 of 8 tested methods) and those which did not (i.e. single linkage).

2) Three hierarchical agglomerative classification methods (i.e. average, flexible-β =-0.25, and Wards linkage) generally outperformed others, particularly with respect to geometric evaluators. Despite this, we cannot strongly recommend one classification method over another. This is true because, despite potential biases (geometric evaluators for compact spherical clusters, and ISAMIC and Morisita's index for single linkage), our

results demonstrate that classifiers may vary in efficacy/character with different ecological datasets. Thus, we support the idea that a “correct” classification method does not exist for all datasets, and encourage objective comparisons (internal evaluation) of the relationship between classification methods and data before choosing which method represents the data best.

3) Differing criteria causes internal evaluators to vary greatly in what they perceive as an optimal solution. Indeed, these contrasting perspectives provide useful information about a classification, and allow a researcher to choose evaluators that seek the clustering qualities he needs (e.g. compact clusters, high fidelity of species to clusters; Table 7.1). On the other hand, concerns such as diametrically opposed classification assessments and sensitivity to outliers emphasize the need to become familiar with internal evaluator biases before using them to gauge classification solutions.

Geometric and non-geometric criteria may offer highly independent interpretations of classification character. Indeed, an effective non-geometric evaluator should be insensitive to the cluster-shape-biases of particular classification methods. Unfortunately, while the two non-geometric evaluators introduced in this paper (ISAMIC and Morisita’s index) are insensitive to cluster geometry, they are highly preferential to single linkage solutions. This is true because outliers isolated in chaining will inevitably contain species with high (or low) within-group constancy. The third introduced evaluator, PARTANA, appears to be a useful geometric strategy which provides assessments highly similar to effective evaluators like C-index and Gamma (Milligan 1981; Milligan and Cooper 1985; Fig. 7.3). Our results emphasize the usefulness of internal evaluators (both geometric and non-geometric) and the need for the continuing development of non-geometric evaluators.

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Literature Cited

Bandyopadhyay, S. 2004. An automatic shape independent clustering technique. Pattern Recogn. 37: 33-45.

Baker, F. B., and L. J. Hubert. 1975. Measuring the power of hierarchical cluster analysis. J. Am. Stat. Assoc. 70, 31-38.

Beals, E. W. 1984. Bray-Curtis ordination: an effective strategy for analysis of multivariate ecological data. Adv. Ecol. Res. 14: 1-55.

Belbin, L., and C. McDonald. 1993. Comparing three classification strategies for use in ecology. J. Veg. Sci. 4: 341-348.

Bolshakova, N., and F. Azuaje. In press. Estimating the number of clusters in DNA microarray data. Method. Inform. Med.

Bray J. R., and J. T. Curtis. 1957. An ordination of the upland forest communties in southern Wisconsin. Ecological Monographs. 27: 325-349.

Brogden, H. E. 1949. A new coefficient: application to biserial correlation and to estimation of selective efficiency. Psychometrika. 14: 169-182.

Cao, Y., Bark, A. W., and W. P. Williams. 1997. A comparison of clustering methods for river benthic community analysis. Hydrobiologia. 347: 25-40.

Cunningham, K. M., and J. C. Ogilvie. 1972. Evaluation of hierarchical grouping techniques: a preliminary study. Comp. J. 15: 209-213.

Dale, M. B. 1991. Knowing when to stop: cluster concept=concept cluster. In Feoli, E. & L. Orloci (eds.), Computer Assisted Vegetation Analysis, Kluwer Academic Publishers, Dordrecht: 149-171.

Dale, M. B. 1995. Evaluating Classification Strategies. J. Veg. Sci. 6: 437-440.

Dubes, R., and A. K. Jain. 1976. Clustering techniques: the user's dilemma. Pattern Recogn. 8: 247-260.

Dufrêne M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetric approach. Ecol. Mong. 67(3): 345-367.

Dunn, O. J. 1964. Multiple comparisons using rank sums. Technometrics 6: 241-252.

Everitt, B. 1977. Cluster analysis. Heinemann Educational Books. London, UK.

Gauch, H. G., and R. H. Whittaker. 1981. Hierarchical classification of community data. J. Ecol. 69: 537-557.

Goodman, L., and W. Kruskal. 1954. Measures of association for cross-validations. J. Am. Stat. Assoc. 732-764.

Hartigan, J. A. 1975. Clustering Algorithms. Wiley. New York, US.

Hartigan, J. A., and M. A. Wong. 1979. A k-means clustering algorithm. Appl. Stat.-J. Roy. St. C. 28: 100-108.

Hill, M. O. 1979. TWINSPAN—A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Ecology and Systematics. Cornell University, Ithaca, NY, US.

Hirano, S., Sun., X., S. and Tsumoto. 2002. Comparison of clustering methods for clinical databases. Inform. Sciences. 159: 155-165.

Horn, H. S. 1966. Measurement of "overlap" in comparative ecological studies. Am. Naturalist. 100: 419-424.

Hubert, L. J., and J. R. Levin. 1975. A general framework for assessing categorical clustering in free recall. Psychol. Bull. 83: 1072-1080.

Hurlbert, S. H. 1978. The measurement of niche overlap and some relatives. Ecology 59: 67-77.

Jacobs, J. 1974. Quantitative measurement of food selection. Oecologia. 14: 412-417.

Kaufman, L., and P. J. Rousseeuw. 1990. Finding groups in data, an introduction to cluster analysis. John Wiley, and Sons, New York, US.

Kruskal, J. B., and M. Wish. 1978. Multidimensional scaling. Sage Publications. Beverly Hills, CA. 93 pp.

Kuiper, F. K., and L. Fisher. 1975. A Monte Carlo comparison of six clustering procedures. Biometrics. 31: 777-783.

Lance, G. N., and W. T. Williams. 1967. A general theory of classification sorting strategies I. Hierarchical systems. Comp. J. 4: 373-380.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software design. Gelenden Beach OR, US.

McCune B., and M. S. Mefford. 1999. PC-ORD: Multivariate analysis of ecological data, ver. 4. MjM software design, Glendale Beach, Oregon, US.

McClain, J. O., and V. R. Rao. 1975. CLUSTISZ: A program to test for the quality of clustering of a set of objects. J. Marketing Res. 12: 456-460.

McGill, R., Tukey, J. W., and W. A. Larsen. 1978. Variations of box plots. Am. Stat. 32: 12-16.

McQuitty, L. L. 1966. Similarity analysis by reciprocal pairs for discrete and continuous data. Educ. Psychol. Meas. 26: 825.

Milligan, G. W. 1980. An examination of six types of error perturbation fifteen Clustering algorithms. Psychometrika. 45: 325-342.

Milligan, G. W. 1981. A Monte Carlo study of thirty internal criterion measures for cluster analysis. Psychometrika. 46(2): 187-199.

Milligan, G. W., and M. C. Cooper. 1985. An examination of procedures for determining the number of clusters in a data set. Psychometrika. 50 (2): 159-179.

Milligan, G. W., and P. D. Isaac. 1980. The validation of four ultrametric clustering algorithms. Pattern Recogn. 12: 41-50.

Orloci, L. 1967. An agglomerative method for classification of plant communities. J. Ecol. 55: 193-206.

Orloci, L. 1978. Multivariate analysis in vegetation research (2nd edition). Dr W. Junk Publishers, Boston, US.

Pielou, E. C. 1984. The interpretation of ecological data. Wiley, New York, US.

R Development Core Team. 2005. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Roberts, D. 2005. Vegetation classification in R, for labdsv ver. 1.1-1, vegetation ecology package. http://www.cran.r-project.org. unpubl.

Roberts, S. J., Everson, R., and I. Rezek. 2000. Maximum certainty data partitioning. Pattern Recogn. 33: 833-839.

Rousseeuw, P. J. 1987. Silhouettes: A graphical aid to the interpretation and validation of cluster analysis. J. Comput. Appl. Math. 20: 53-65.

Smith, E. P., and T. M. Zaret. 1984. Bias in estimating niche overlap. Ecology. 63: 1248- 1258.

Sneath, P. H. A., and R. R. Sokal. 1973. Numerical taxonomy, the principles and practice of numerical exploration. W. H. Freeman and Company. San Francisco, CA USA.

Sokal, R. R., and C. D. Michener. 1958. A statistical method for evaluating systematic relationships. University of Kansas Science Bulletin. 38: 1409-1438.

Sokal, R. R., and F. F. Rohlf. 1962. The comparison of dendrograms by objective methods. Taxon. 11: 33-40.

Sokal, R. R., and P. H. A. Sneath. 1963. Principles of numerical taxonomy. W. H. Freeman and Company. San Francisco, CA US.

Weaver, T., and K. Aho. 2006. Identification of community types of southeast Montana as targets for mine reclamation. In 2006 Billings Land Reclamation Symposium, June 5-8, 2006, Billings MT . Jointly published by BLRS and ASMR 3134 Montavista Rd., Lexington KY 40502.

Ward, J. H., Jr. 1963. Hierarchical grouping to optimize an objective function. J. Am. Stat. Assoc. 58: 236-244.

CHAPTER 8

MEASURING WATER RELATIONS AND pH OF CRYPTOGAM ROCK-SURFACE ENVIRONMENTS[*]

Introduction

Rock surface characteristics (e.g., water absorption, water retention, pH, and nutrient and toxin availability) are important to organisms which live on them (e.g., mosses and lichens). In soils these characteristics greatly affect plant productivity (Lambers et al. 1998), and are easily measured because soils have large non-lithic surface areas for water and ion exchange. As a result, well-tested methods for the measurement of soil environmental characteristics are available (e.g., Campbell & Gee 1996; Gardner 1996). In contrast, a lack of standard methods for measuring these properties for rock surfaces limits the work of lichenologists, bryologists and ecologists studying rock outcrop communities.

Measuring Water Retention/Absorption

While water stored on rock surfaces may buffer against cryptogam dehydration, little information exists in the ecological literature about the water absorption/storage characteristics of rock substrates (Brodo 1973; Pentecost 1980; Smith 1982). This is of concern since water is an important variable in determining community composition on

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both rock outcrops (Foote 1966; Larson et al. 2000) and bark (Hale 1955; Kalgutkar & Bird 1969).

Lack of information concerning rock surface water relations may be due to a lack of standard procedures for their measurement. Although classic ecological methods for estimating water absorption/retention of bark surfaces are available (Barkman 1958; Brodo 1968; Smith 1982), few comparable methods exist for rock surfaces. Techniques for describing rock-water relations have been developed in non-ecological fields (e.g., capillary imbibition, Benavente 2004; Richardson 1991; water absorption of inundated rock samples, Mod'd et al. 1996), and have generally not been used by ecologists. As a result we find essentially no procedures in the ecological/bryological literature for studying three important aspects of rock surface water relations: 1) the quantity of water held at saturation, 2) the amount of atmospheric water that can be absorbed, and 3) water supply capacity (i.e. the length of time a saturated rock remains wet).

Measuring Surface pH

While cryptogams respond to substrate pH, controlling mechanisms are often uncertain since acidity/alkalinity has many correlates. For instance, pH regulates the availability of mineral nutrients (e.g., P, Fe) and toxins (Killham 1994). Regardless of the specific mechanism it is apparent that substrate pH is often strongly correlated with moss and lichen distribution and performance (Bates 1978; Brodo 1973; Garty et al. 1997; Schmidt et al. 2001; many others).

Despite its importance to cryptogam ecology, techniques for measuring rock surface pH are also inadequate. One conventional method requires crushing rocks without regard to physical/chemical differences between surfaces and un-weathered and uninhabitable inner rock areas (Cook 2000; Fujita et al. 2003; Tulve & Young 1997). A second approach is to measure the pH of water running over a substrate without consideration of substrate surface area, solvent volume, initial water chemistry (e.g., acid rain) or contaminants (Murphy et al. 1983; Pentecost 1980).

Kricke (2002) and Schmidt et al. (2001) have proposed methods for measuring the surface pH of bark to describe lichen habitat. However, while these protocols are useful (quick and field applicable), they are less appropriate for measurements of rock surface pH. For instance, while bark pH may equilibrate with a solvent after only four minutes (Schmidt et al. 2001) we expect rocks to reach equilibrium with solution much more slowly.

Objectives

We present here methods for: 1) measuring water absorption by rock surfaces exposed to a simulated saturation event (e.g., rain, spring thaw), 2) measuring water absorption from atmospheres of known humidities, 3) measuring water retention of saturated rocks, and 4) measuring rock surface pH by methods which are compatible with the slow rates of ion release from lithic surfaces. In addition we offer an inexpensive method for measuring surface area to convert water absorption/retention and pH responses into cryptogam-relevant units (i.e., cm^2 of surface). We demonstrate these techniques by contrasting the surface characteristics of two types of rocks (andesite and limestone) that provide habitat for moss and lichen communities in Yellowstone National Park, U.S.A. (Eversman et al. 2002).

Methods

Rock samples were obtained from nine paired cliff locations where a limestone layer (sedimentary) was unconformably overlain by an andesitic (siliceous, volcanic) layer. The cliffs were located on two mountains: Abiathar and Barronette Peak in northeast Yellowstone National Park, WY, U.S.A. (44°58’N, 110°05’W, elev. 2500 m). To simulate the environment of cryptogam-inhabited cliff faces only rocks with weathered surfaces (i.e. not products of recent fracturing) were collected. From a larger sample 54 specimens were chosen (three limestone and three andesite samples from each of the nine cliff locations). Rock samples whose surfaces were chipped or abraded during measurements were excluded from analysis.

Measuring Water Holding Capacity

We determined the water holding capacity of rocks during a saturation event (e.g., rain, snowmelt) by measuring the increase in rock mass between dehydrated and saturated states. Rocks were cleaned, oven-dried at 70°C for 48 hours, and immediately transported to a scale in an airtight container filled with desiccant (to minimize water absorption prior to weighing). To find their dry weights, rocks were removed from the desiccator individually and weighed to the nearest 0.1 mg. Rocks were then immersed in water for 10 minutes, removed and shaken vigorously to remove non-absorbed water, and reweighed. The weight of any water left on the scale was subtracted before calculating water-holding capacity.

Measuring Absorption of Atmospheric Water

To measure the amount of atmospheric water substrates can potentially make available to cryptogams, we placed oven-dried rocks into a sealed humidity chamber and repeatedly weighed them as they absorbed water from air of known humidity. We used the same preparatory techniques as for absorption of liquid water. That is, rocks were cleaned, oven-dried at 70°C for 48 hours and were transported to a scale using a desiccator to minimize water absorption. Rocks were removed from the desiccator individually and were weighed immediately to find their dry weights. Water absorption from dry (20% relative humidity), moist (75% RH) and wet air (100% RH), was measured using a humidity chamber. The chamber was a large plastic box (30 × 60 cm) with a small, sliding, air-tight door in its lid (Fig. 8.1). To produce humid air, a small humidifier (Robitusin DH-5650) was placed inside the chamber. The humidifier was left on until the desired relative humidity level was reached. To continually monitor humidity, a relative humidity sensor (Vernier Software model RH-DIN) was placed in the chamber, and attached through a serial interface (Vernier software) to a computer which served as a datalogger (Fig. 8.1). Humidity levels were verified with a dry/wet bulb psychrometer (Casella #4053) at all three humidity levels. Rocks were weighed to the nearest 0.1 mg at approximately 10 minute intervals for the first hour, at half hour intervals for the next four hours, and at approximately 24 hours. Between readings rocks were placed on a 0.5 cm mesh screen within the chamber to ensure that water absorbance occurred on all surfaces (Fig. 8.1).

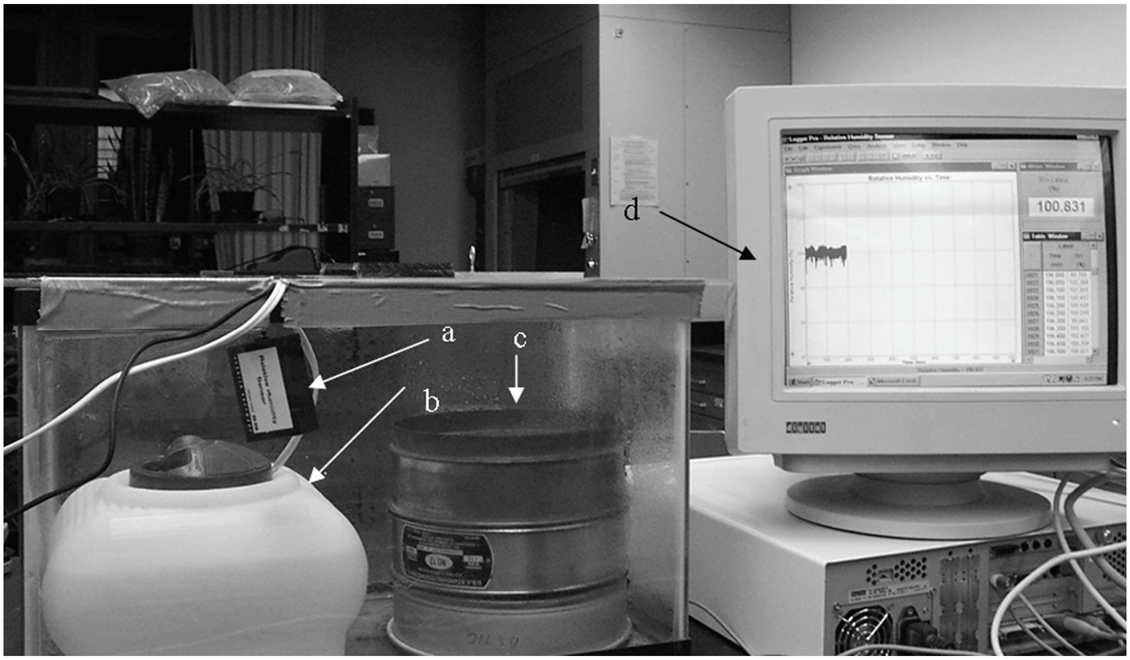

Figure 8.1. Relative humidity chamber. (a) relative humidity sensor, (b) humidifier, (c) wire mesh rack, (d) computer serving as a relative humidity data logger.

Measuring Water Release/Retention

To measure the rate and duration of water release, saturated rocks were weighed repeatedly while drying in room conditions (20°C and 20% relative humidity). Note that this measure and measurements of water holding capacity, described above, can be accomplished in a single operation. To saturate rocks, samples were submerged in water for 10 min, removed and shaken to rid them of non-absorbed water. As rocks dried, loss of weight was recorded to the nearest 0.1 mg at 10 minute intervals for one hour, at half hour intervals for the next four hours, and at approximately 24 hours. Between readings, rocks were placed on a wire rack to insure even drying. Note that our method for measuring water retention parallels a protocol used by Pentecost (1980) for comparing rhyolite and pumice water relations.

Measuring Acidity/Alkalinity

To measure the effect of rock surfaces on H^+/OH^- concentrations in adjacent solution, we determined the change in ion concentration caused by samples in known volumes of solvent over time. Rocks were submerged in known volumes of 0.1 M KCl solution, and pH was measured with standard electrodes (Fisher Scientific Accumet 13-620-531 and 13-620-183). KCl was used as a solvent since it enhances rates of cation exchange compared to deionized water (Farmer et al. 1990; Kricke 2002). Note that for maximum accuracy KCl should be degassed by boiling it for several minutes before submerging rocks, and then sealed during measurements. Measurements were taken at 1, 2, 5, 10, 20, 30, 40, 50, 60, 90, 120 and 150 minutes.

Measuring Surface Area

When considering ecologically important rock surface processes, measurements should be expressed with respect to cryptogam-relevant units (e.g., cm^2 surface area). To do so we calculated surface area by measuring the increase in rock mass after applying a monolayer of homogenous sand grains with a known mass per unit surface area. We sieved 30-weight silica landscaping sand to isolate sand grains 250–350 μm in diameter. To find how much sand represented a 100 cm^2 (10,000 mm^2) surface area, we applied a thin layer of spray-on adhesive (3M #62-4977-4930-9) to a sample ($n = 5$) of 10 × 10 cm index cards, tared, then covered the paper with a single layer of sand and reweighed it. Rocks samples were prepared in the same way. To find rock surface area, rock-sand weight was compared to the 100 cm^2 standard (Equation 8.1). Rock measurements (water holding capacity, absorption of atmospheric water, water retention, and pH) were adjusted to surface area units using Equations 8.1–8.3.

Our method for measuring rock surface area was adapted from a protocol for measuring conifer needle surface area with glass beads of known diameter and mass (Davies & Benecke 1980; Thompson & Leyton 1971). For our purposes this method is superior to measures based on gas adsorption (i.e., Brunauer et al. 1938; Gregg & Sing 1967), because it operates at a cryptogam appropriate scale, and does not include unoccupied pore space beneath the surface in measurements.

Equations

$$\mathrm{SW(g)} \times \frac{1\ \mathrm{cm}^2}{\mathrm{M(g)}} = \mathrm{SA(cm^2)} \tag{8.1}$$

$$\mathrm{H_2O\ absorption\ or\ loss\ (mL)/SA(cm^2) = H_2O\ absorption\ or\ loss\ (mL\ cm^{-2})} \tag{8.2}$$

$$\mathrm{pH} = -\log[\mathrm{H}^+] \quad \text{or conversely,} \quad [\mathrm{H}^+] = 10^{-\mathrm{pH}}$$

$$[\mathrm{H}^+_{\mathrm{i}}] - [\mathrm{H}^+_{\mathrm{f}}] = \Delta[\mathrm{H}^+] \quad \text{or conversely,} \quad (1 \text{ x } 10^{-14}/[\mathrm{H}^+_{\mathrm{i}}]) - (1 \text{ x } 10^{-14}/[\mathrm{H}^+_{\mathrm{f}}]) = \Delta[\mathrm{OH}^-]$$

$$\frac{\Delta\ \mathrm{mol\ OH^-}}{\mathrm{KCl(L)}} \times \frac{\mathrm{Svol.\ KCl(L)}}{1} \times \frac{1}{\mathrm{SA(cm^2)}} = \Delta\ \mathrm{mol\ OH^-\ cm^{-2}} \tag{8.3}$$

Where: sand weight (SW) = weight of rocks with sand - weight of rocks without sand, M = mass of 1 cm^2 of sand (we found that 1 cm^2 of 30# silica landscaping sand weighed approximately 0.03 g), SA = surface area, $[\mathrm{H}^+_{\mathrm{f}}]$ = final concentration of hydrogen ions, $[\mathrm{H}^+_{\mathrm{i}}]$ = initial concentration of hydrogen ions, and Svol. = volume of KCl used to inundate samples.

Other Measures

Three additional measures were made using conventional methods. The mineralogy of substrates was determined with x-ray diffraction techniques (Moore & Reynolds 1997) using a powder x-ray diffractometer (Syntag Inc.). The presence of $CaCO_3$ on rock surfaces was determined with "fizz tests" by applying 0.5 M HCl to rock surfaces (Brice & Levin 1960). Density was measured by weighing rocks, determining volume displacement in a graduated cylinder and dividing mass by volume (Davis & Reitan 1976).

Results

Water Absorption and Retention

Absorption of liquid water by andesite was much greater than limestone after a simulated saturation event (Kruskal-Wallis non-parametric tests; $p < 0.001$, $H = 27.19$; Fig. 8.2; Table 8.1). In addition, andesite atmospheric water absorption was greater than limestone at all three humidity levels, for all time intervals after 15 minutes ($p \leq 0.003$; Fig. 8.3; Table 8.1). After 22 hours at 100% RH, andesite absorbed 0.029 mL cm^{-2}; this is nearly half the water content of completely saturated andesite (0.06 mL cm^{-2}), and three times the water content of completely saturated limestone (0.01 mL cm^{-2}; Table 8.1). Limestone absorbed relatively little atmospheric water. Even after 22 hours at 100% RH only 0.0004 mL cm^{-2} was absorbed by limestone samples (Table 8.1).

The greater water holding capacity of andesite allowed it to release water over much longer periods than limestone. More than 26 hours after saturation, andesite continued to retain relatively large quantities of water (0.009 mL cm^{-2}), while saturated limestone samples were essentially dry in less than 2 hours (Fig. 8.2; Table 8.1).

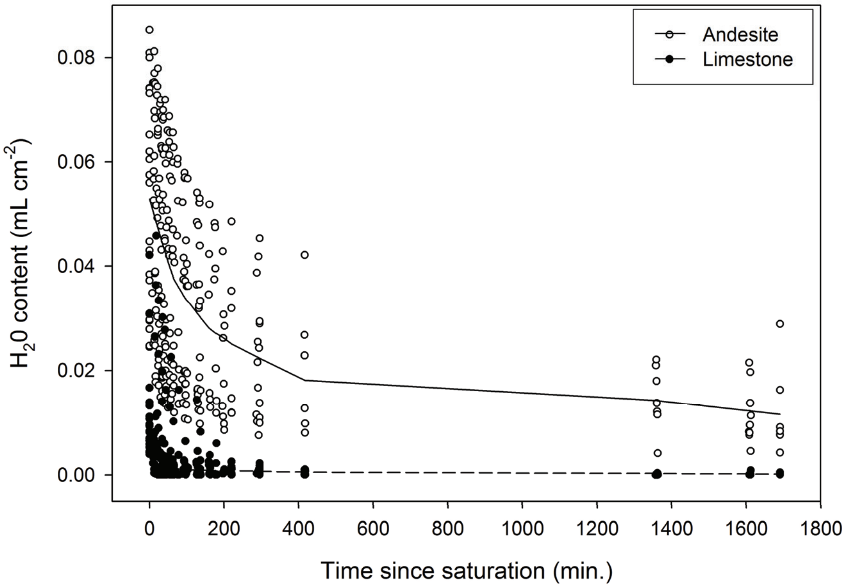

Figure 8.2. Water loss from saturated rock surfaces (mL cm^{-2} min^{-1}). Differences between substrates were significant at time = 0 minutes (i.e., during saturation), and remained significant after 26 hours. Lines are lowess smoothers.

<u>Acidity/Alkalinity</u>

The pH equilibration time for rock samples was much longer than the four minutes reported for bark (Schmidt et al. 2001). Both rock types equilibrated with 0.1 M KCl solution after approximately 2.5 hours (Fig. 8.4). While both rock types increased solution alkalinity, limestone samples equilibrated with KCl at a much higher pH (8.68) than andesite (6.60) ($p < 0.001$; Table 8.1). Differences in ion concentration (Δmoles OH$^-$ cm^{-2}) between solutions containing limestone and andesite rocks were detectable within 15 minutes ($p = 0.0005$; Table 8.1). These differences continued to increase over time (Fig. 8.4).

Discussion

Porosity

The superior water absorbing/retention power of andesite is largely due to its high porosity. Porous rock surfaces provide channels for capillary absorption/retention and liquid water stored in protected reservoirs (Benavente et al. 2004). In addition, minute projections on rough/porous surfaces may act as nuclei for condensation of water droplets (Pentecost 1980). The high porosity of andesite was demonstrated both by streams of air bubbles released from samples during saturation, and the low density of our andesitic rocks relative to limestone ($p < 0.001$, $H = 24.49$; Table 8.1).

Water Absorption

Limestone and andesite rock samples absorbed water from the environment as both liquid and vapor. Liquid water captured by substrates from saturation events (e.g., rain, snowmelt) is beneficial to many cryptogam species, and may profoundly affect rock outcrop community structure (Brodo 1973, Larson et al. 2000, Pentecost 1980). In many regions, however, acquisition of rainwater alone may be insufficient or too unreliable to support cryptogam survival and development. For instance, summer precipitation in the study site region is infrequent (rain showers fall on only 26% of July–August days) and limited (64% of showers that do occur deliver less than 4.0 mm of water). Frequency and amount of summer rainfall is similar in other ecosystems of the Northern Rockies including shortgrass prairie, foothills prairie and Douglas fir (*Pseudotsuga menziesii*) montane zones (Weaver 1985).

Water acquired from condensation of vapor may provide more consistent recharge of substrate reservoirs than liquid water, particularly in mesic-dry environments. Our experiment demonstrated the potential for such recharge at humidities of 100%, 75% and even 20% RH. Andesite samples were particularly effective in absorbing atmospheric water (Fig. 8.3, Table 8.1). The water absorption power of our andesite is probably due to both its vesicular/porous surface, noted above, and its hydrophilic smectite clay content (Pusch & Yong 2003; Table 8.1).

Atmospheric water condensation (dew) occurs at high humidities when the ground is cooler than the air (Geiger et al. 2003; Kramer 1983). Since solid surfaces cool more rapidly than air at night, water vapor condenses nightly on substrates at between 80–90% RH in cool climates and as low as 60% RH in warmer regions (Geiger et al. 2003). In our region, average early morning relative humidity (5:00 am) exceeds 80% every month at lower altitudes, and is predicted to be higher at high elevations and in cliff/canyon areas (Finklin 1983). Thus, repeated nocturnal condensation may provide more hours of wet substrate than rainfall, particularly in dry climates (cf. Azevedo & Morgan 1974; Oliver 2002; Vogelman et al. 1968). Atmospheric water absorption may be particularly important in cliff environments where rain water received by rock surfaces is restricted by slope (Larson et al. 2000).

Table 8.1. Surface characteristics of andesite and limestone rocks. *P*-values are for hypotheses of no difference between substrates. *N* = number of rock samples compared with Kruskal-Wallis nonparametric tests. Significance levels were adjusted for simultaneous inference using Dunn's (1964) procedure.

	Andesite		Limestone		
	Median	N	Median	N	*P*-val.
Rock character					
General mineralogy (x-ray crystallography)	andesine, augite, smectite clay		calcite, dolomite		
Density (g cm^{-3})	2.26	27	2.72	27	<0.001
Liquid water absorption					
H_2O content (mL cm^{-2}) of saturated rocks	0.06	22	0.01	20	<0.001
Absorption of atmospheric water					
H_2O abs. at 20% RH (mL cm^{-2}) after 10 mins.	0.0003	18	<0.0001	27	<0.001
after 22 hours	0.005	12	0.0001	18	<0.001
H_2O abs. at 75% RH (mL cm^{-2}) after 10 mins.	0.001	6	0.0001	9	0.001
after 23 hours	0.02	6	0.0008	8	0.002
H_2O abs. at 100% RH (mL cm^{-2}) after 15 mins.	0.002	7	0.0001	6	0.003
after 22 hours	0.029	22	0.0004	19	<0.001
Water retention/storage					
H_2O content (mL cm^{-2}) after drying 26.5 hours	0.009	15	0.0001	13	<0.001
pH—acidity/alkalinity					
Ca presence ("fizz test" with 0.5 M HCl)	100% Ca-	27	100% Ca+	27	
Log(mol OH^- increase) cm^{-2} after 15 mins.	-8.63	19	-7.23	19	<0.005
Final (equilibrium) pH – initial (KCl) pH = Δ***pH***	6.6-6.1=**0.5**	26	8.7-6.1=**2.6**	26	<0.001

Water Release/Retention

The duration of substrate water supply strongly affects cryptogam community composition on both bark (e.g., Hale 1955) and rock-surfaces (Larson et al. 2000; Pentecost 1980). Our experiments show that in a dry, low-energy environment, saturated andesite continued to retain water for over 26 hours (1600 mins.), while limestone stored water for less than 2 hours (Fig. 8.2). Although not shown in Fig. 8.2, saturated andesite rocks continued to release water for more than 48 hours at 20°C and 20% RH.

Water stored from vapor condensation should also affect cryptogam communities. Our results indicate that after equilibrating with saturated air (Fig. 8.3), andesite can supply water for more than 24 hours in a dry environment. This information can be read from the andesite drying curve (Fig. 8.2) by beginning at the 100% RH saturation point (Water content ≈ 0.03 mL cm^{-2}, Time ≈ 140 mins.), and applying the curve to the remaining water. The capacity of andesite to retain both liquid and condensed water is again due to its porosity and/or hydrophilic mineralogy; characteristics that are strongly correlated to substrate evaporation resistance in soil models (Aluwihare & Watanabe 2003; Yamanaka et al. 1997; many others).

We expect water storage related community differences between andesite and limestone to be greatest on shaded north-facing cliffs. In north-facing environments water storage differences between substrates are maintained due to relatively small amounts of evaporation. In contrast, on south-facing cliffs, differences in the duration of water supply are reduced, because while the duration of limestone water storage after saturation (≅ 1 hour) cannot be greatly shortened, the duration of andesite water retention (> 48 hours) will be greatly shortened by radiation driven evaporation.

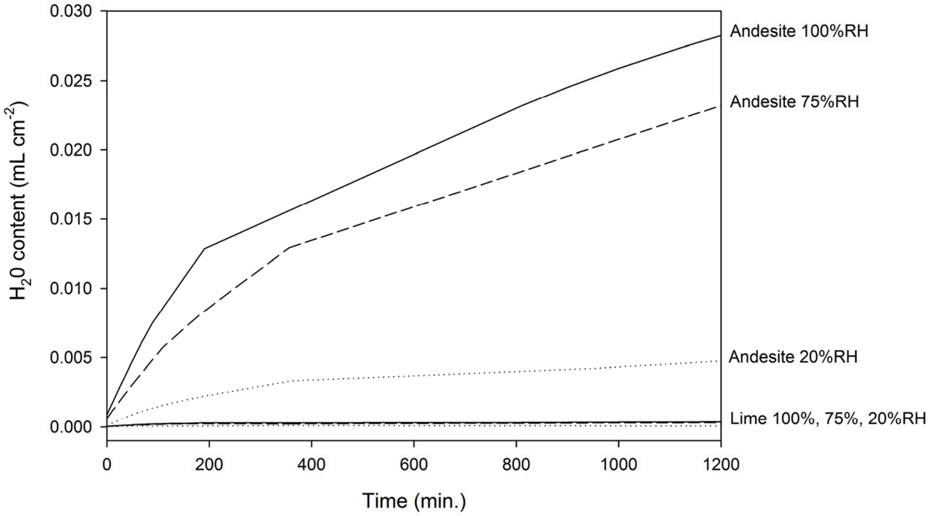

Figure 8.3. Absorption of atmospheric water (RH 20%, 75% and 100%) by andesite and limestone. Water content differences between substrates were statistically significant at all three humidities after 15 minutes. Lines are lowess smoothers.

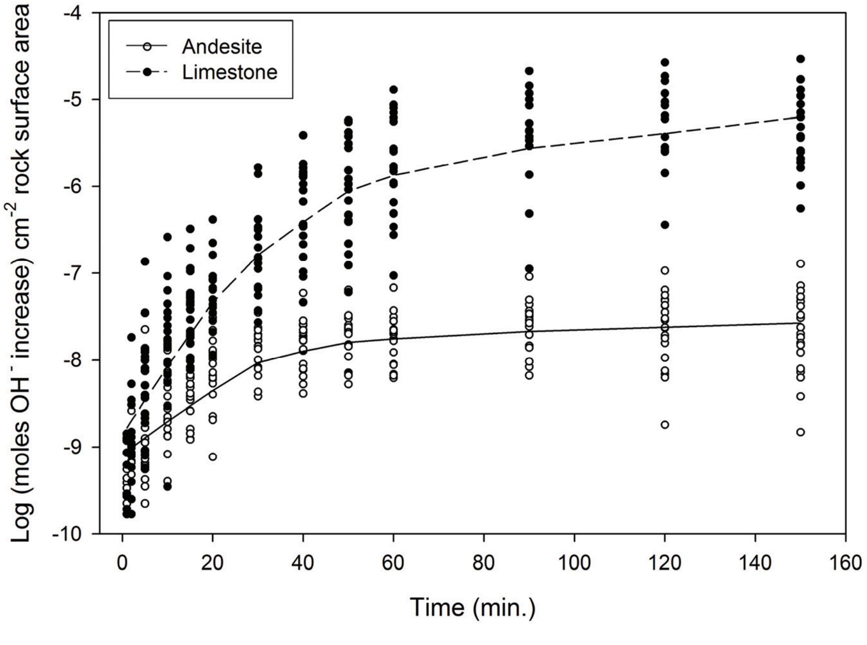

Figure 8.4. Equilibration of pH for samples in KCl solution [log(Δmoles OH$^-$ ions) cm^{-2} min^{-1}]. Differences between substrates were statistically significant after 15 minutes. Lines are lowess smoothers.

Physiological Implications of Substrate Water Relations

Water absorption and retention/storage of substrates may affect cryptogams in two important ways. First, an unknown fraction of water supplied by the substrate will be available to cryptogams at physiologically useful water potentials. Second, the remaining water, contained in surfaces distant from cryptogams or held at unavailable water potentials may also provide benefit. This is because evaporation of unusable water (resulting in increased water potential of the surrounding air) should reduce both cryptogam transpiration/water loss and evaporation from cryptogam-usable reservoirs (cf. Lambers et al. 1998, pg. 185). The importance of these factors will vary with environmental conditions and the water use strategies (e.g., ectohydric, endohydric physiology) of particular cryptogam species (cf. Proctor 1982).

It should be emphasized that cryptogams will also affect the water relations of rock outcrops. For instance pores formed by saxicolous (rock-inhabiting) species may drastically increase the water retention capacity of rock surfaces, facilitating cryptogam reestablishment after fires (Garty 1977). The lichen *Lecidea tenebrica* may increase the water retention capacity of rhyolite rock surfaces, though it appears to have little effect on evaporation rates (Pentecost 1980). This interaction will undoubtedly vary among cryptogam life forms (e.g. mosses lichens, hepatics) and species.

Surface Chemistry

Along with surface water relations, surface chemistry is important to rock dwelling communities since cryptogams absorb and accumulate nutrients, ions and toxic substances released from substrates by weathering and biological activity (Bates 1978, Smith 1962). Chemical differences between substrates, particularly the presence/absence of calcium noted in our study, may result in highly dissimilar flora on adjacent rock outcrops (Table 8.1; Brodo 1973; Smith 1982). Similarly, hydrogen ion concentration (pH), the substrate chemical component most frequently measured by lichenologists and bryologists, is a correlate of cryptogam performance and distribution on both lithic and non-lithic surfaces (Smith 1982). The acidity/alkalinity of substrates may act directly on cryptogams, or indirectly by altering diffusion rates and the availability of nutrients and toxins (Brodo 1973, Smith 1982).

The high alkalinity of limestone in our experiment is due to the H^+ buffering characteristics of its major constituent, calcite, $CaCO_3$ (Table 8.1). The slight but measurable alkalinity of andesite is probably due to secondary alterations of rock surfaces which produce hydroxyl-bearing minerals (T. Feeley pers. comm. 2005), and/or to $CaCO_3$ depositions from water or air.

In accordance with convention we report the equilibrium pH of andesite and limestone in solution (Table 8.1). However, to describe rock surface acidity/alkalinity, we favor Δ moles H^+ cm^{-2}, or Δ moles OH^- cm^{-2} as a measure, i.e., the change in ion concentration caused by the interaction of a solution with an area of surface (Table 8.1; Fig. 8.4; Stumm & Morgan 1996). While surfaces of solids can donate or bind H^+ ions to alter the pH of a solution they are in contact with, they do not have pH *per se*. By expressing acidity/alkalinity on a surface area basis we acknowledge that ion exchange of a solid depends on both its surface area and its mineral content (Dzombak & Morel 1990; Stumm & Morgan 1996)

It should be noted that neither our method, nor methods of others (e.g., Bates 1978; Farmer et al. 1990; Kricke 2002; Schmidt et al. 2001) consider slight variations in ratios of surface area to solvent volume. Such variation may cause measurements (e.g., ion concentration cm^{-2}) to be confounded by the law of mass action (Brown et al. 1994). In addition, previous methods, including ours, do not address models of solid-liquid interfaces which allow for non-uniform distributions of ions in solution (e.g., Delahay 1965).

While untested, our method should be useful for measuring the availability of other materials (e.g., toxins and nutrients) on rock surfaces. That is, one can immerse a weathered sample in solution, measure the change in concentration of an ion of interest with either chemical methods or appropriate electrodes (Anker et al. 1981; Brinckoff 1978; Diggens et al. 1972; Midgely 1985; for Ca^+; NO_3^-; Na^+; and Cl^- respectively), and express the change with respect to surface area. These measures will provide important additional information about nutrient availability, toxicity, weathering rates, and substrate stability.

Conclusions

Surface conditions (water relations and chemistry) are important to cryptogams occupying lithic substrates, necessitating defensible methods for measurement. We validated original methods for quantitatively measuring substrate environments, and demonstrated that adjacent rock faces may differ significantly with respect to surface characteristics (water absorption, water retention and pH) important to their cryptogam constituents. Using our methods it should also be possible to measure exchange of other ions at rock surfaces including nutrients and toxins. These methods and their extensions will be useful to lichenologists, bryologists and ecologists interested in rock outcrop communities.

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Literature Cited

Aluwihare, S. & K. Watanabe. 2003. Measurement of evaporation on bare soil and estimating surface resistance. Journal of Environmental Engineering 129: 1157–1198.

Anker, P. E., D. Wieland, R. E. Dohner, R. Asper & W. Simon. 1981. Neural carrier based ion-selective electrode for the determination of total calcium in blood serum. Analytical Chemistry 53: 1970–1974.

Azevedo, J. & D. L. Morgan. 1974. Fog precipitation in coastal California forests. Ecology. 55: 1135–1141.

Barkman, J. J. 1958. Phytosociology and Ecology of Cryptogamic Epiphytes. Van Gorcum, Assen, Netherlands.

Bates, J. W. 1978. The influence of metal availability on the bryophyte and macrolichen vegetation of four rock types on Skye and Rhum. Journal of Ecology. 66: 457-482.

Benavente, D., M. A. García del Cura, R.. Fort & S. Ordóñez. 2004. Durability estimation of porous building stones from pore structure and strength. Engineering geology. 74: 113-127.

Brice, J. C. & H. L. Levin 1960. Laboratory Studies in Earth History. Wm. C. Brown Co., Dubuque, Iowa, U.S.A.

Brinckoff, H. C. 1978. Analysis of the nitrate content of water and effluent water; Application of plastic membrane nitrate selective electrode in water quality monitors. Environmental Science and Technology 12: 1392–1394.

Brodo, I. M. 1968. The lichens of New York: A vegetational and floristic analysis. New York State Museum Science Service Bulletin 410: 1–330.

Brodo, I. M. 1973. Substrate ecology. Pages 401–441. *In* V. Ahmadjihan and M. E. Hale (eds.). The Lichens. Academic Press, New York and London.

Brown, T. L., H. E. Lemay & B. E. Bursten. 1994. Chemistry: The Central Science. Prentice-Hall, Engelwood Cliffs, NJ, U.S.A.

Brunauer, S., P. H. Emmett & E. Teller. 1938. Adsorption of gasses in multimolecular levels. Journal of the American Chemical Society 60: 309–313.

Campbell, G. S. & G. W. Gee. 1996. Water potential, miscellaneous methods. Pages 619–632. *In* A. Klute (ed.), Methods of Soil Analysis, part 1—physical and mineralogical methods. Second edition. American Society of Agronomy, Inc. and Soil Science Society of America, Madison, WI, U.S.A.

Cook, S. J. 2000. [Abstract] Surficial geochemical expressions of buried mineral deposits; results of regional lake sediments and water geochemical mapping surveys in the Nechako Plateau, central British Columbia. Page 8. *In* Geological Society of America, Cordilleran section, 96th annual meeting. Geological Society of America, Boulder, CO, U.S.A.

Davies, C. E., & U. Benecke. 1980. Fluidized bed coating of conifer needles with glass beads for determination of surface area. Forestry Science 26: 29–32.

Davis, S. & P. Reitan. 1976. Geology, Our Physical Environment. McGraw-Hill, Boston, MA, U.S.A.

Delahay, P. 1965. Double Layer and Electrode Kinetics. Interscience Publishers, New York, U.S.A.

Diggens, A. A., K. Parker & H. M. Weber. 1972. The continuous determination of sodium in high purity water by using a sodium monitor incorporating a sodium-responsive glass electrode. Analyst 97: 198–203.

Dunn, O. J. 1964. Multiple comparisons using rank sums. Technometrics 6: 241–252.

Dzombak, D. A. & F. M. M. Morel. 1990. Surface Complexation Modeling; Hydrous Ferric-oxide. Wiley-Interscience, New York, U.S.A.

Eversman, S., C. M. Wetmore, K. Glew & J. P. Bennett. 2002. Patterns of lichen diversity in Yellowstone National Park. The Bryologist 105: 27–42.

Farmer, A. M., J. W. Bates & N. B. Bell. 1990. A comparison of methods for the measurement of bark pH. The Lichenologist 22: 191–197.

Finklin, A. I. 1983. Weather and Climate of the Selway-Bitteroot Wilderness. Northwest Naturalist Books, University Press of Idaho, Moscow, ID, U.S.A.

Foote, K. G. 1966. The vegetation of lichens and bryophytes on limestone outcrops in the Driftless Area of Wisconsin. The Bryologist 69: 265–292.

Fujita, T., D. Suigiyama, S. W. Swanton & B. J. Myatt. 2003. Observation and characterization of colloids derived form leached cement hydrates, Pages 3–16. *In*

Kim Jae & H. Horst (eds.), 8th conference on chemistry migration behaviour of actinides and fission products in the geosphere. Journal of Contaminant Hydrology. Elsevier, Amsterdam, Netherlands.

Gardner, W. H. 1996. Soil water content. Pages 493–541. *In* A. Klute (ed.), Methods of Soil Analysis, part 1—physical and mineralogical methods. Second edition. American Society of Agronomy, Inc. and Soil Science Society of America, Madison, WI, U.S.A.

Garty, J. 1992. The postfire recovery of rock-inhabiting algae, microfungi and lichens. Canadian Journal of Botany. 70: 301-312.

Garty, N. Kloog, R. Wolfson, Y. Cohen, A. Karnielli & A. Avni. 1997. The influence of air pollution on the concentration of mineral elements, on the spectral reflectance response and on the production of stress-ethylene in the lichen *Ramalina duriaei*. New Phytologist 137: 587–597.

Geiger, R., R. H. Aeon & P. Todhunter. 2003. The Climate Near the Ground. 6th edition. Rowman and Littlefield. Lanham, MD., U.S.A.

Gregg, S. J. & K. S. W. Sing. 1967. Adsorption, Surface Area and Porosity. Academic Press, New York, U.S.A.

Hale, M. E., Jr. 1955. Phytosociology of corticolous cryptogams in the upland forest of southern Wisconsin. Ecology 36: 45–63.

Kalgutkar, R. M. & C. D. Bird. 1969. Lichens found on *Larix lyallii* and *Pinus albicaulis* in southwestern Alberta, Canada. Canadian Journal of Botany 47: 627–648.

Killham, K. 1994. Soil Ecology. Cambridge University Press, Cambridge, U.K.

Kramer, P. J. 1983. Water Relations of Plants. Academic Press, New York, U.S.A.

Kricke, R. 2002. Measuring bark pH. Pages 333–336. *In* P. L. Nimis, C. Scheidegger & P. A. Wolseley (eds.), Monitoring Lichens—Monitoring with Lichens. Kluwer Academic Publishers, Dodrecht, Netherlands.

Lambers, H., F. S. Chapin III & T. L. Pons. 1998. Plant Physiological Ecology. Springer-Verlag, New York, U.S.A.

Larson, D., U. Mattes & P. E. Kelly. 2000. Cliff Ecology. Cambridge University Press, Cambridge, U.K.

Midgely, D. 1985. Determination of chloride and fluoride in boronated waters. Analyst 110: 841–845.

Mod'd, B. K., R. J. Howarth, & C. H. Bland. 1996. Rapid prediction of building research establishment limestone durability class from porosity and saturation. Quarterly Journal of Engineering Geology. 29: 285-297.

Moore, D. M. & R. C. Reynolds. 1997. X-ray Diffraction and the Identification and Analysis of Clay Minerals. Oxford University Press, Oxford, U.K.

Murphy, T. P., K J. Hall & I. Yesaki. 1983. Coprecipitation of phosphate with calcite in a naturally eutrophic lake. Limnology and Oceanography 28: 58–69.

Oliver, J. 2002. Fog harvesting along the west coast of South Africa, a feasibility study. Water South Africa. 28: 349–360.

Pentecost, A. 1980. The lichens and bryophytes of rhyolite and pumice-tuff rock outcrops in Snowdonia, and some factors affecting their distribution. Journal of Ecology 68: 251–267.

Proctor, M. C. F. 1982. Physiological ecology: water relations, light and temperature responses, carbon balance. Pages 333-381. *In* A. J. E. Smith (ed.), Bryophyte Ecology. Chapman and Hall, London, UK.

Pusch, R. & R. Yong. 2003. Water saturation and retention of hydrophilic clay buffer—microstructural aspects. Applied Clay Science 23: 61–68.

Richardson, B. A. 1991. The durability of porous stones. Stone industries. 26(10): 22-55.

Schmidt, J., R. Kricke & G. B. Feige. 2001. Measurement of bark pH with a modified flathead electrode The Lichenologist 33: 456–460.

Smith, A. J. E. 1982. Epiphytes and epiliths. Pages 191-227. *In* A. J. E. Smith (ed.), Bryophyte Ecology. Chapman and Hall, London, UK.

Smith, D. C. 1962. The biology of lichen thalli. Cambridge Philosophical Society Biological Reviews 37: 537–570.

Stumm, W. & J. J. Morgan. 1996. Aquatic Chemistry. Wiley-Interscience, New York, U.S.A.

Thompson, F. B. & L. Leyton. 1971. Method for measuring the leaf surface area of complex shoots. Nature 229: 572.

Tulve, N., & T. C. Young. 1997. [Abstract] Aggregation properties of colloidal particles from the Fox River, Green Bay, Wisconsin. Page 248. *In* Geological Society of America, 1997 annual meeting. Geological Society of America, Boulder, CO, U.S.A.

Vogelman, H. W., T. Siccama, D. Leedy & D. C. Ovitt. 1968. Precipitation from fog in the Green Mountains of Vermont. Ecology 49: 1205–1207.

Weaver, T. 1985. Summer showers: their sizes and interception by surface soils. American Midland Naturalist 114: 409–413.

Yamanaka, T., A. Takeda & F. Sugita. 1997. A modified surface resistance approach for representing bare-soil evaporation: Wind tunnel experiments under various atmospheric conditions. Water Resources Research 33: 2117–2128.

CHAPTER 9

MEASURING SOIL WATER POTENTIAL WITH GYPSUM BLOCKS: CALIBRATION AND SENSITIVITY

Introduction

Processes including photosynthesis, respiration, and growth are strongly associated with plant water potential (Lambers et al. 1998). This is because plant physiological processes depend largely on water uptake (determined by soil water potential) and losses (largely determined by the water potential gradient from soil to stoma). As a result plant ecologists need effective methods to determine soil water potential.

Gypsum block sensors are an inexpensive and reliable tool for measuring soil water and comparing water potential across a diversity of sites (Gardner 1986, Bouyoucos and Mick 1940). The measurement depends on the regular increase in conductivity of the blocks with increasing soil water content. Slight dissolution of blocks creates a weak in-block ion solution which also controls against the confounding effect of soil salinity on conductivity, at least at low soil salt concentrations (Weaver 1987). Other methods for measuring soil water potential are reviewed by Gardner (1986).

Objectives

This chapter provides four products: **1)** First we demonstrate a new gypsum block calibration procedure involving equilibration of sensors in soils of known water potentials. Our method improves on conventional procedures by simultaneously providing useful measurement units [water potential; megapascals (MPa)] and shortening calibration times (cf. Gee and Campbell 1986). For instance, a common calibration procedure measures block conductivity in soils of known water content [(wet soil mass – dry soil mass)/dry soil mass]. Since this method does not correlate block response to water potential, its results are generally limited to soils which are similar to those used in creating the calibration curve (Gardner 1986). A second common method involves imbedding blocks in soils, reducing water potential incrementally, and measuring water potential at these increments (e.g. Klute 1986, Weaver 1987). While this procedure produces a calibration curve in water potential units, it is very slow (> 6 months, Weaver 1987), and will overestimate water potential if the system is not brought to full equilibrium. **2)** Second, we determine equilibration times for dry blocks inserted in samples of a sandy loam at five water potentials. **3)** Third, we provide calibration curves for two types of commercial plaster blocks (Boyoucous and Delmhorst GB-1). **4)** Lastly we measure the useful range of each block type by determining the range in which soil water potentials are statistically distinguishable.

Methods

We studied two types of commercial blocks, Delmhorst GB-1 (2.5 cm x 2 cm diameter) available from Forestry Suppliers (205 West Rankin Street, P.O. Box 8397 Jackson, MS 39284-8397), and Bouyoucos (3 x 4 x 1.5 cm) manufactured by Beckman Instruments (PO Box 3100, 2500 Harbor Boulevard, Fullerton, CA). Readings were made with a Delmhorst KS-D1 digital soil moisture meter available from Forestry Suppliers.

To calibrate the blocks we measured their electrical resistance at seven known water potentials and plotted water potential against resistance. Calibration involved six steps. **1.** As a calibration medium we chose a sandy loam (60% sand, 16% silt, 24% clay) since its silt component would allow good contact with blocks while its sand component would facilitate mixing and prevent mudding. **2.** A water retention curve was created for this soil by measuring water contents at -0.03, -0.1, -0.3, -0.5, -0.8, and -1.5 MPa. The soil water potentials were measured with a pressure membrane/ceramic plate apparatus by the MSU soil testing laboratory (cf. Gardner 1986). Water contents were measured gravimetrically (wt/wt). A regression of water content and water potential was linear after power transformation ($r^2 = 0.993$), allowing interpolation of water potentials. **3.** We wished to test responses of sensors with a range of water potentials from approximately -0.01 to -1.5 MPa. We adjusted soil samples to desired water potentials by weighing them, calculating the water content for a desired water potential, and repeatedly misting with water, and mixing until the desired water content was reached. Water contents were gravimetrically verified. Gravimetric determinations showed that the water potentials created were -0.02, -0.05, -0.08, -0.2, -0.6, -1.2, and -4.4 MPa. **4)** Soils with the seven different water potentials were stored in separate cylinders (16cm high and 16cm dia.). Three Delmhorst and three Bouyoucos blocks were buried in each can. The soils were firmly packed. Since they were to equilibrate with the soils, the blocks touched neither each other, the walls of the can, nor the surface of the soil. To prevent loss of water by evaporation/condensation cans were stored at a uniform 21ºC, sealed with duct tape, and enclosed with polyethylene bags. Sensor leads extended outside the bags and were sealed with vulcanizing rubber so drying air did not enter as sensors were read. That slight water loss did not occur was demonstrated by making gravimetric measures in closing the experiment. **5.** To determine the block equilibration time, sensor readings were taken ten times over a thirty-six day period, at 0, 8, 27, 99, 166, 267, 335, 439, 600, 774, and 875 hours. **6.** Post-equilibration readings were regressed against soil water potential.

Analysis

A one-way ANOVA was run comparing sensor responses from the seven different water potential levels. Regressions were run in S-Plus using the nlm package (R core development team 2006). Formulae were verified with MATHCAD.

Results

Regardless of the soil water potential both Bouyoucos and Delmhorst blocks equilibrated with soils in approximately 100 hours (Fig 9.1). Equilibration may have been slightly faster in wetter soils.

Calibration curves for Bouyoucos and Delmhorst blocks were constructed by plotting block readings against known soil water potentials (Fig. 9.2). Since the blocks equilibrated in 100 hours, readings taken thereafter were used in creating the calibration curve and for other statistical analyses. Exact model predictions of water potentials at particular sensor responses are provided in Table 9.1.

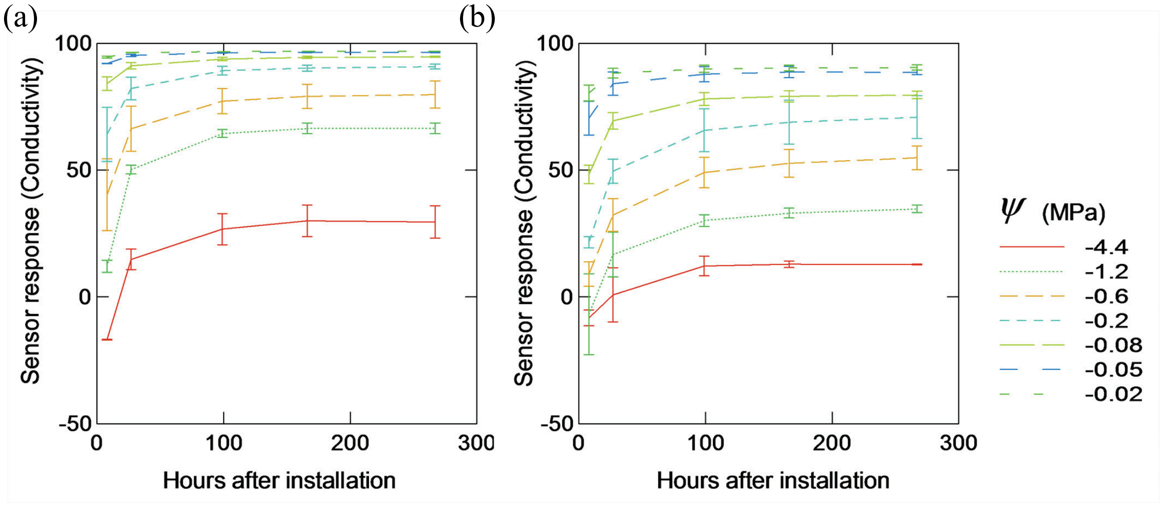

Figure 9.1. Time required for equilibration of (a) Bouyoucos and (b) Delmhorst sensors in soils with water potentials of -0.02 to -4.4 MPa. Bars indicate ±SE.

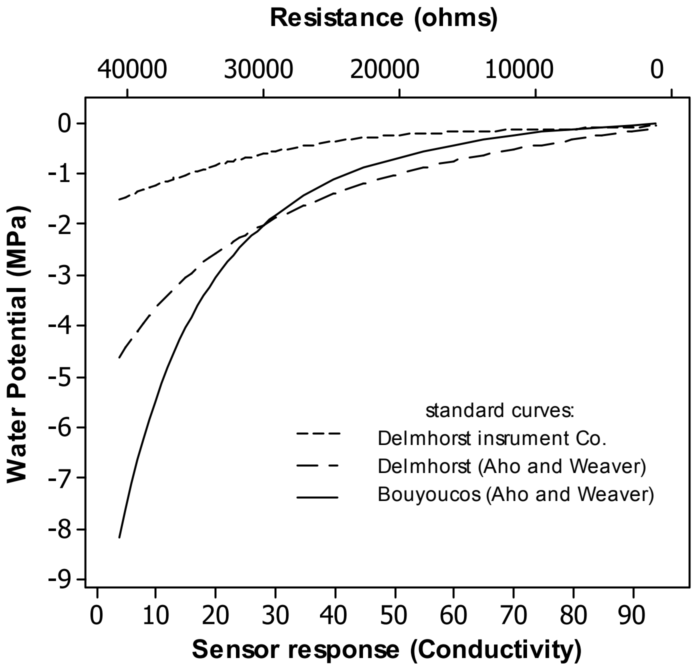

Figure 9.2. Relationship of soil water potential to meter reading and approximate electrical resistance (ohms) for Bouyoucos and Delmhorst sensors (Eqs. 9.1-9.2). A calibration curve provided by Delmhorst Inst Co. for use with their meter and blocks is also shown (see Eq. 9.3).

$$\psi(B) = \exp\left[\frac{-\ln\left(17.9493 - \ln\left(\frac{B+35.1-129.88}{B+35.1}\right) - 3.832\right)}{19.439} \Big/ 0.13206 \right]$$

(9.1) Bouyoucos (Aho and Weaver)

$$\psi(D) = \exp\left[\frac{-\ln\left(16.041 - \ln\left(\frac{D+35.1-131.728}{D+35.1}\right) - 2.393\right)}{19.439} \Big/ 0.13206 \right]$$

(9.2) Delmhorst (Aho and Weaver)
$r^2 = .99997$

<u>For $0 > \psi > -0.15$ MPa</u>

$\psi(D) = -(13.729 - 0.4343D + .00524D^2 - 0.0000226D^3)/10$

<u>For $-0.15 > \psi > -1.5$ MPa</u>

$\psi(D) = -(17.09 - 0.5619D + .00652D^2 - 0.000024D^3)/10$

(9.3) Delmhorst Instrument Co. (P. Laurentzi per. comm. 2001), $r^2 = .982$

Where Ψ = water potential (MPa), B = Bouyoucos sensor reading, D = Delmhorst sensor reading, $\Psi(B)$ = water potential for Bouyoucos sensor, $\Psi(D)$ = water potential for Delmhorst sensor.

Table 9.1. Soil water potentials at particular sensor responses for Bouyoucos and Delmhorst GS-1 sensors.

Meter reading	Bouyoucos Ψ (MPa)	Delmhorst Ψ (MPa)
90	-0.03	-0.15
80	-0.12	-0.32
70	-0.24	-0.51
60	-0.42	-0.74
50	-0.69	-1.02
40	-1.12	-1.38
30	-1.81	-1.87
25	-2.34	-2.19
20	-3.05	-2.57
15	-4.04	-3.04
10	-5.47	-3.64
5	-7.63	-4.43

While drier treatments were easily distinguished (-4.4 to -0.08 MPa) sensor responses were too similar to detect differences among the wettest soils (Fig 9.3). Delmhorst sensors distinguished responses from all but the three wettest treatments: -4.4

MPa < -1.2 MPa < -0.6MPa < -0.2 MPa ≤ -0.08 MPa ≤ 0.05 MPa ≤ 0.02 MPa (Fig 9.3b, $P < 0.001$, df=134). Bouyoucos sensors distinguished responses from all but the two wettest treatments: -4.4 MPa < -1.2 MPa < -0.6MPa < -0.2 MPa < -0.08 MPa < -0.05 MPa ≤ 0.02 MPa (Fig. 9.3a, $P < 0.001$, df = 133).

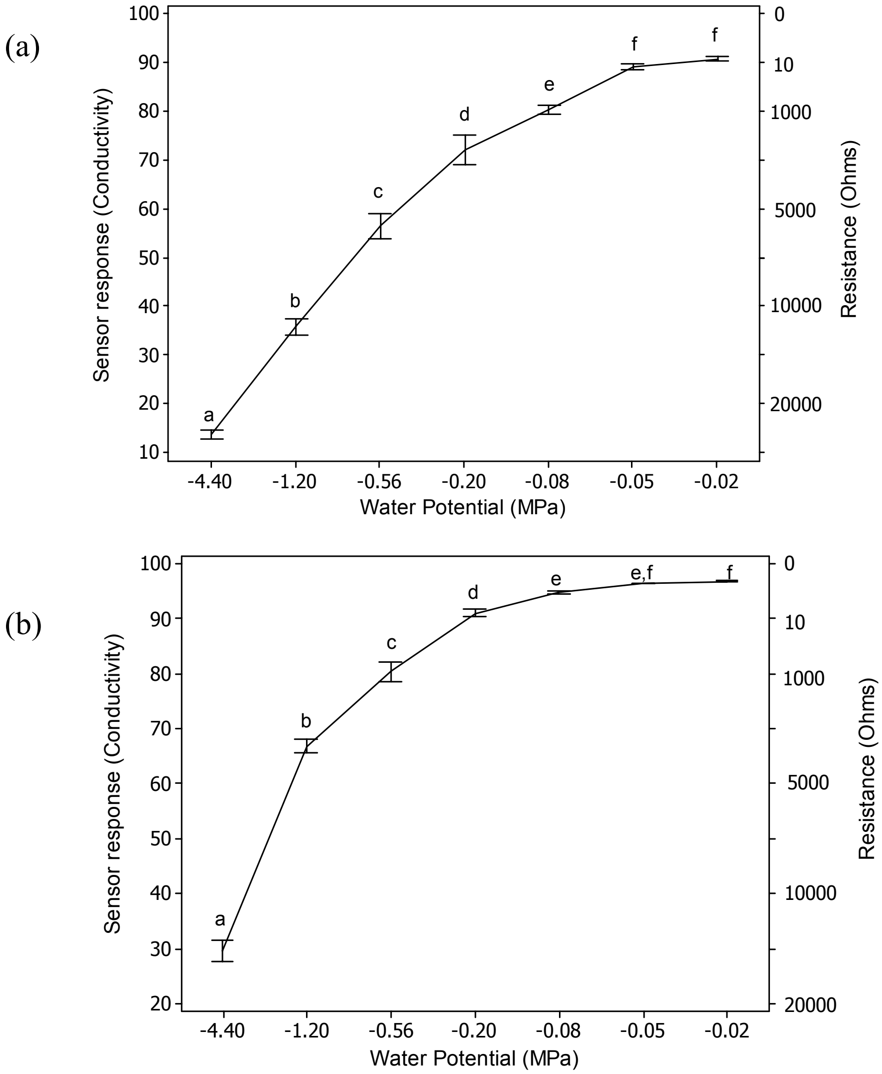

Figure 9.3. Distinguishable water potential levels with (a) Bouyoucos and (b) Delmhorst sensors. Treatments with significant differences in water potential levels are marked with different letters (Tukey's pairwise comparisons, $\alpha = 0.05$). Bars indicate 95% confidence intervals.

Discusssion

Gypsum blocks are suitable for many applications in terrestrial ecology. They are inexpensive and dependable. Gypsum blocks can also compare water stress across soils with different textures and organic matter contents. Readings are repeatable (Fig. 9.1) and distinguishable in the range of greatest interest to ecologists and agriculturists (≅ -1.0 to -3.0 MPa, Fig. 9.3). They do not readily distinguish wetter soil treatments, however, (< 0.05 MPa) because calibration curves become asymptotic near field capacity (Figs. 9.2-9.3, Campbell and Gee 1986).

Because calibration curves differ among block species, users need curves specific to their blocks. While there may be some variance among manufacturing runs, our curves (Fig. 9.2, Table 9.1) should serve those using Bouyoucos or Delmhorst blocks. With large data sets it will be more convenient and precise to convert meter readings to water potentials using equations 9.1-9.2 than interpolating values from Table 9.1 or Fig. 9.2.

Sensor readings may lag behind soil water conditions while blocks are either wetting or drying. Because dry blocks in moister soils take about four days to equilibrate (Fig. 9.1), sensor readings will underestimate water potentials if blocks are recently installed or if surrounding soils have been recently wet. In soils with different textures we expect equilibration time to increase with sand content since soil coarseness decreases contact with sensors.

On the other hand, wet blocks in drier soils may equilibrate even more slowly due to the slow loss of moisture from blocks. Water exchange is slow because water moves slowly from a fine-pored (block) to a coarser-pored (soil) medium (cf. Brady 1974). In addition, in a field situation, water deep in impenetrable blocks is further removed from absorbing roots than that it is in adjacent root permeated soils. Thus recently wetted blocks will tend to overestimate soil potentials. Such overestimates might appear, for example, when soils dry around blocks previously saturated by melting snow or flooding. Similarly, overestimates will appear when blocks are installed wet or in a slurry (as often recommended by block manufacturers), and may persist for weeks or months. Evidence for overestimation is seen in a comparison of calibration curves in Figure 9.2. Note that the manufacturer curve predicts wetter values through most of the -0.1 to -1.5 MPa range than our curves.

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Literature cited

Bouyoucos, C. J., and A. H. Mick. 1940. An electrical resistance method for the continuous measurement of soil moisture under field conditions. Michigan Agric. Exp. Stn. Tech. Bull. East Lansing, MI.

Brady, N. C. 1974. The nature and properties of soils. MacMillan Publishers, New York, USA.

Gardner, W. H. 1986. Soil water content. pgs 493-541. *In* A. Klute ed. 1986. Methods of soil analysis, part 1-physical and mineralogical methods, second edition. American Society of Agronomy, inc. Soil Science Society of America. Madison WI.

Campbell, G. S., and G. W. Gee. 1986. Water potential, miscellaneous methods. Pgs 619-632. *In* A. Klute ed. 1986. Methods of soil analysis, part 1-physical and mineralogical methods, second edition. American Society of Agronomy, inc. Soil Science Society of America. Madison WI.

Klute, A. 1986. Water retention, laboratory methods. Pgs 645-652. *In* A. Klute ed. 1986. Methods of soil analysis, part 1-physical and mineralogical methods, second edition. American Society of Agronomy, inc. Soil Science Society of America. Madison WI.

Lambers, H., Chapin III, F.S., and T.L. Pons. 1998. Plant physiological ecology. Springer-Verlag NY. 540 pp.

R Development Core Team. 2005. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Weaver, T. 1987. Effect of salinity on soil water measurement with gypsum resistance blocks. Mont Acad Sci Proc 47:109-112.

CHAPTER 10

CONCLUSIONS

This dissertation describes the ecology of alpine and cliff environments in the North-Central Rocky Mountain and GYE region. My principal conclusions/products are summarized below by chapter.

Indicator Species for Water and Temperature Conditions in Alpine Ecosystems

Chapter 2 describes species distributions with respect to moisture and temperature gradients using two approaches. Responses to gradient *segments* were measured using fidelity, constancy, cover and indicator species analysis scores as responses. We also examined the *continuous* relationships between species abundance and water/temperature using kernel-based Nonparametric Regression Models. We successfully determined optima on both water and temperature gradients for most of the 59 species studied. From our results we propose a quantitative method for estimating soil water and temperature conditions at alpine sites throughout the Northern Rockies.

Alpine Communities, Ecology, and Flora of Mount Washburn

This chapter describes the alpine ecosystem of Mount Washburn in Yellowstone National Park. Six communities were objectively identified use classification and pruning analysis. One type is indicated by *Erigeron rydbergii* and *Oxytropis lagopus.* Both species have a limited geographic range and are endemic to the Greater Yellowstone Ecosystem. The environmental variables most strongly correlated with vegetation cover and richness were surface soil characteristics (i.e. soil availability and quality). Soil water availability was an important variable in determining community composition. The low richness of the Washburn Range is consistent with characteristics of small isolated alpine island ecosystems indicating it may be particularly vulnerable to habitat fragmentation/degradation.

Alpine Communities of the Absaroka Volcanics

This chapter describes alpine vegetation for nine andesitic mountains, a substrate essentially unstudied in the Northern Rockies. The vegetation and environment of fifteen communities nested hierarchically within four "supergroups" (i.e. ledge, talus, ridge/turf and snowbank) were described. Indicator species identified in chapter 2 were used to estimate (relative) water and temperature conditions in community environments. Among measured environmental factors the best predictors of alpine community composition were soil accumulation/development and elevation. Floristically the Absaroka Volcanic alpine vegetation is unexpectedly similar to distant andesitic-alpine areas in Colorado and New Mexico.

Local and Regional Variation in Alpine Vegetation (North-Central Rockies)

To examine variation in the North Rocky Mountain alpine we compared four regions in (the Washburn Range, the Northern Absarokas, the Beartooth Plateau, and Beartooth Butte) stratified by topography (talus , ridgetops, south slopes, north slopes and snowbanks). The study area resembled typical alpine ecosystems around the world. Universal vegetation characteristics include fluctuation from open fellfields and windswept ridges, to forb-graminoid meadows, and wet late-melt meadows and bogs at the base of leeward slopes. Typical environmental characteristics include the importance of soil accumulation and soil development to community variability and productivity. Within this universal framework study site ecosystems varied with respect to local (topographic), regional (substrate and climate), and particularly combinations of local and regional factors. Support for the strength of these scale factors was provided by rejection of null predictions from this unified neutral theory of biodiversity and biogeography which attributes community variability purely to dispersal and ecological drift.

Water and Substrate Control of Cliff Communities (North-Central Rocky Mountains)

Sub-alpine cliff communities in northeast YNP were studied with respect to water (dry, intermediate, and wet), substrate (andesite and limestone), and combinations of water and substrate treatments. We analyzed distributional trends for major life forms (i.e. mosses, lichens and vascular plants) and individual species, and determined indicator species for describing cliff moisture and substrate. Our analyses suggest regulation of cliff community composition by three environmental forces. First, cover of major life-forms varies on a water gradient due to differential inputs of liquid water. Second, species composition varies on the water gradient due to substrate water relations differences (andesite had superior water absorption/retention capacities compared to limestone). Third, species composition also varies on a substrate gradient associated mineralogy (e.g. pH and the availability of nutrients or toxins).

Using Geometric and Non-Geometric Internal Evaluators to Compare Eight Commonly Used Vegetation Classification Methods

In chapter 7 five classification evaluators were used to compare the performance of eight classification methods commonly used by vegetation ecologists. Among non-geometric evaluators, we introduce an adapted form of Morisita's index of niche overlap, and DUARM (an algorithm which measures the degree to which species are either always present or always absent within clusters). Flexible beta ($\beta = -0.25$), average linkage, and Ward's linkage generally outperformed other methods across a large number of clustering solutions. While often favoring the same classification methods, our results indicate that geometric and non-geometric evaluators may have largely independent perspectives of classification solution efficacy.

Measuring Water Relations and pH of Cryptogam Rock-Surface Environments

In this chapter we introduce simple and inexpensive methods for measuring water absorption, water release, pH, and surface area of rock surfaces. By use of these techniques we found andesitic rocks absorbed more water from atmospheric and liquid sources, released it over longer periods of time, and were less basic than limestone rocks in northeast YNP.

Sensitivity and Calibration of Gypsum Block Water Sensors

We examined two types of gypsum block water sensors (Delmhorst GS-1, and Bouyoucos) to accomplish four goals. 1) To demonstrate a new calibration procedure for gypsum blocks. 2) To determine equilibration times for gypsum blocks inserted in soils with particular water potentials (-4.4 to -0.2 MPa). 3) To provide calibration curves for commercially available instruments. 4) To measure the sensitivity of the sensors by determining what soil water potentials were statistically distinguishable. Our procedure yielded calibration curves applicable to blocks of similar manufacture. Blocks imbedded in soils with water potentials levels ranging from (-4.4 to -0.2 MPa) equilibrated after approximately 100 hours. Soil sensor responses were statistically distinguishable for water potentials between -4.4 and -0.5. Blocks in two wetter soils -0.05 and -0.02 MPa were not distinguishable from each other with either sensor.

APPENDICES

APPENDIX A

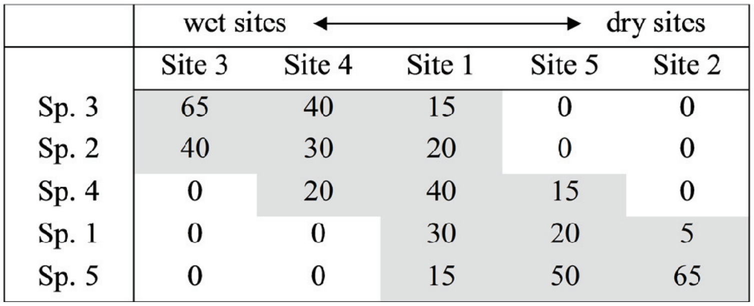
APPENDICES PERTAINING TO CHAPTER 2--

INDICATOR SPECIES FOR WATER AND TEMPERATURE CONDITIONS IN ALPINE ECOSYSTEMS

Appendix A.1:
A Dot Product Based Algorithm for Sorting Rows in Ordered Relevé Tables

A large number of ecologists have used sorted tables to describe patterns of data across gradients (Braun-Blanquet 1964, Hill 1973)[†]. Perhaps the most common method to order a data matrix is to: 1) arrange columns (sites) in an order representing positions along a gradient (e.g. dry to wet), then 2) sort the species according to their dominance within the arranged columns (Table A.1.1).

Table A.1.1. Hypothetical sorted table with five species and five sites. Sites have been arranged to represent a gradient. Species have been sorted with respect to the column order so that they are ranked from wet sites to dry sites preference. Responses are percent cover. Cells with responses > 0 are shaded.



	wet sites ←		→		dry sites
	Site 3	Site 4	Site 1	Site 5	Site 2
Sp. 3	65	40	15	0	0
Sp. 2	40	30	20	0	0
Sp. 4	0	20	40	15	0
Sp. 1	0	0	30	20	5
Sp. 5	0	0	15	50	65

Hand sorting tables becomes burdensome for large complex datasets, and a large degree of subjectivity can be introduced (i.e. where does one put multimodal, randomly, or uniformly distributed species?). As a result, a number of methods have been developed to automatically sort the order of rows (species) with respect to the gradient represented by the order of columns algorithms (e.g. Tichy 2002). One method is to use weighted averaging so that species abundances are weighted by responses of the environmental variable determining the order of columns (Ter Braak and Looman 1986). While this method often produces good results, it is hampered by the distribution shape

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[†] For bibliographic information in Appendix A see the Chapter 2 literature cited section

of the gradient (Jongman 1995). To address this problem I propose using a dot product algorithm (Stewart 2003, pg. 807) to find the order of rows. Consider an *n* x *s* matrix *M*, where *s* = the number of species, *n* = the number of sites, and *c* is a constant.

1. Create a vector *v*, of length *n* which is uniformly distributed from –*c* to +*c*. Thus, if *n* = 5, and *c* = 1, then *v* = (-1.0, -0.5, 0.0, 0.5, 1.0).
2. Take the dot product of *v* and the vector of abundances of spp 1 from sites 1 through *n* (Eq. A.1.1).
$$D_1 = v_1 sp1_1 + v_2 sp1_2 ... + ... v_n sp1_n \qquad \text{(A.1.1)}$$
3. Create the vector *D* by calculating its elements D_1, D_2 …D_s.
4. Sort the rows in *M* with the respect to descending values of *D*.

A hypothetical dataset sort using the dot product function SORTID is shown in Fig. A.1.1. Code for the function to be used with R (R Development Core Team 2005) is shown at the end of this appendix.

Note that *v* need not be uniformly distributed (see step 1 in the algorithm description above). To account for distribution shape in the gradient, any distribution (e.g. normal, lognormal, Poisson) may be used.

(a)

	# of days Ψ<-0.12 Mpa
site1	0
site2	1
site3	4
site4	5
site5	7

(b)

$M =$

	site1	site2	site3	site4	site5
sp1	20	23	47	32	10
sp2	0	0	2	1	5
sp3	0	1	10	20	30
sp4	40	30	23	0	10
sp5	0	20	40	20	5

(c)

	D
sp1	5.5
sp2	-5.5
sp3	-39.5
sp4	45
sp5	-5

(d)

	site1	site2	site3	site4	site5
sp4	40	30	23	0	10
sp1	20	23	47	32	10
sp5	0	20	40	20	5
sp2	0	0	2	1	5
sp3	0	1	10	20	30

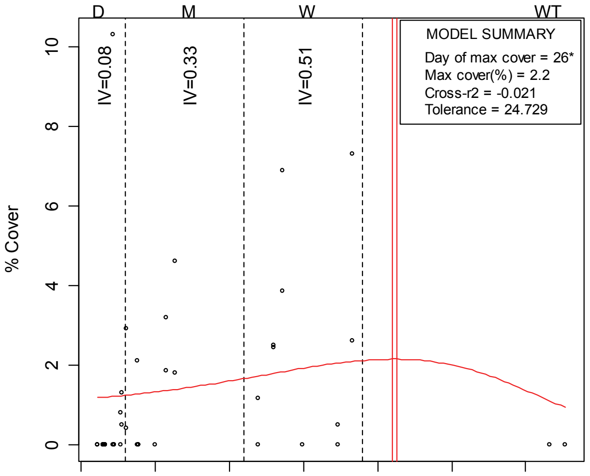
Fig. A.1.1. Example of SORTID results (a) Environmental data (b) M = Vegetation data matrix. (c) The D vector was calculated using SORTID defaults. Thus v is assumed to a uniformly distributed vector of length 5 (i.e. number of sites) with a range of -1 to 1. (d) The matrix M is sorted by SORTID with respect to descending values of D.

```
############################### SORTID ################################
## Given a matrix with species in rows and an order of columns       ##
## representing some gradient of sites; SORTID sorts rows with       ##
## respect to the order of columns to create a sorted relevé table   ##
## ala Braun-Blanquet.                                               ##
##                                                                   ##
##                                                                   ##
## taxa = a matrix as described above                                ##
## v = any number greater than 0.                                    ##
##                                                                   ##
## as the gradient constant increases the emphasis placed on the     ##
## order of columns is further reinforced.                           ##
##                                                                   ##
## Code: Aho(2006)                                                   ##
##                                                                   ##
#######################################################################

sortid<-function(taxa,v=1){
      vec<-seq(v,-v,length.out=ncol(taxa))

      ## creates a continuous weighting vector with a length equaling the
      ## length of the gradient (i.e. the number of columns in the taxa matrix)
      ## which you wish to describe.

      row1<-as.matrix(t(apply(taxa,1,function(x){x*vec})))

      ## responses for each row (species) in the taxa matrix are multiplied by
      ## the associated cell in the vec vector, i.e. the dot product of a row
      ## of species responses and the vec vector is taken.

      D<-as.matrix(apply(row1,1,sum))

      ## finds where each species should be put in the sorted matrix by summing
      ## across rows in the row1 matrix

      sort1<-order(D,decreasing=T)
      s<-taxa[sort1,]

      ## sorts matrix
      result<-list()
      result$sorted.table<-s
      result$D<-D
      result

                                                }
```

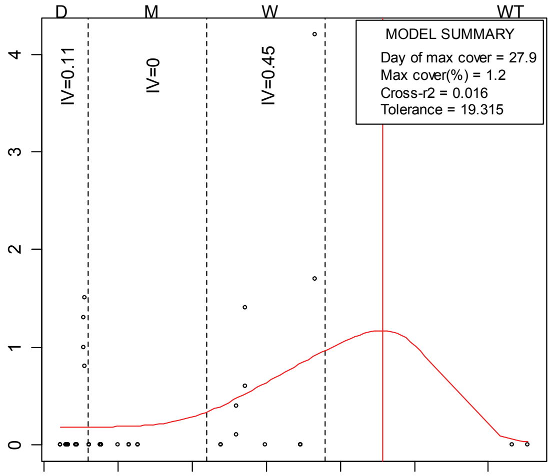
Appendix A.2: Non-parametric moisture models

The figures in this appendix show NPR response curves for all 59 species versus soil water, where soil water is defined as the number of days when soil water potential is less than -0.12 MPa (Chapter 3). Vertical dashed lines show the separation between soil water categories (D, M, W, and WT). Vertical solid lines indicate the number of days along the predictor axis when the optimal response is predicted to occur. The term “IV” represents ISA indicator value scores for each category (Dufrêne and Legendre 1997). The model summary box in each figure lists: 1) day of maximum response (also indicated by the solid vertical line), 2) the predicted maximum cover, 3) the cross r^2 evaluation for the model (see methods), and 4) The tolerance (optimal kernel width) of the model (see methods).

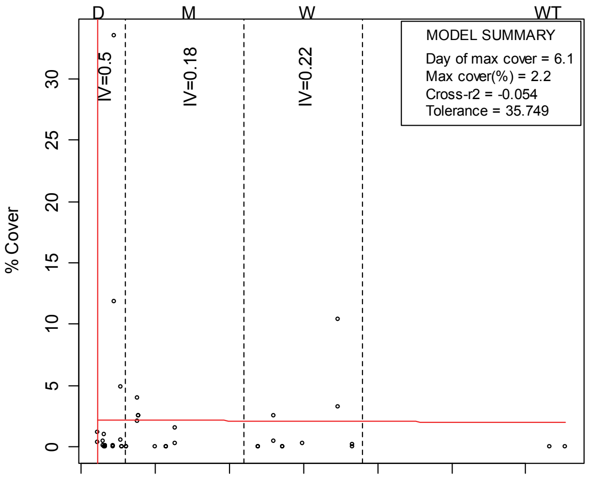
Achillea millefolium



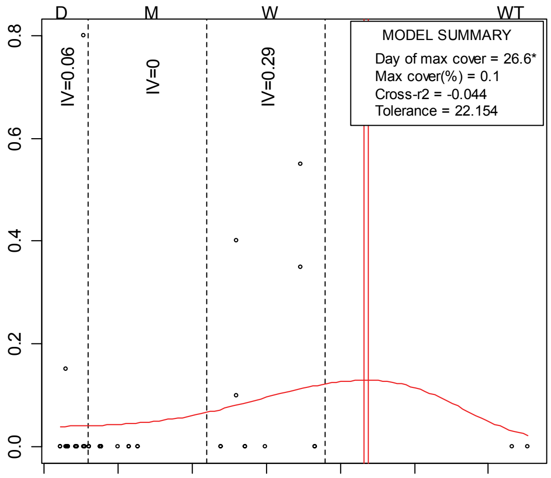
Agoseris glauca



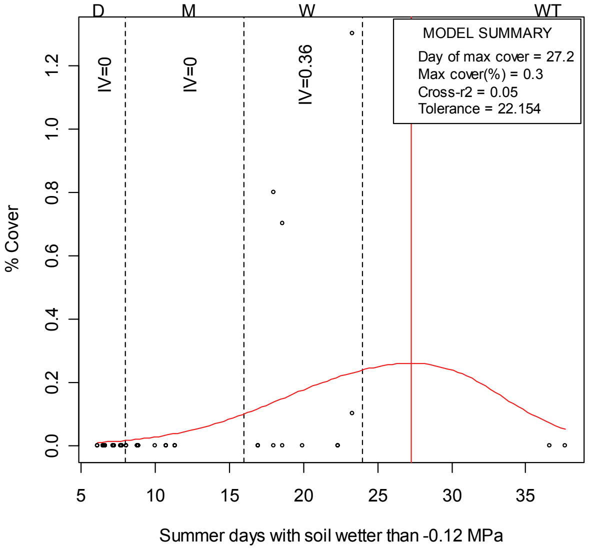
All mosses



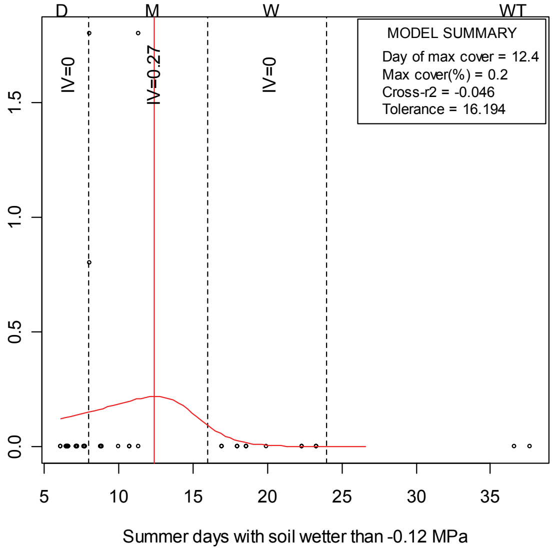
Androsace septentrionalis



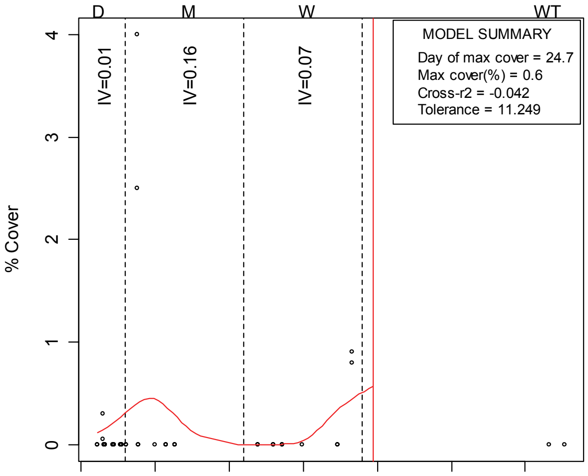
Antennaria media



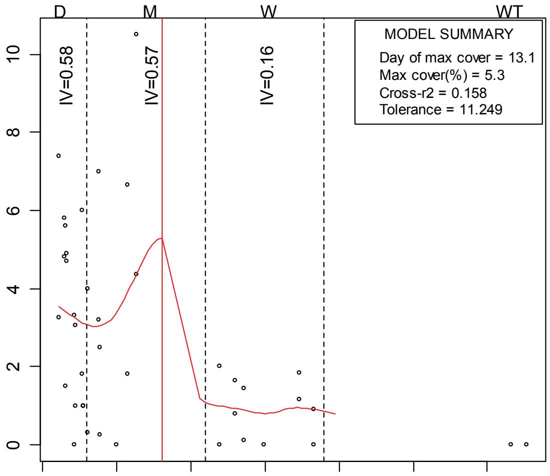
Antennaria microphylla



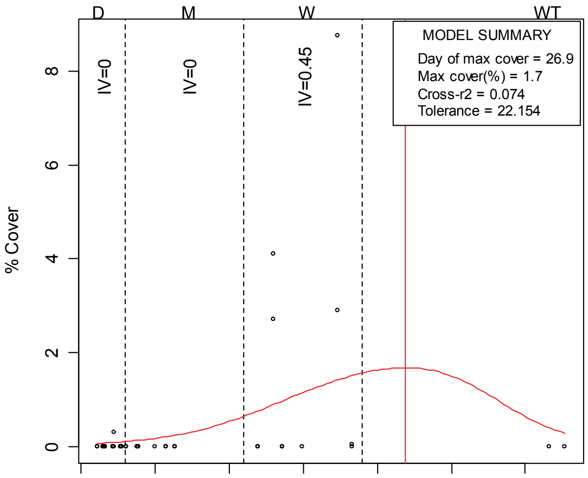
Arenaria congesta



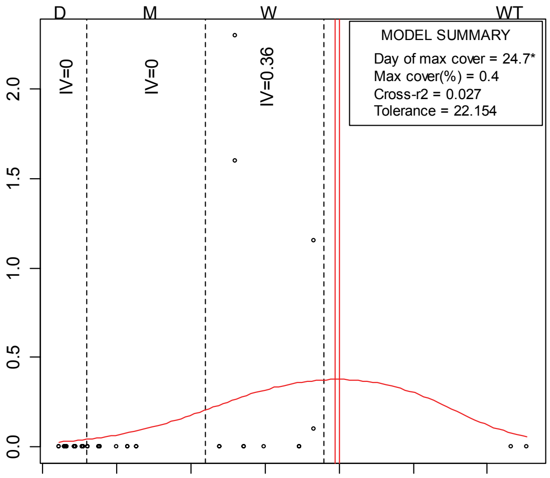
Arenaria obtusiloba



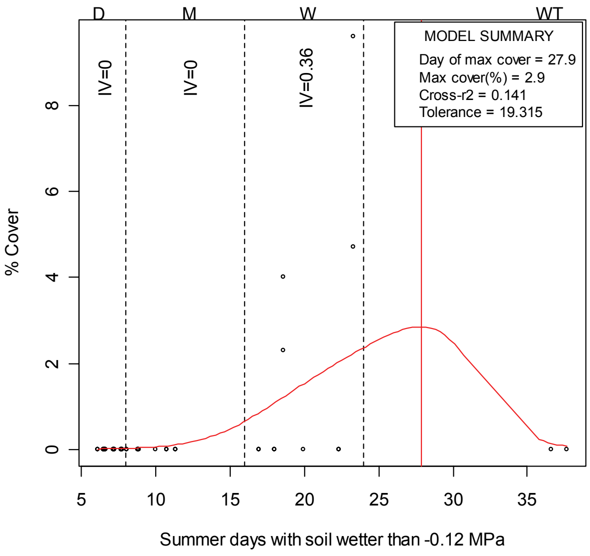
Artemisia scopulorum



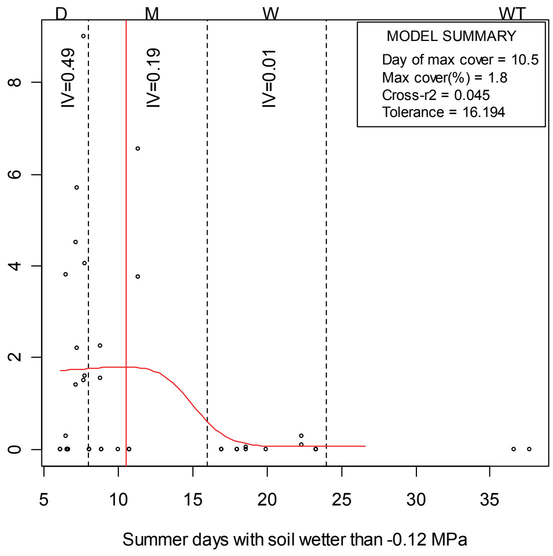
Aster alpigenus

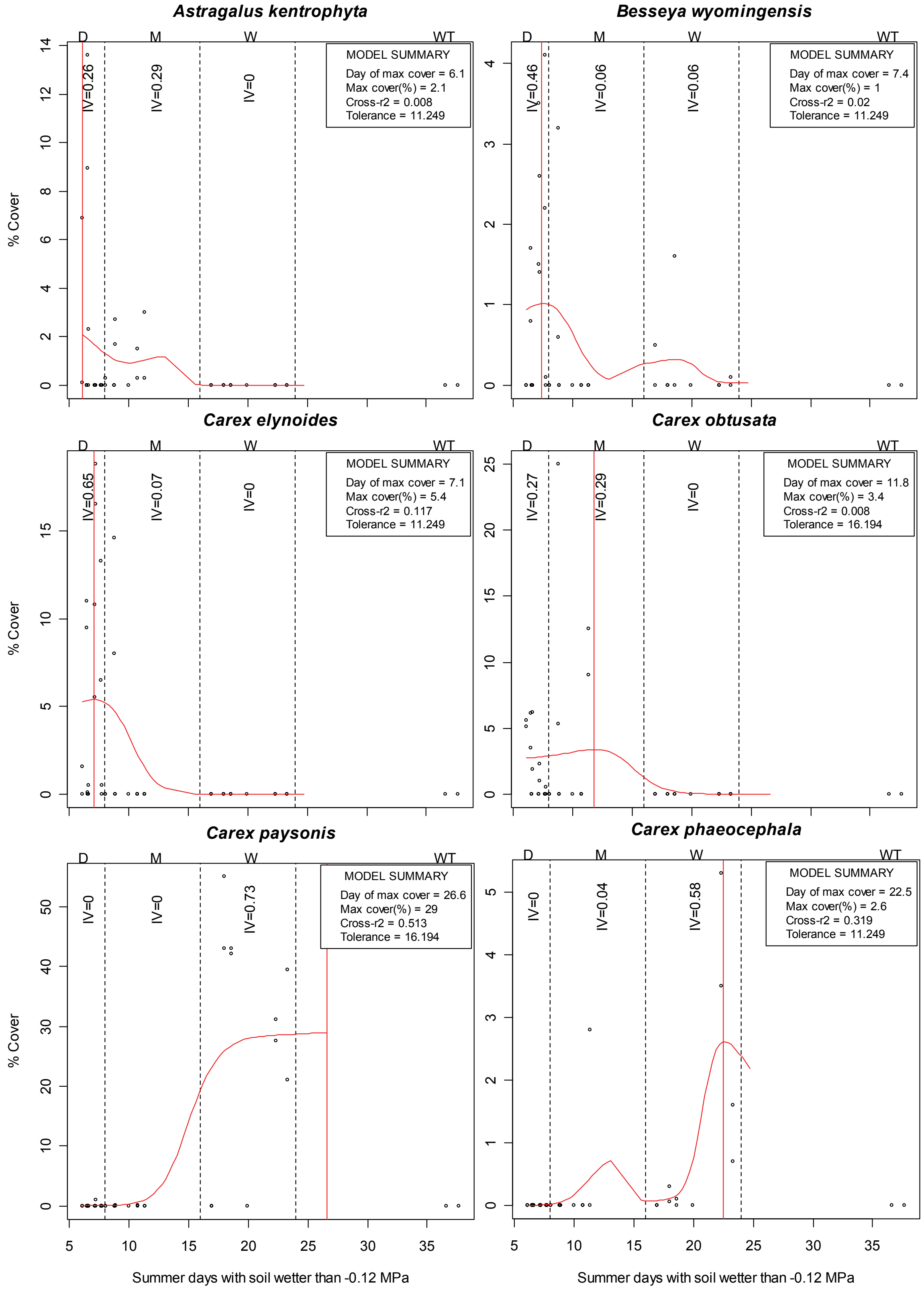


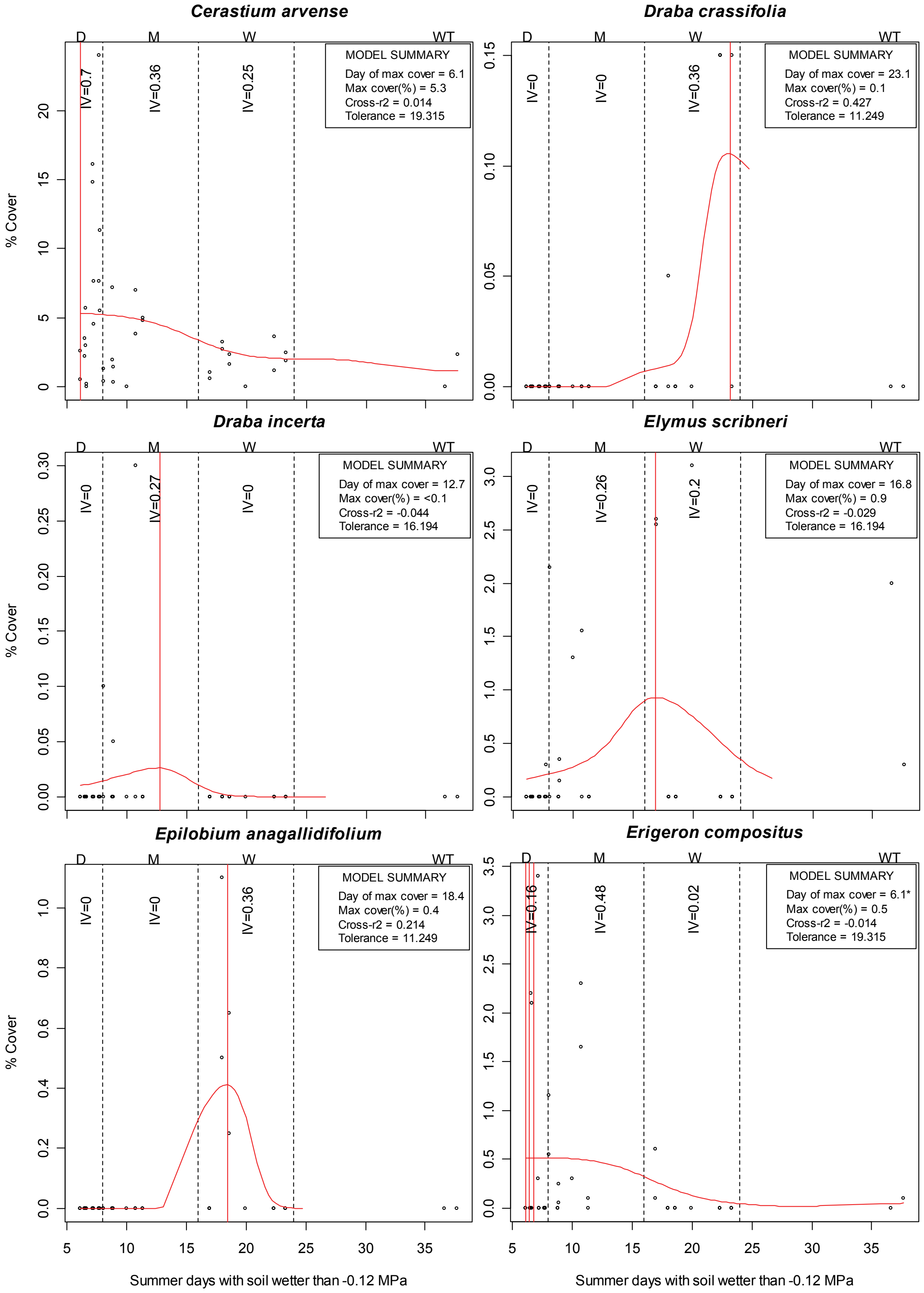
Aster foliaceus v. apricus

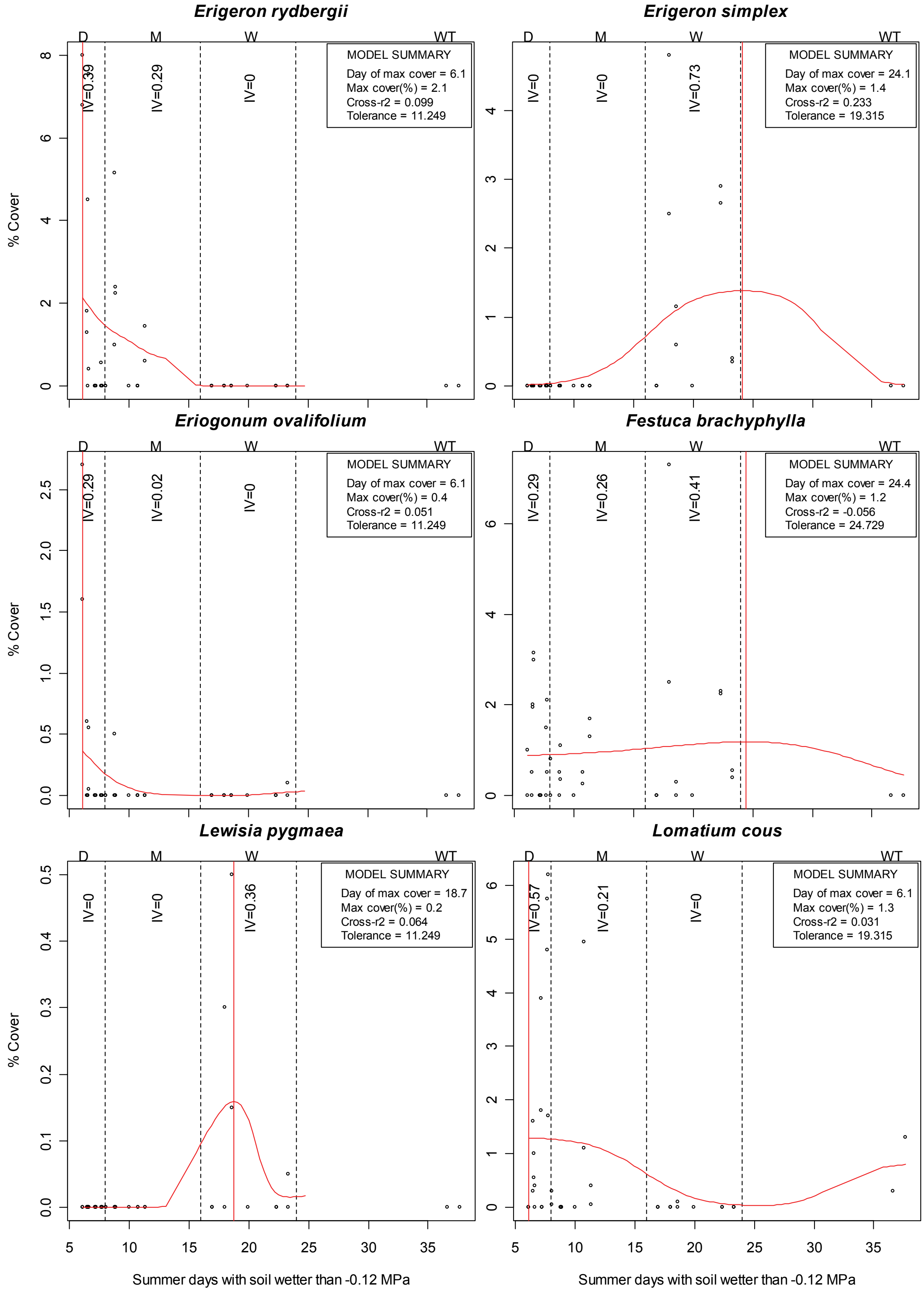


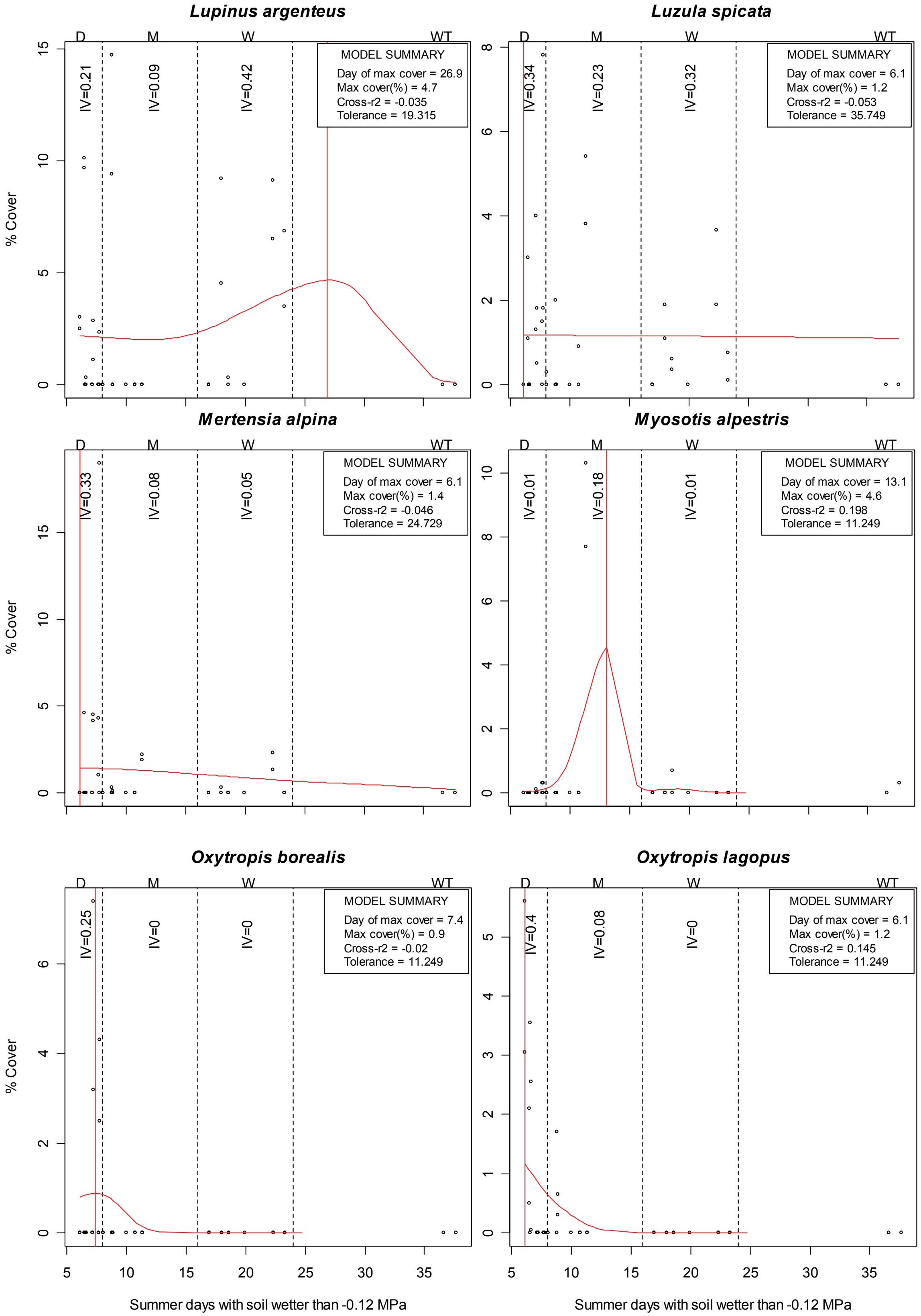
Astragalus alpinus

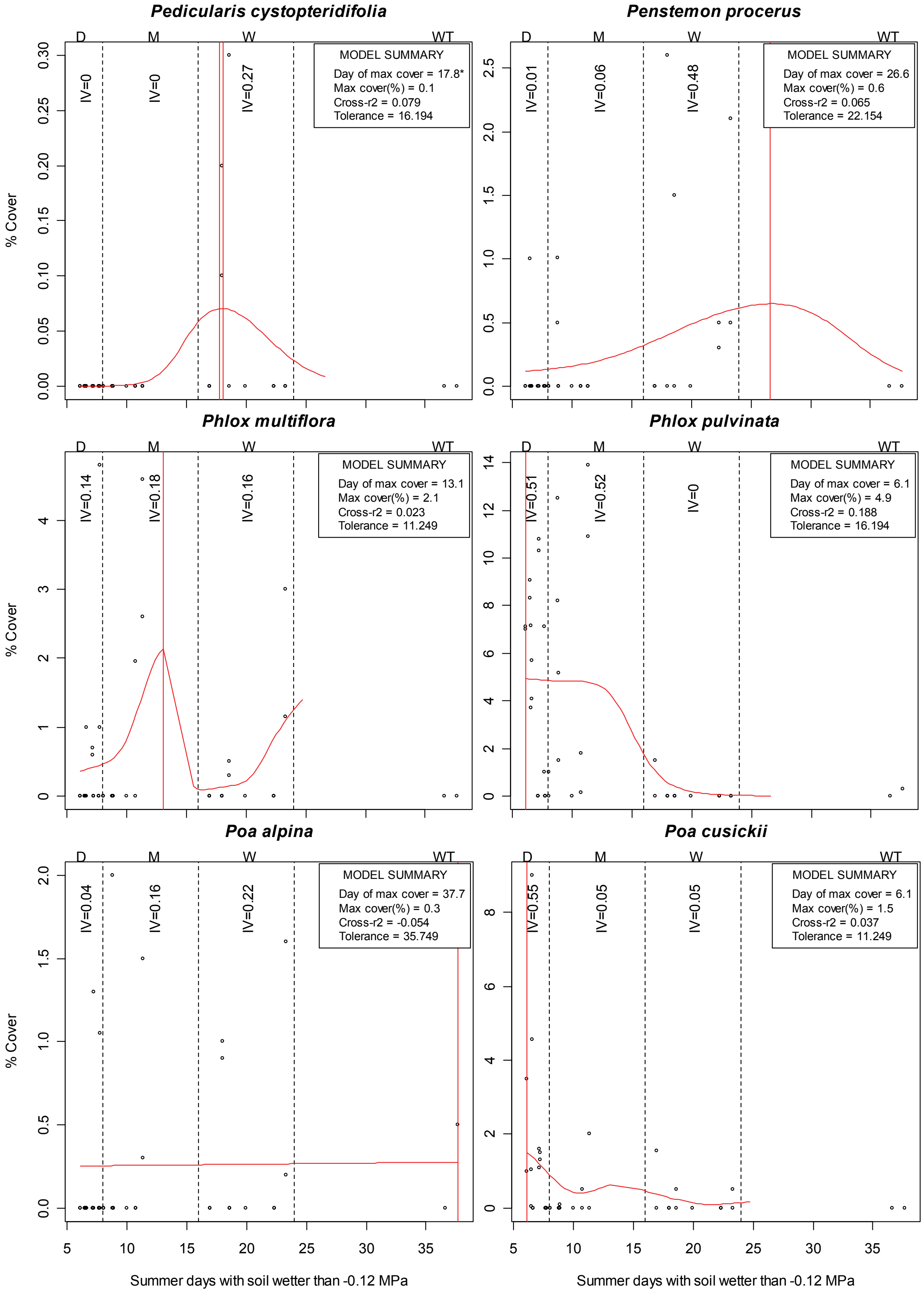


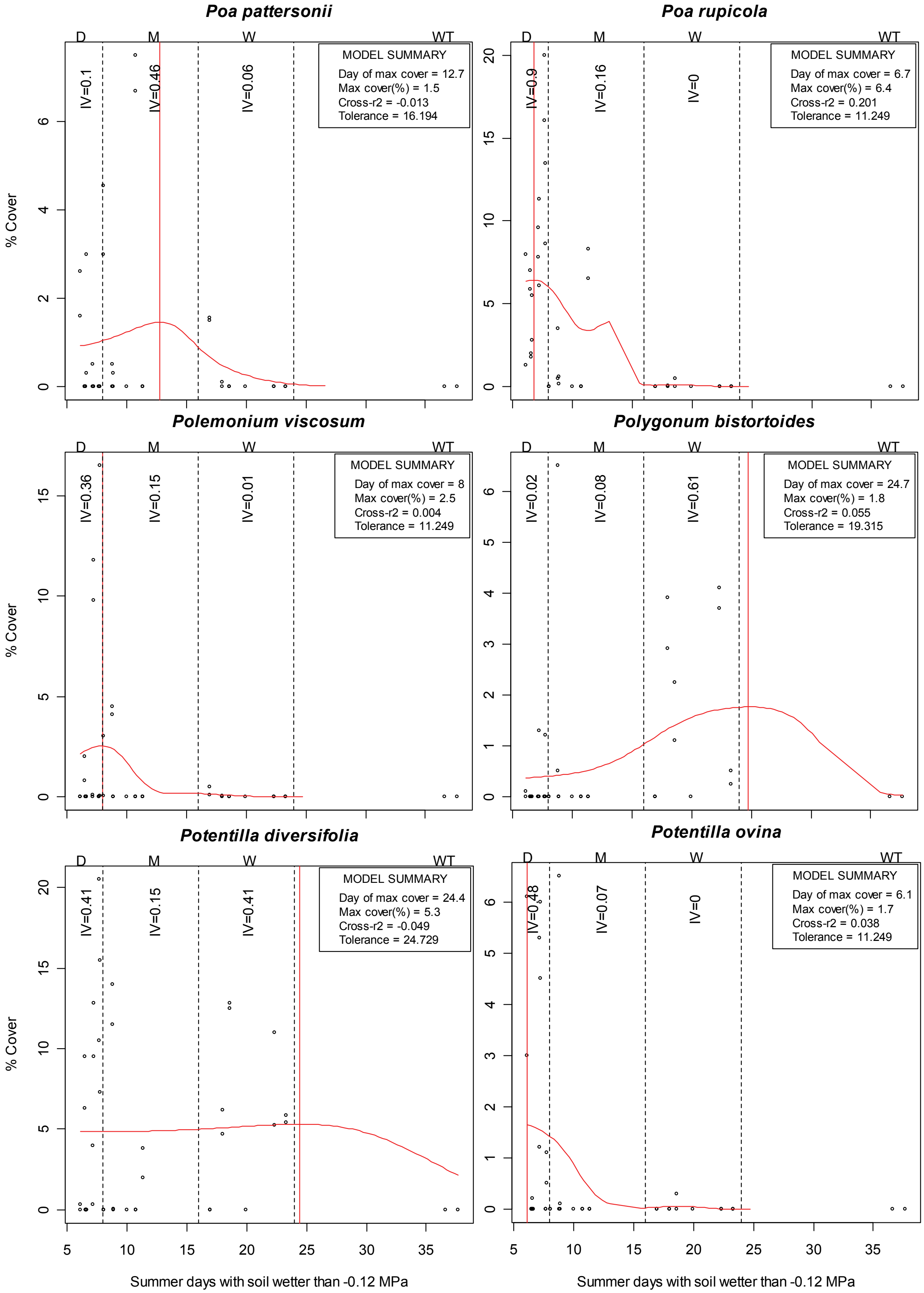

Astragalus kentrophyta
D
M
W
WT
IV=0.26
IV=0.29
IV=0
MODEL SUMMARY
Day of max cover = 6.1
Max cover(%) = 2.1
Cross-r2 = 0.008
Tolerance = 11.249
% Cover
0
2
4
6
8
10
12
14
Besseya wyomingensis
D
M
W
WT
IV=0.46
IV=0.06
IV=0.06
MODEL SUMMARY
Day of max cover = 7.4
Max cover(%) = 1
Cross-r2 = 0.02
Tolerance = 11.249
0
1
2
3
4
Carex elynoides
D
M
W
WT
IV=0.65
IV=0.07
IV=0
MODEL SUMMARY
Day of max cover = 7.1
Max cover(%) = 5.4
Cross-r2 = 0.117
Tolerance = 11.249
% Cover
0
5
10
15
Carex obtusata
D
M
W
WT
IV=0.27
IV=0.29
IV=0
MODEL SUMMARY
Day of max cover = 11.8
Max cover(%) = 3.4
Cross-r2 = 0.008
Tolerance = 16.194
0
5
10
15
20
25
Carex paysonis
D
M
W
WT
IV=0
IV=0
IV=0.73
MODEL SUMMARY
Day of max cover = 26.6
Max cover(%) = 29
Cross-r2 = 0.513
Tolerance = 16.194
% Cover
0
10
20
30
40
50
Carex phaeocephala
D
M
W
WT
IV=0
IV=0.04
IV=0.58
MODEL SUMMARY
Day of max cover = 22.5
Max cover(%) = 2.6
Cross-r2 = 0.319
Tolerance = 11.249
0
1
2
3
4
5
5
10
15
20
25
30
35
Summer days with soil wetter than -0.12 MPa
5
10
15
20
25
30
35
Summer days with soil wetter than -0.12 MPa

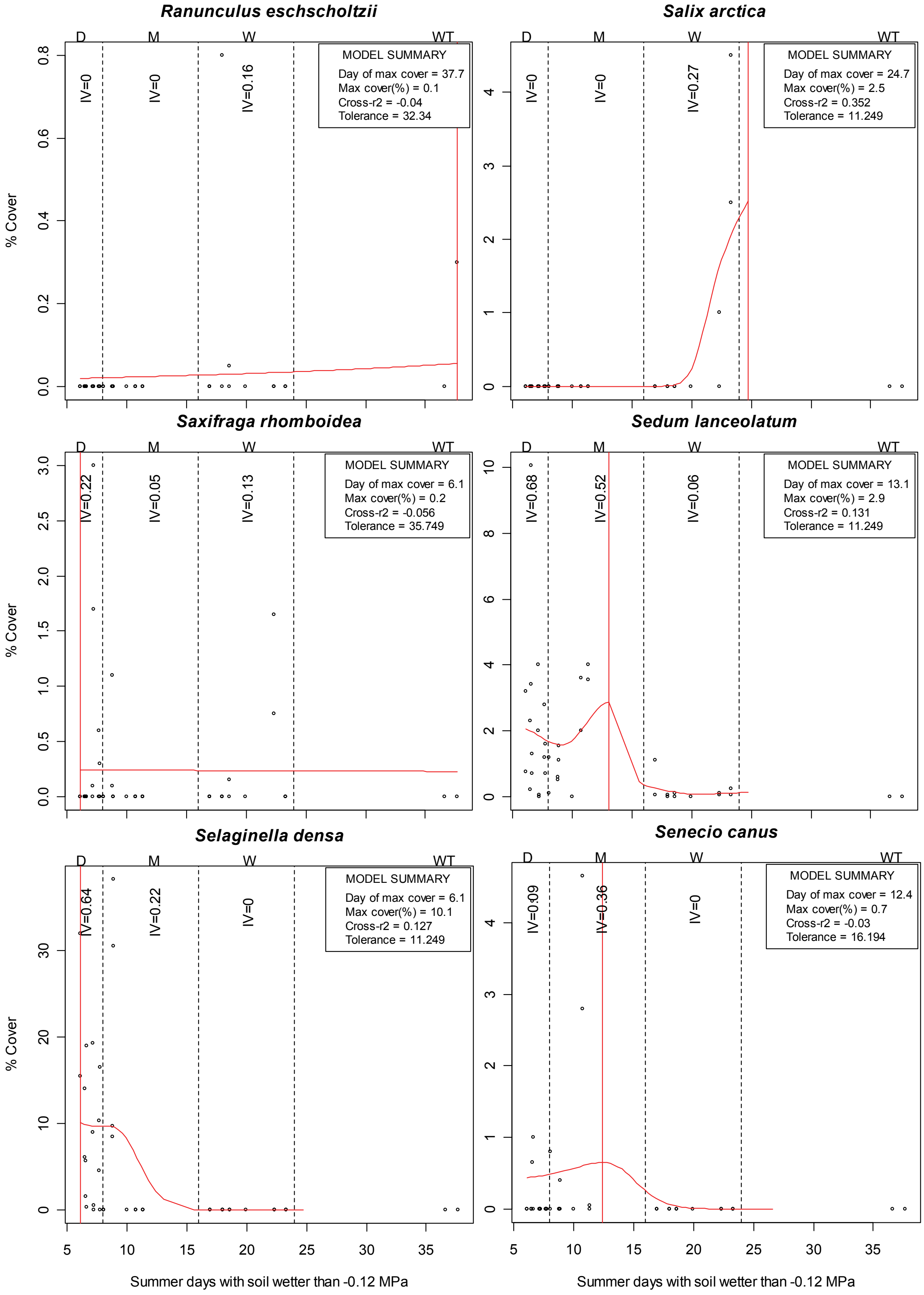

Cerastium arvense
Draba crassifolia
Draba incerta
Elymus scribneri
Epilobium anagallidifolium
Erigeron compositus
D
M
W
WT
% Cover
IV=0.7
IV=0.36
IV=0.25
MODEL SUMMARY
Day of max cover = 6.1
Max cover(%) = 5.3
Cross-r2 = 0.014
Tolerance = 19.315
IV=0
IV=0
IV=0.36
MODEL SUMMARY
Day of max cover = 23.1
Max cover(%) = 0.1
Cross-r2 = 0.427
Tolerance = 11.249
IV=0
IV=0.27
IV=0
MODEL SUMMARY
Day of max cover = 12.7
Max cover(%) = <0.1
Cross-r2 = -0.044
Tolerance = 16.194
IV=0
IV=0.26
IV=0.2
MODEL SUMMARY
Day of max cover = 16.8
Max cover(%) = 0.9
Cross-r2 = -0.029
Tolerance = 16.194
IV=0
IV=0
IV=0.36
MODEL SUMMARY
Day of max cover = 18.4
Max cover(%) = 0.4
Cross-r2 = 0.214
Tolerance = 11.249
IV=0.16
IV=0.48
IV=0.02
MODEL SUMMARY
Day of max cover = 6.1*
Max cover(%) = 0.5
Cross-r2 = -0.014
Tolerance = 19.315
5
10
15
20
25
30
35
Summer days with soil wetter than -0.12 MPa
Summer days with soil wetter than -0.12 MPa

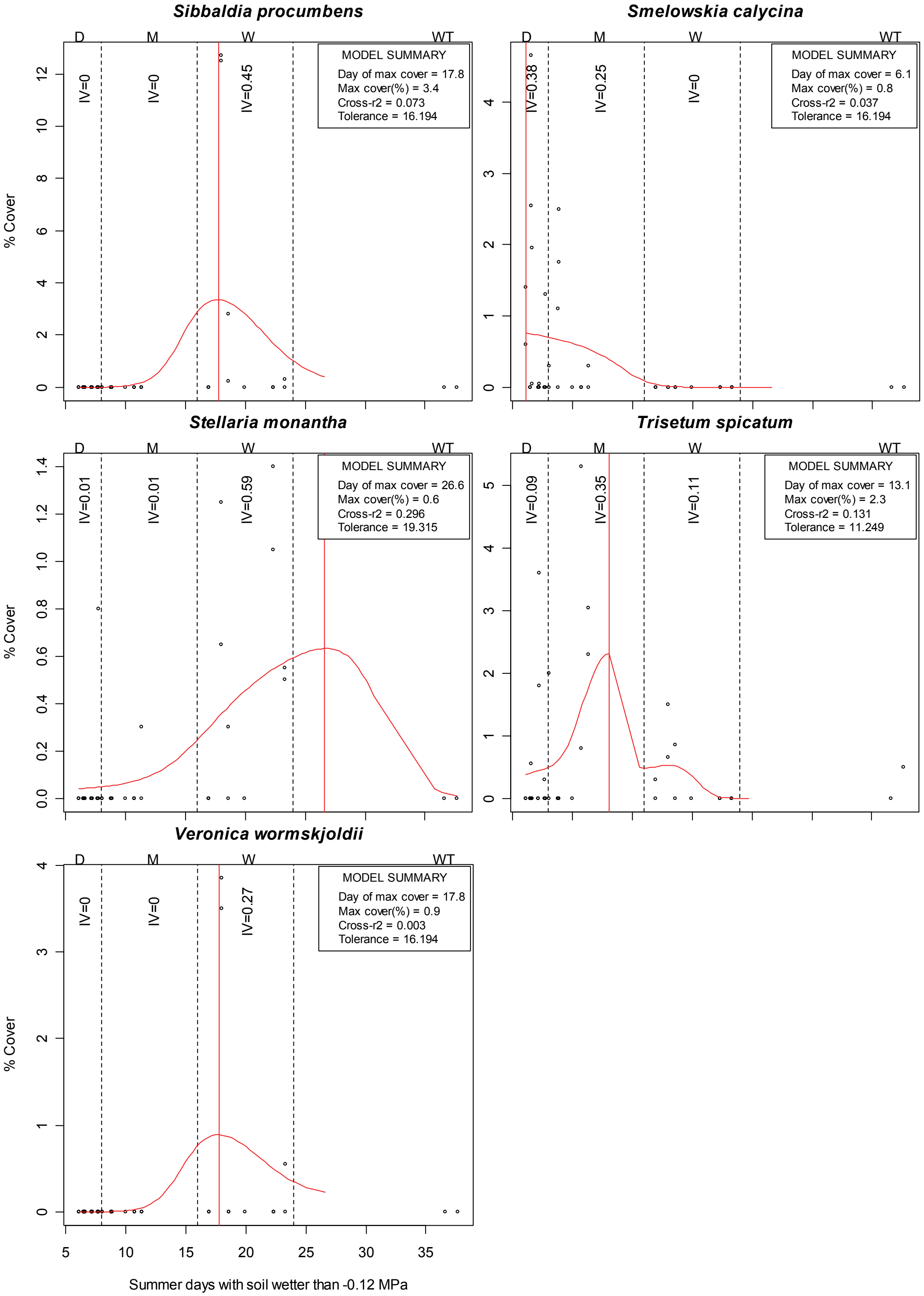

Erigeron rydbergii
D
M
W
WT
IV=0.39
IV=0.29
IV=0
MODEL SUMMARY
Day of max cover = 6.1
Max cover(%) = 2.1
Cross-r2 = 0.099
Tolerance = 11.249
% Cover
Erigeron simplex
IV=0
IV=0
IV=0.73
MODEL SUMMARY
Day of max cover = 24.1
Max cover(%) = 1.4
Cross-r2 = 0.233
Tolerance = 19.315
Eriogonum ovalifolium
IV=0.29
IV=0.02
IV=0
MODEL SUMMARY
Day of max cover = 6.1
Max cover(%) = 0.4
Cross-r2 = 0.051
Tolerance = 11.249
Festuca brachyphylla
IV=0.29
IV=0.26
IV=0.41
MODEL SUMMARY
Day of max cover = 24.4
Max cover(%) = 1.2
Cross-r2 = -0.056
Tolerance = 24.729
Lewisia pygmaea
IV=0
IV=0
IV=0.36
MODEL SUMMARY
Day of max cover = 18.7
Max cover(%) = 0.2
Cross-r2 = 0.064
Tolerance = 11.249
Lomatium cous
IV=0.57
IV=0.21
IV=0
MODEL SUMMARY
Day of max cover = 6.1
Max cover(%) = 1.3
Cross-r2 = 0.031
Tolerance = 19.315
5
10
15
20
25
30
35
Summer days with soil wetter than -0.12 MPa


Lupinus argenteus
D
M
W
WT
IV=0.21
IV=0.09
IV=0.42
MODEL SUMMARY
Day of max cover = 26.9
Max cover(%) = 4.7
Cross-r2 = -0.035
Tolerance = 19.315
% Cover
0
5
10
15
Luzula spicata
D
M
W
WT
IV=0.34
IV=0.23
IV=0.32
MODEL SUMMARY
Day of max cover = 6.1
Max cover(%) = 1.2
Cross-r2 = -0.053
Tolerance = 35.749
0
2
4
6
8
Mertensia alpina
D
M
W
WT
IV=0.33
IV=0.08
IV=0.05
MODEL SUMMARY
Day of max cover = 6.1
Max cover(%) = 1.4
Cross-r2 = -0.046
Tolerance = 24.729
% Cover
0
5
10
15
Myosotis alpestris
D
M
W
WT
IV=0.01
IV=0.18
IV=0.01
MODEL SUMMARY
Day of max cover = 13.1
Max cover(%) = 4.6
Cross-r2 = 0.198
Tolerance = 11.249
0
2
4
6
8
10
Oxytropis borealis
D
M
W
WT
IV=0.25
IV=0
IV=0
MODEL SUMMARY
Day of max cover = 7.4
Max cover(%) = 0.9
Cross-r2 = -0.02
Tolerance = 11.249
% Cover
0
2
4
6
Oxytropis lagopus
D
M
W
WT
IV=0.4
IV=0.08
IV=0
MODEL SUMMARY
Day of max cover = 6.1
Max cover(%) = 1.2
Cross-r2 = 0.145
Tolerance = 11.249
0
1
2
3
4
5
5
10
15
20
25
30
35
Summer days with soil wetter than -0.12 MPa
5
10
15
20
25
30
35
Summer days with soil wetter than -0.12 MPa


Pedicularis cystopteridifolia
D
M
W
WT
IV=0
IV=0
IV=0.27
MODEL SUMMARY
Day of max cover = 17.8*
Max cover(%) = 0.1
Cross-r2 = 0.079
Tolerance = 16.194
0.00
0.05
0.10
0.15
0.20
0.25
0.30
% Cover
Penstemon procerus
IV=0.01
IV=0.06
IV=0.48
MODEL SUMMARY
Day of max cover = 26.6
Max cover(%) = 0.6
Cross-r2 = 0.065
Tolerance = 22.154
0.0
0.5
1.0
1.5
2.0
2.5
Phlox multiflora
IV=0.14
IV=0.18
IV=0.16
MODEL SUMMARY
Day of max cover = 13.1
Max cover(%) = 2.1
Cross-r2 = 0.023
Tolerance = 11.249
0
1
2
3
4
% Cover
Phlox pulvinata
IV=0.51
IV=0.52
IV=0
MODEL SUMMARY
Day of max cover = 6.1
Max cover(%) = 4.9
Cross-r2 = 0.188
Tolerance = 16.194
0
2
4
6
8
10
12
14
Poa alpina
IV=0.04
IV=0.16
IV=0.22
MODEL SUMMARY
Day of max cover = 37.7
Max cover(%) = 0.3
Cross-r2 = -0.054
Tolerance = 35.749
0.0
0.5
1.0
1.5
2.0
% Cover
Poa cusickii
IV=0.55
IV=0.05
IV=0.05
MODEL SUMMARY
Day of max cover = 6.1
Max cover(%) = 1.5
Cross-r2 = 0.037
Tolerance = 11.249
0
2
4
6
8
5
10
15
20
25
30
35
Summer days with soil wetter than -0.12 MPa
Summer days with soil wetter than -0.12 MPa

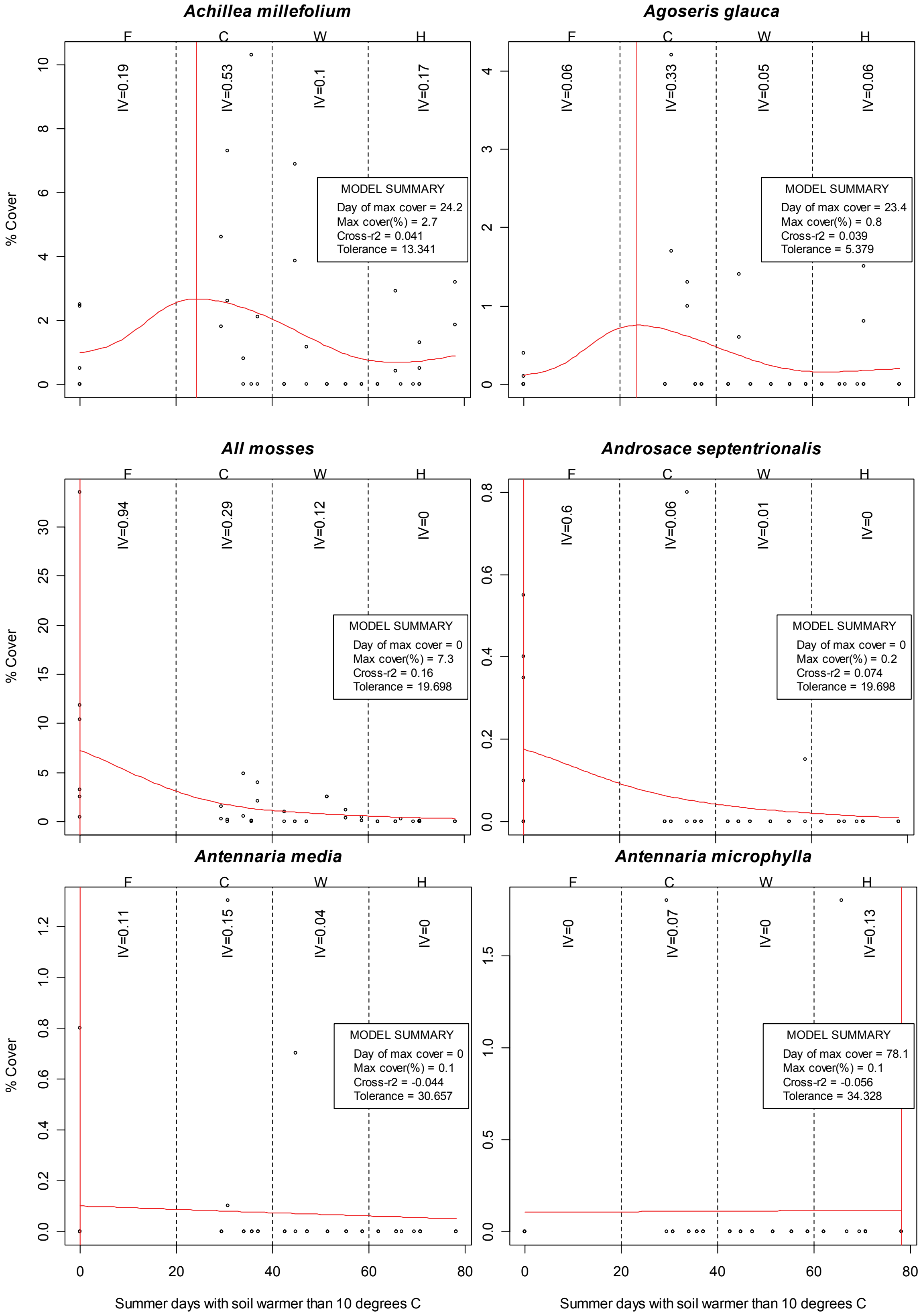

Poa pattersonii
D
M
W
WT
IV=0.1
IV=0.46
IV=0.06
MODEL SUMMARY
Day of max cover = 12.7
Max cover(%) = 1.5
Cross-r2 = -0.013
Tolerance = 16.194
% Cover
0
2
4
6
Poa rupicola
D
M
W
WT
IV=0.9
IV=0.16
IV=0
MODEL SUMMARY
Day of max cover = 6.7
Max cover(%) = 6.4
Cross-r2 = 0.201
Tolerance = 11.249
0
5
10
15
20
Polemonium viscosum
D
M
W
WT
IV=0.36
IV=0.15
IV=0.01
MODEL SUMMARY
Day of max cover = 8
Max cover(%) = 2.5
Cross-r2 = 0.004
Tolerance = 11.249
% Cover
0
5
10
15
Polygonum bistortoides
D
M
W
WT
IV=0.02
IV=0.08
IV=0.61
MODEL SUMMARY
Day of max cover = 24.7
Max cover(%) = 1.8
Cross-r2 = 0.055
Tolerance = 19.315
0
1
2
3
4
5
6
Potentilla diversifolia
D
M
W
WT
IV=0.41
IV=0.15
IV=0.41
MODEL SUMMARY
Day of max cover = 24.4
Max cover(%) = 5.3
Cross-r2 = -0.049
Tolerance = 24.729
% Cover
0
5
10
15
20
Potentilla ovina
D
M
W
WT
IV=0.48
IV=0.07
IV=0
MODEL SUMMARY
Day of max cover = 6.1
Max cover(%) = 1.7
Cross-r2 = 0.038
Tolerance = 11.249
0
1
2
3
4
5
6
5
10
15
20
25
30
35
Summer days with soil wetter than -0.12 MPa
5
10
15
20
25
30
35
Summer days with soil wetter than -0.12 MPa

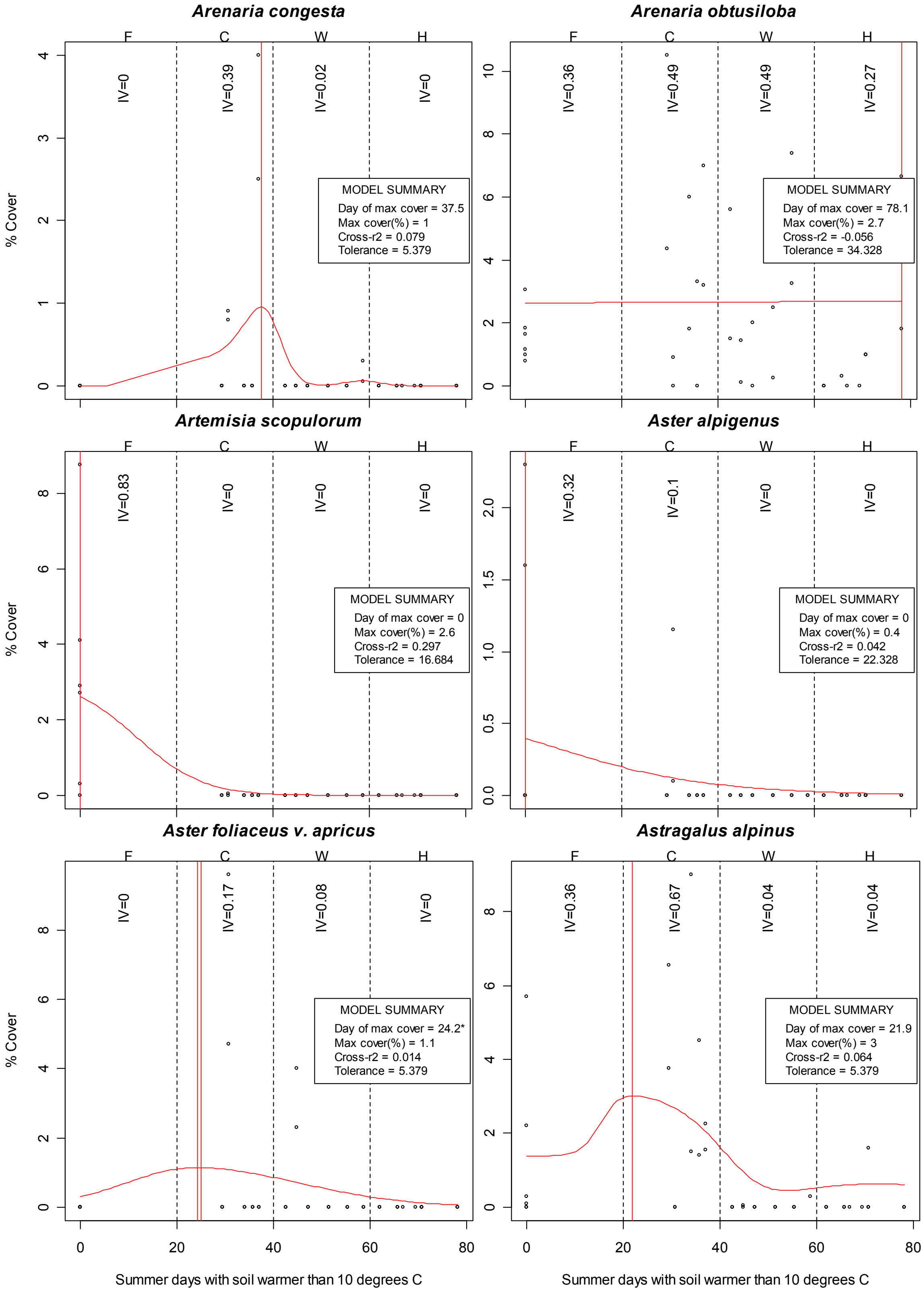

Ranunculus eschscholtzii
D
M
W
WT
IV=0
IV=0
IV=0.16
MODEL SUMMARY
Day of max cover = 37.7
Max cover(%) = 0.1
Cross-r2 = -0.04
Tolerance = 32.34
% Cover
0.0
0.2
0.4
0.6
0.8
Salix arctica
IV=0
IV=0
IV=0.27
MODEL SUMMARY
Day of max cover = 24.7
Max cover(%) = 2.5
Cross-r2 = 0.352
Tolerance = 11.249
0
1
2
3
4
Saxifraga rhomboidea
IV=0.22
IV=0.05
IV=0.13
MODEL SUMMARY
Day of max cover = 6.1
Max cover(%) = 0.2
Cross-r2 = -0.056
Tolerance = 35.749
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Sedum lanceolatum
IV=0.68
IV=0.52
IV=0.06
MODEL SUMMARY
Day of max cover = 13.1
Max cover(%) = 2.9
Cross-r2 = 0.131
Tolerance = 11.249
0
2
4
6
8
10
Selaginella densa
IV=0.64
IV=0.22
IV=0
MODEL SUMMARY
Day of max cover = 6.1
Max cover(%) = 10.1
Cross-r2 = 0.127
Tolerance = 11.249
0
10
20
30
Senecio canus
IV=0.09
IV=0.36
IV=0
MODEL SUMMARY
Day of max cover = 12.4
Max cover(%) = 0.7
Cross-r2 = -0.03
Tolerance = 16.194
0
1
2
3
4
5
10
15
20
25
30
35
Summer days with soil wetter than -0.12 MPa

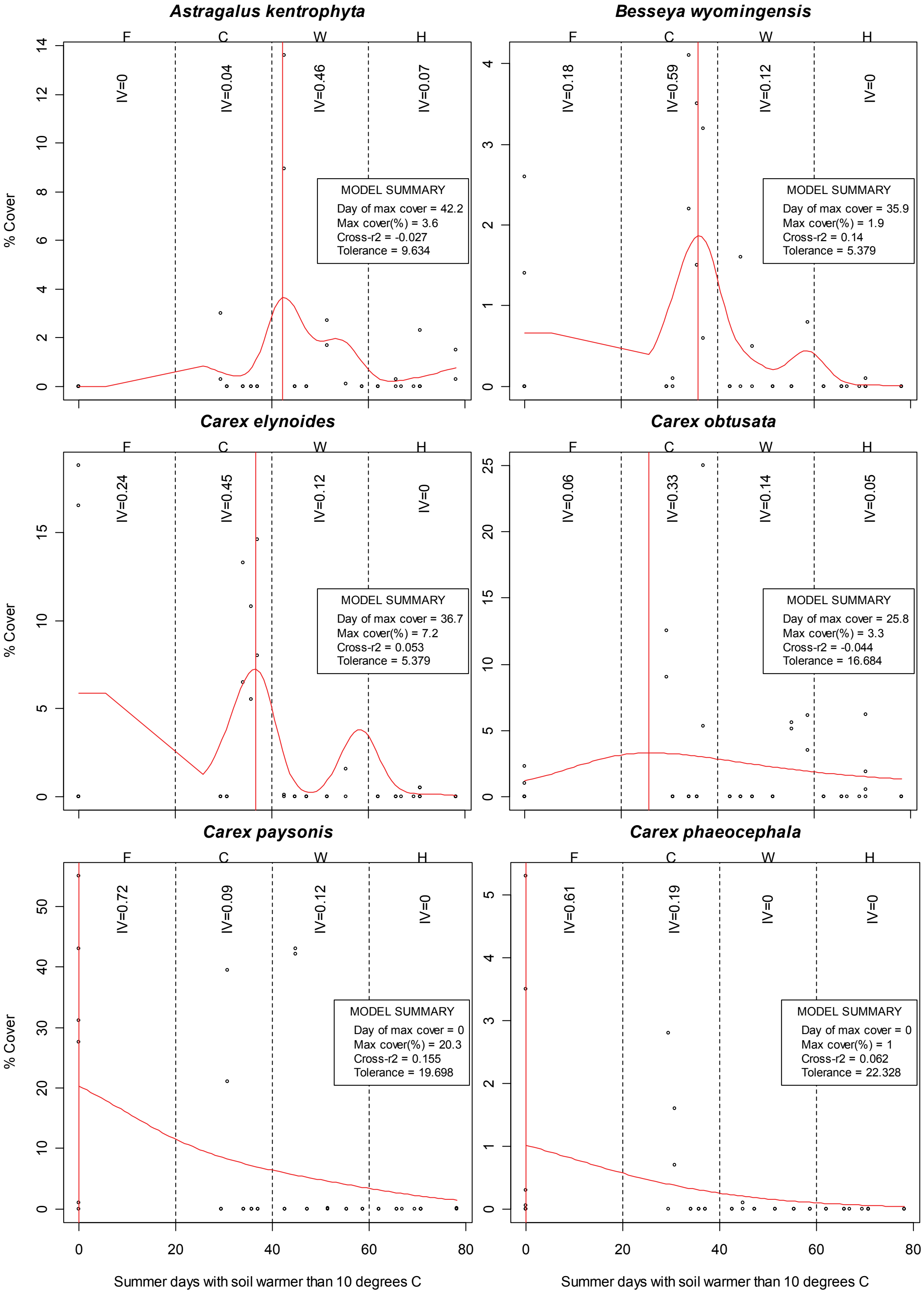

Sibbaldia procumbens
D
M
W
WT
IV=0
IV=0
IV=0.45
MODEL SUMMARY
Day of max cover = 17.8
Max cover(%) = 3.4
Cross-r2 = 0.073
Tolerance = 16.194
% Cover
0
2
4
6
8
10
12
Smelowskia calycina
D
M
W
WT
IV=0.38
IV=0.25
IV=0
MODEL SUMMARY
Day of max cover = 6.1
Max cover(%) = 0.8
Cross-r2 = 0.037
Tolerance = 16.194
0
1
2
3
4
Stellaria monantha
D
M
W
WT
IV=0.01
IV=0.01
IV=0.59
MODEL SUMMARY
Day of max cover = 26.6
Max cover(%) = 0.6
Cross-r2 = 0.296
Tolerance = 19.315
% Cover
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
Trisetum spicatum
D
M
W
WT
IV=0.09
IV=0.35
IV=0.11
MODEL SUMMARY
Day of max cover = 13.1
Max cover(%) = 2.3
Cross-r2 = 0.131
Tolerance = 11.249
0
1
2
3
4
5
Veronica wormskjoldii
D
M
W
WT
IV=0
IV=0
IV=0.27
MODEL SUMMARY
Day of max cover = 17.8
Max cover(%) = 0.9
Cross-r2 = 0.003
Tolerance = 16.194
% Cover
0
1
2
3
4
5
10
15
20
25
30
35
Summer days with soil wetter than -0.12 MPa

Appendix A.3: Nonparametric temperature models

The figures in this section show NPR response curves for all 59 species versus soil temperature, where soil temperature is defined as the number of days when soils are warmer than 10ºC (Chapter 3). Vertical dashed lines show the separation between soil water categories (F, C, W, and H). Vertical solid lines indicate the number of days along the predictor axis when the optimal response is predicted to occur. The term "IV" represents ISA indicator value scores for each category (Dufrêne and Legendre 1997). The model summary box in each figure lists: 1) day of maximum response (also indicated by the solid vertical line), 2) the predicted maximum cover, 3) the cross r^2 evaluation for the model (see methods), and 4) The tolerance (optimal kernel width) of the model (see methods).


Achillea millefolium
F
C
W
H
IV=0.19
IV=0.53
IV=0.1
IV=0.17
MODEL SUMMARY
Day of max cover = 24.2
Max cover(%) = 2.7
Cross-r2 = 0.041
Tolerance = 13.341
% Cover
0
2
4
6
8
10
Agoseris glauca
F
C
W
H
IV=0.06
IV=0.33
IV=0.05
IV=0.06
MODEL SUMMARY
Day of max cover = 23.4
Max cover(%) = 0.8
Cross-r2 = 0.039
Tolerance = 5.379
0
1
2
3
4
All mosses
F
C
W
H
IV=0.94
IV=0.29
IV=0.12
IV=0
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = 7.3
Cross-r2 = 0.16
Tolerance = 19.698
% Cover
0
5
10
15
20
25
30
Androsace septentrionalis
F
C
W
H
IV=0.6
IV=0.06
IV=0.01
IV=0
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = 0.2
Cross-r2 = 0.074
Tolerance = 19.698
0.0
0.2
0.4
0.6
0.8
Antennaria media
F
C
W
H
IV=0.11
IV=0.15
IV=0.04
IV=0
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = 0.1
Cross-r2 = -0.044
Tolerance = 30.657
% Cover
0.0
0.2
0.4
0.6
0.8
1.0
1.2
Antennaria microphylla
F
C
W
H
IV=0
IV=0.07
IV=0
IV=0.13
MODEL SUMMARY
Day of max cover = 78.1
Max cover(%) = 0.1
Cross-r2 = -0.056
Tolerance = 34.328
0.0
0.5
1.0
1.5
0
20
40
60
80
Summer days with soil warmer than 10 degrees C
0
20
40
60
80
Summer days with soil warmer than 10 degrees C


Arenaria congesta
F
C
W
H
IV=0
IV=0.39
IV=0.02
IV=0
MODEL SUMMARY
Day of max cover = 37.5
Max cover(%) = 1
Cross-r2 = 0.079
Tolerance = 5.379
% Cover
0
1
2
3
4
Arenaria obtusiloba
F
C
W
H
IV=0.36
IV=0.49
IV=0.49
IV=0.27
MODEL SUMMARY
Day of max cover = 78.1
Max cover(%) = 2.7
Cross-r2 = -0.056
Tolerance = 34.328
0
2
4
6
8
10
Artemisia scopulorum
F
C
W
H
IV=0.83
IV=0
IV=0
IV=0
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = 2.6
Cross-r2 = 0.297
Tolerance = 16.684
% Cover
0
2
4
6
8
Aster alpigenus
F
C
W
H
IV=0.32
IV=0.1
IV=0
IV=0
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = 0.4
Cross-r2 = 0.042
Tolerance = 22.328
0.0
0.5
1.0
1.5
2.0
Aster foliaceus v. apricus
F
C
W
H
IV=0
IV=0.17
IV=0.08
IV=0
MODEL SUMMARY
Day of max cover = 24.2*
Max cover(%) = 1.1
Cross-r2 = 0.014
Tolerance = 5.379
% Cover
0
2
4
6
8
0
20
40
60
80
Summer days with soil warmer than 10 degrees C
Astragalus alpinus
F
C
W
H
IV=0.36
IV=0.67
IV=0.04
IV=0.04
MODEL SUMMARY
Day of max cover = 21.9
Max cover(%) = 3
Cross-r2 = 0.064
Tolerance = 5.379
0
2
4
6
8
0
20
40
60
80
Summer days with soil warmer than 10 degrees C


Astragalus kentrophyta

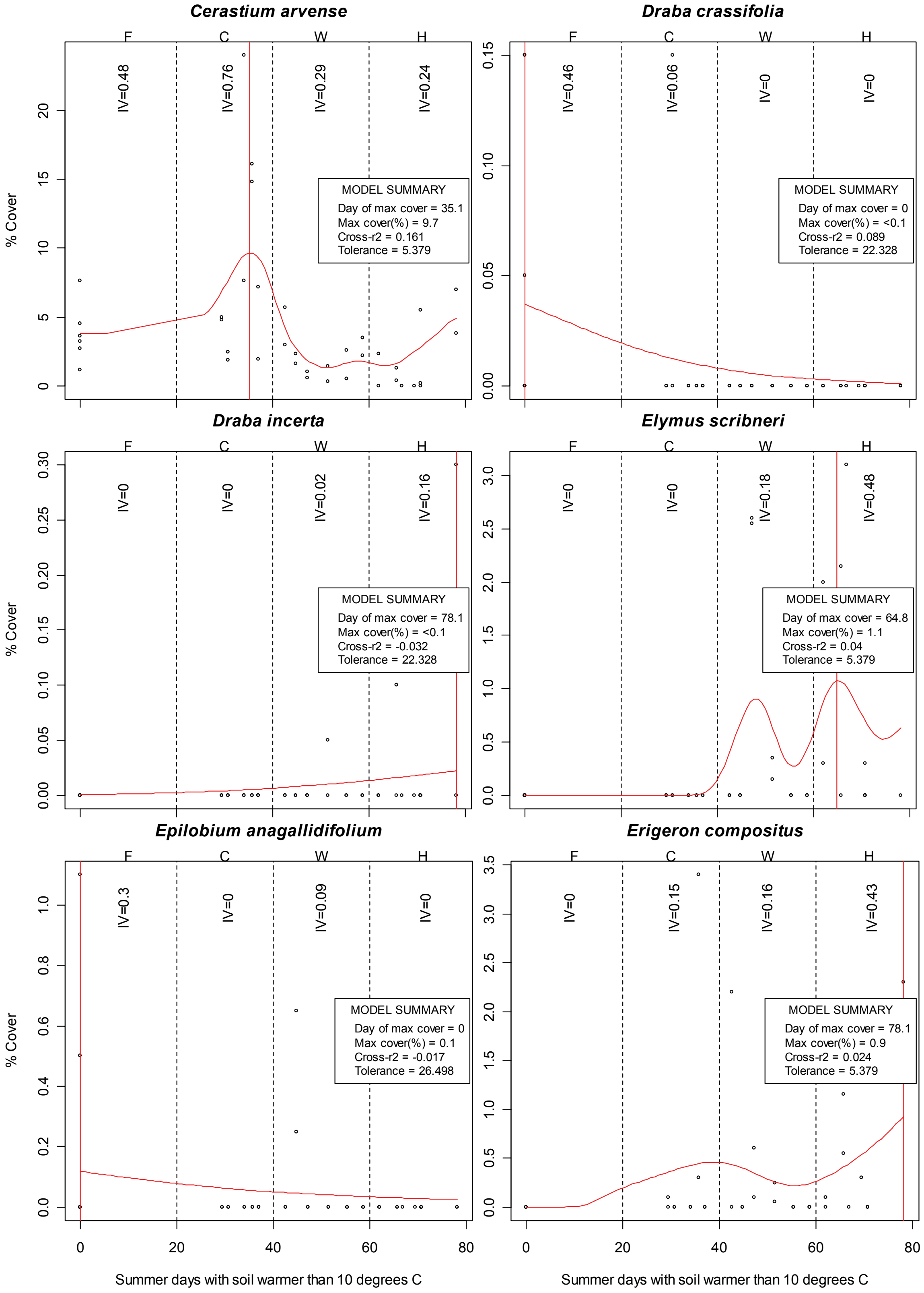
Besseya wyomingensis

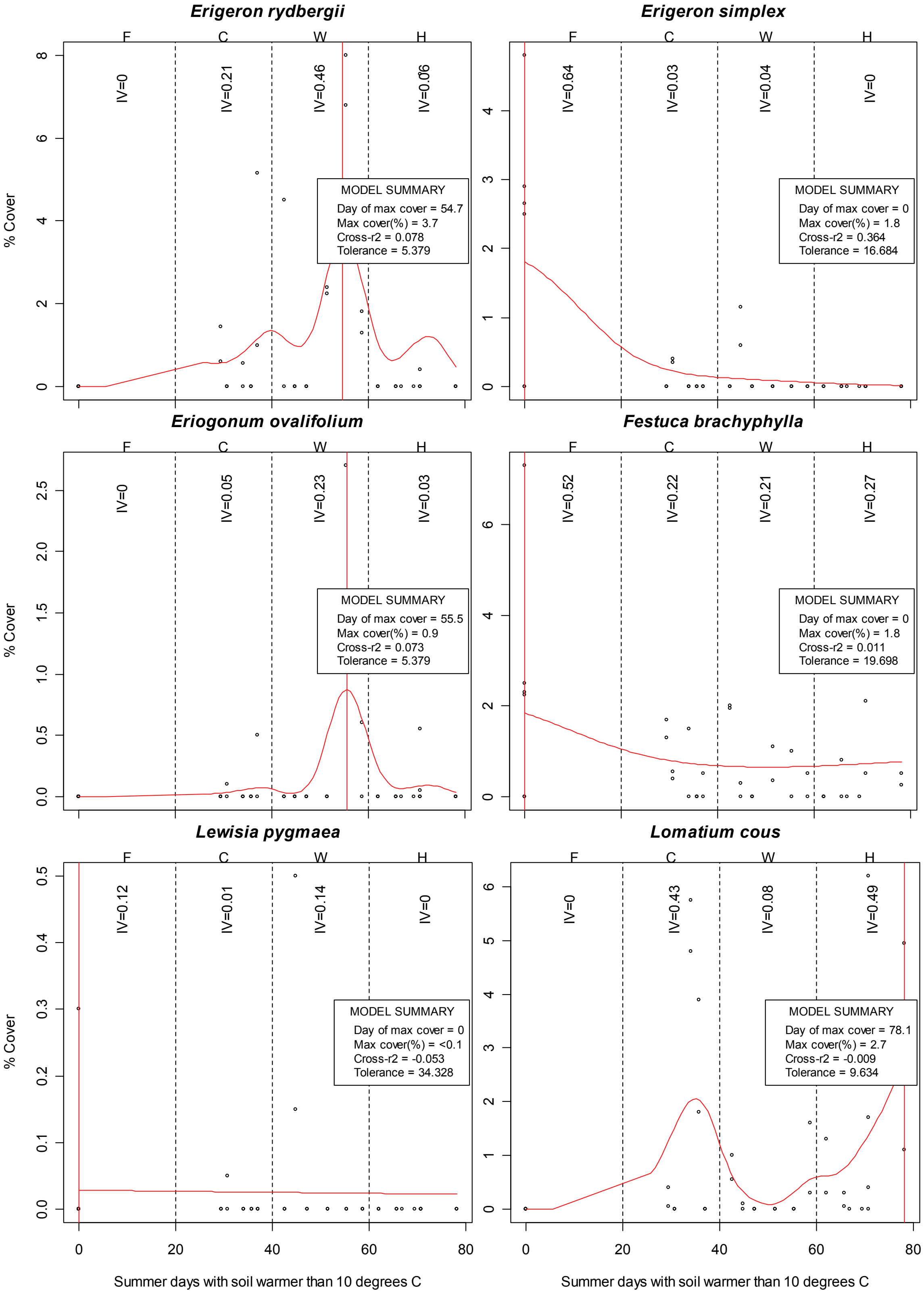
Carex elynoides

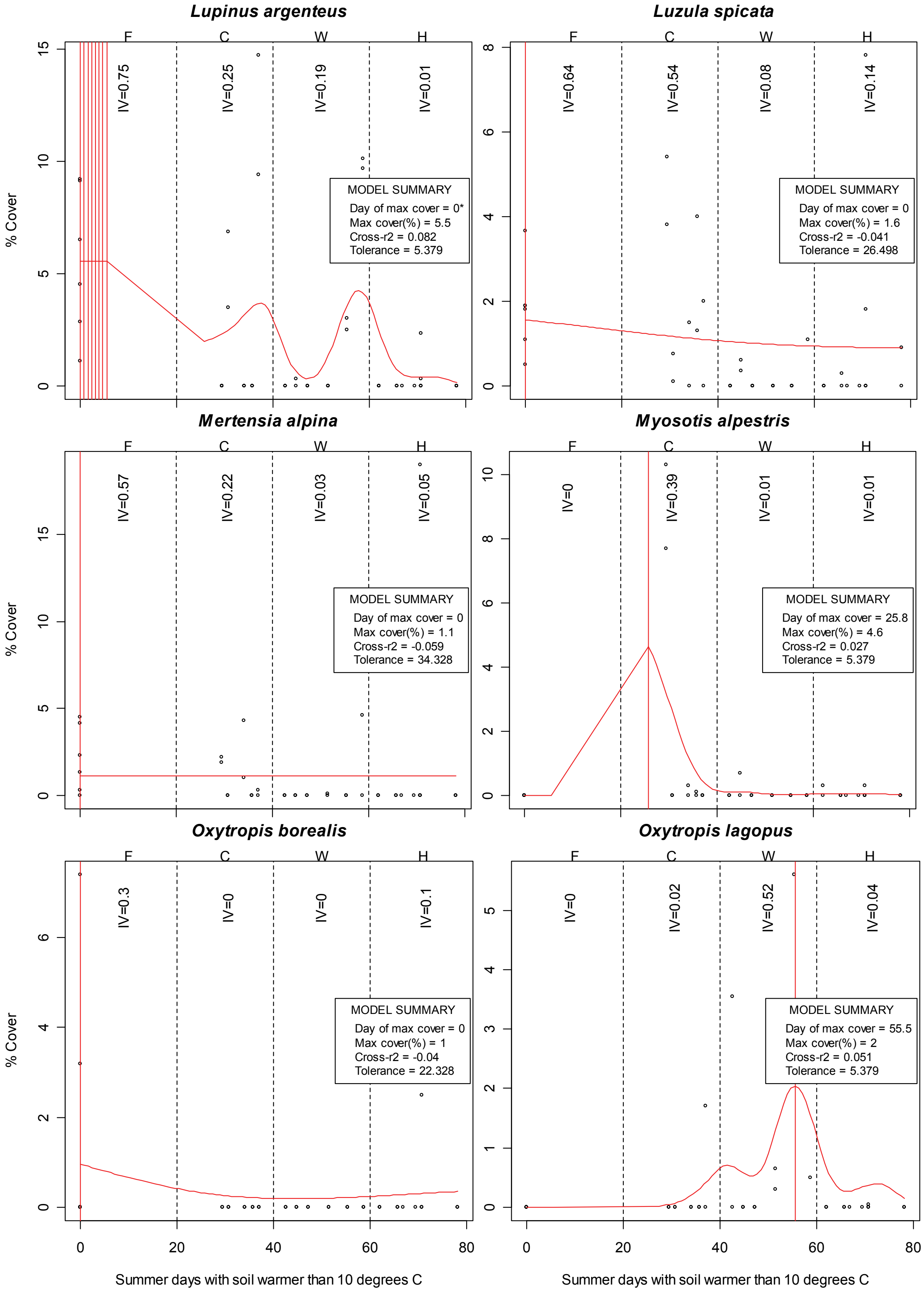
Carex obtusata

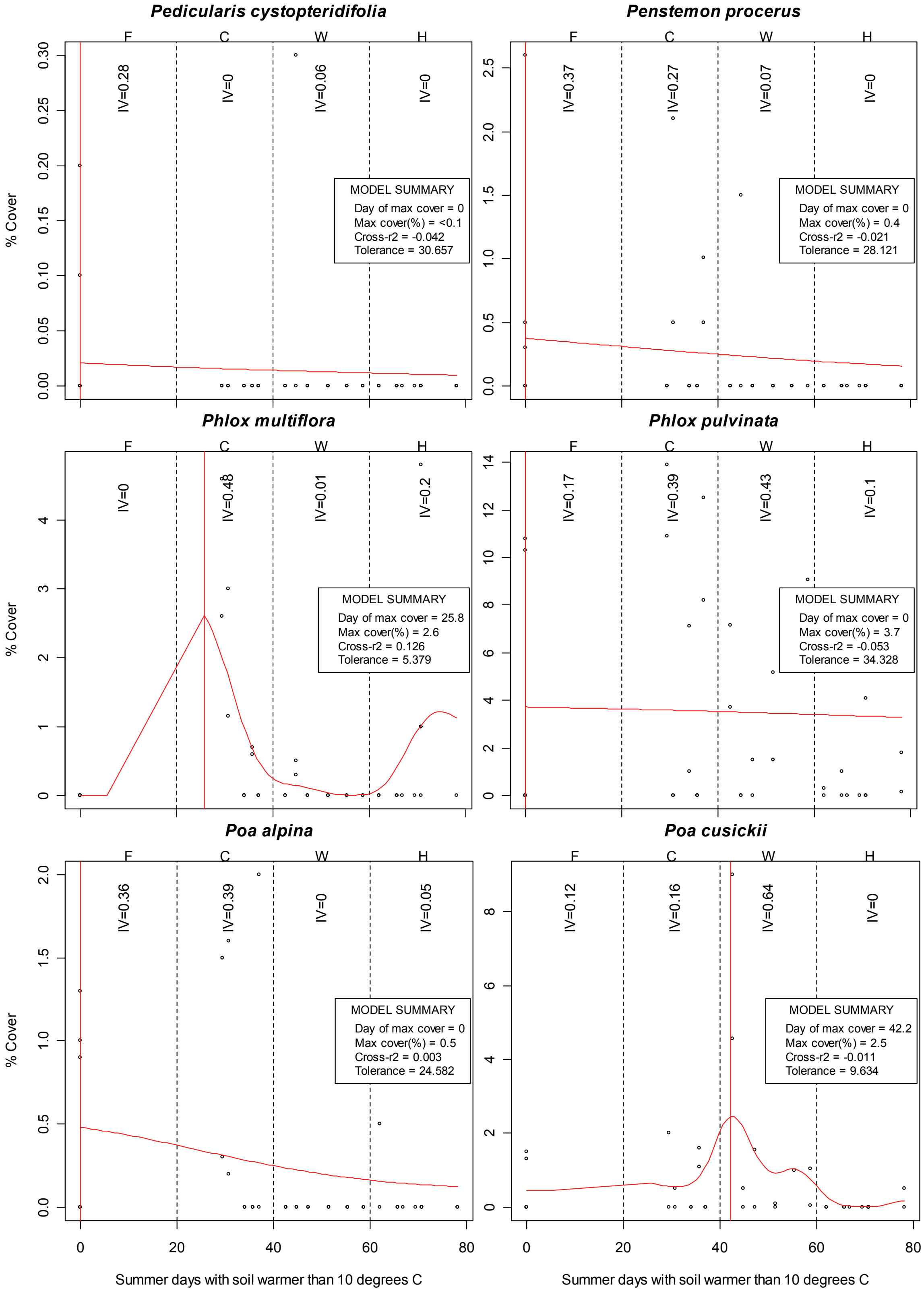
Carex paysonis

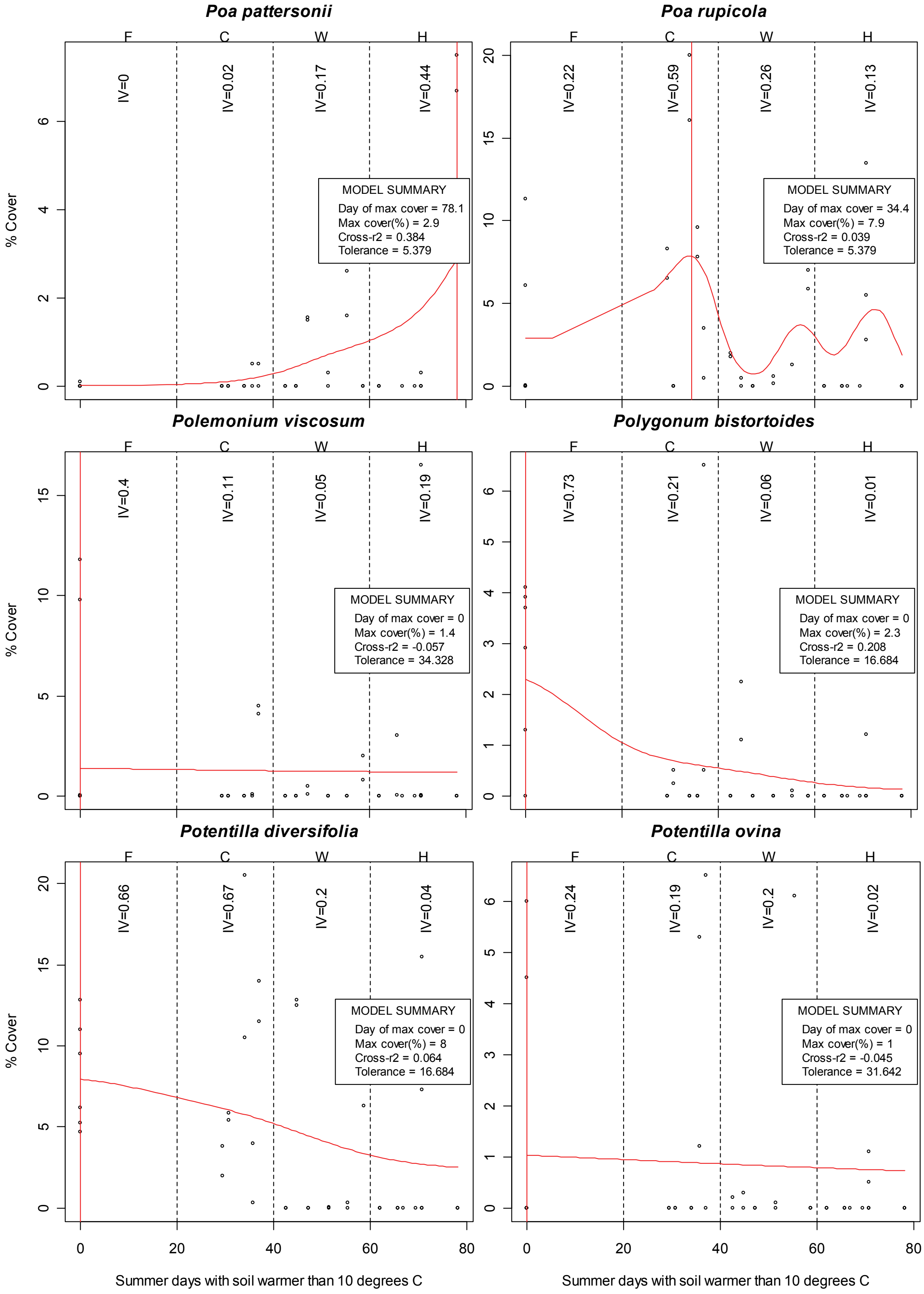
Carex phaeocephala

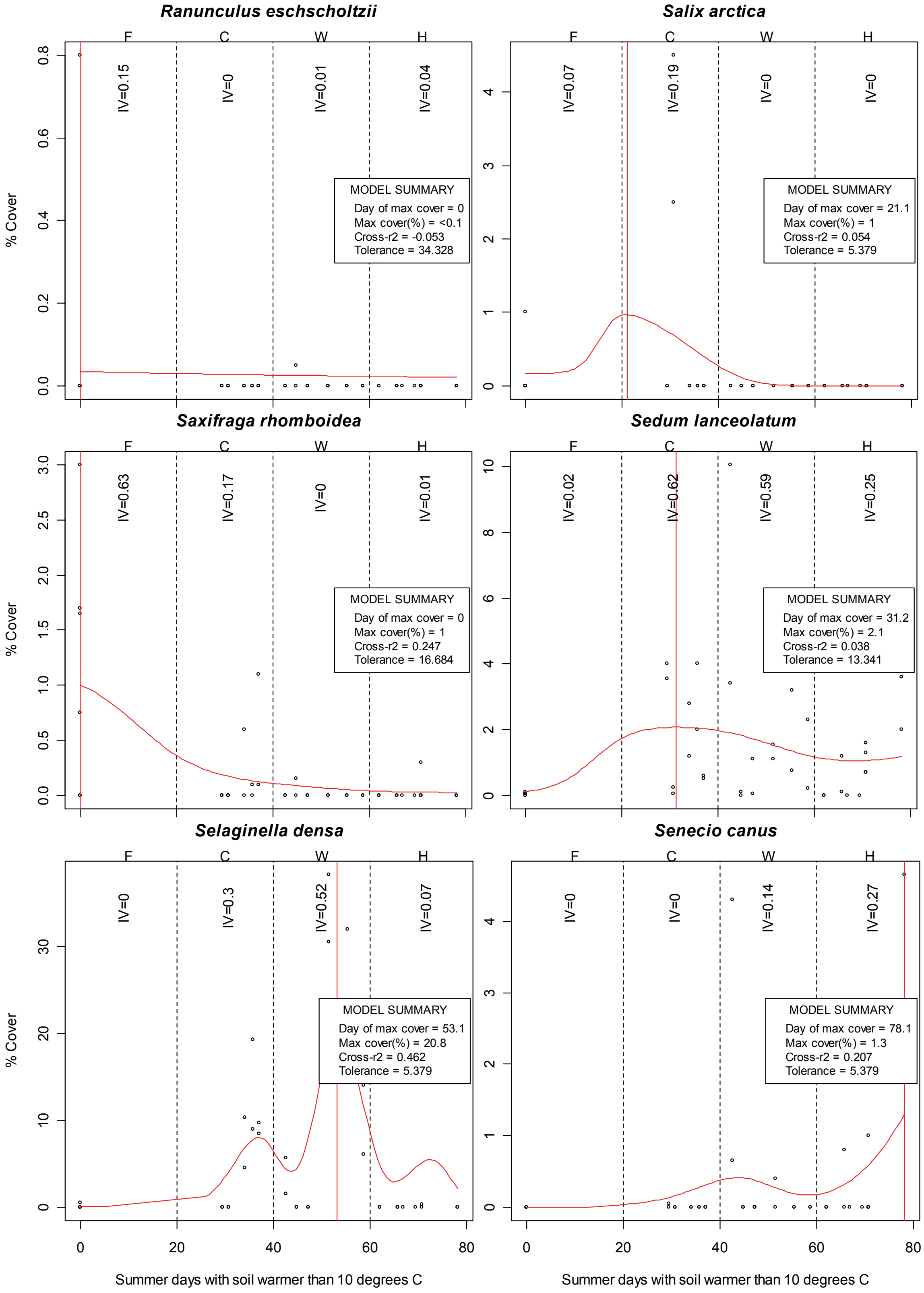

Cerastium arvense
F
C
W
H
IV=0.48
IV=0.76
IV=0.29
IV=0.24
MODEL SUMMARY
Day of max cover = 35.1
Max cover(%) = 9.7
Cross-r2 = 0.161
Tolerance = 5.379
% Cover
0
5
10
15
20
Draba crassifolia
F
C
W
H
IV=0.46
IV=0.06
IV=0
IV=0
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = <0.1
Cross-r2 = 0.089
Tolerance = 22.328
0.00
0.05
0.10
0.15
Draba incerta
F
C
W
H
IV=0
IV=0
IV=0.02
IV=0.16
MODEL SUMMARY
Day of max cover = 78.1
Max cover(%) = <0.1
Cross-r2 = -0.032
Tolerance = 22.328
% Cover
0.00
0.05
0.10
0.15
0.20
0.25
0.30
Elymus scribneri
F
C
W
H
IV=0
IV=0
IV=0.18
IV=0.48
MODEL SUMMARY
Day of max cover = 64.8
Max cover(%) = 1.1
Cross-r2 = 0.04
Tolerance = 5.379
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Epilobium anagallidifolium
F
C
W
H
IV=0.3
IV=0
IV=0.09
IV=0
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = 0.1
Cross-r2 = -0.017
Tolerance = 26.498
% Cover
0.0
0.2
0.4
0.6
0.8
1.0
0
20
40
60
80
Summer days with soil warmer than 10 degrees C
Erigeron compositus
F
C
W
H
IV=0
IV=0.15
IV=0.16
IV=0.43
MODEL SUMMARY
Day of max cover = 78.1
Max cover(%) = 0.9
Cross-r2 = 0.024
Tolerance = 5.379
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
0
20
40
60
80
Summer days with soil warmer than 10 degrees C

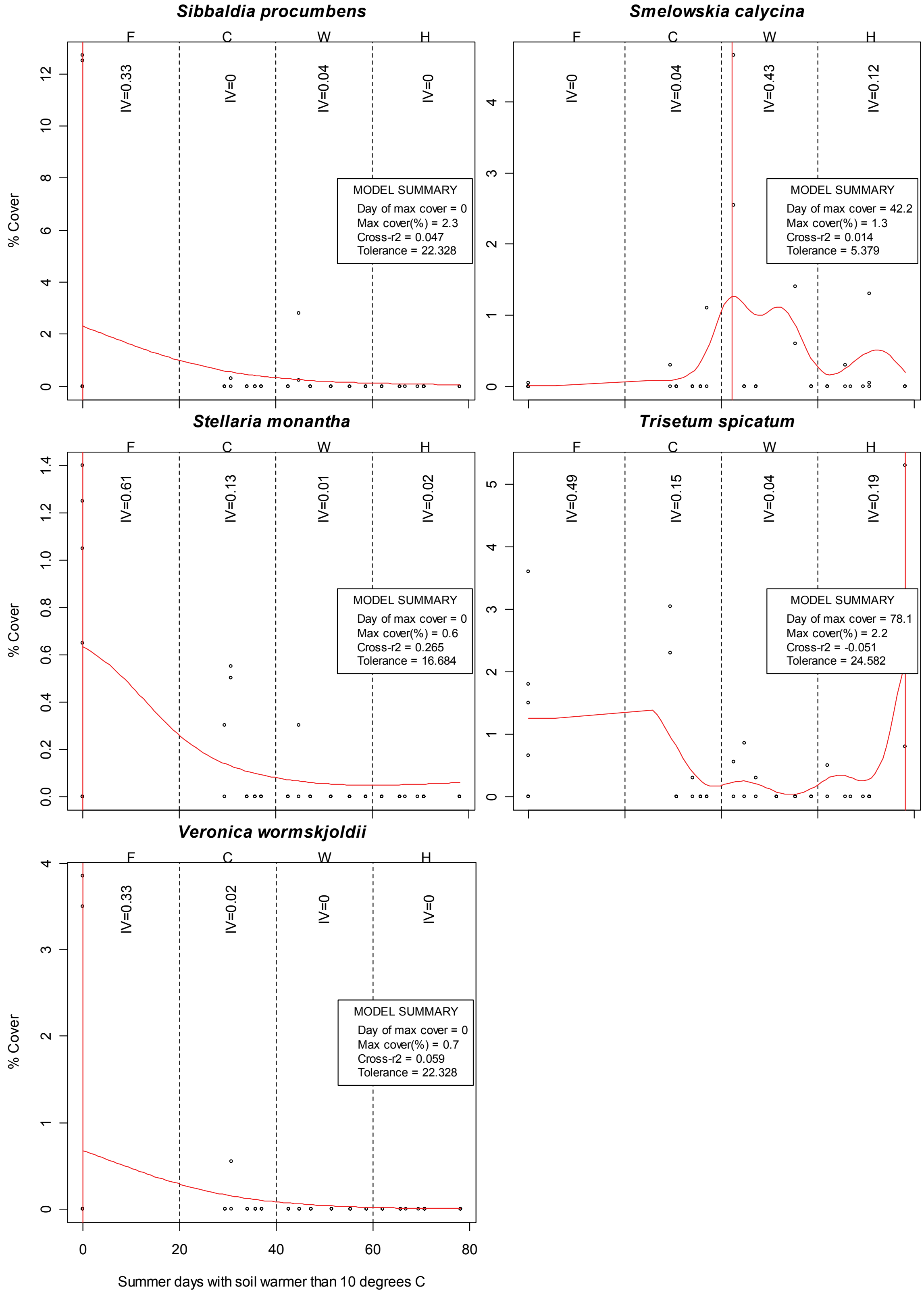

Erigeron rydbergii
F
C
W
H
IV=0
IV=0.21
IV=0.46
IV=0.06
MODEL SUMMARY
Day of max cover = 54.7
Max cover(%) = 3.7
Cross-r2 = 0.078
Tolerance = 5.379
% Cover
0
2
4
6
8
Erigeron simplex
F
C
W
H
IV=0.64
IV=0.03
IV=0.04
IV=0
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = 1.8
Cross-r2 = 0.364
Tolerance = 16.684
0
1
2
3
4
Eriogonum ovalifolium
F
C
W
H
IV=0
IV=0.05
IV=0.23
IV=0.03
MODEL SUMMARY
Day of max cover = 55.5
Max cover(%) = 0.9
Cross-r2 = 0.073
Tolerance = 5.379
% Cover
0.0
0.5
1.0
1.5
2.0
2.5
Festuca brachyphylla
F
C
W
H
IV=0.52
IV=0.22
IV=0.21
IV=0.27
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = 1.8
Cross-r2 = 0.011
Tolerance = 19.698
0
2
4
6
Lewisia pygmaea
F
C
W
H
IV=0.12
IV=0.01
IV=0.14
IV=0
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = <0.1
Cross-r2 = -0.053
Tolerance = 34.328
% Cover
0.0
0.1
0.2
0.3
0.4
0.5
Lomatium cous
F
C
W
H
IV=0
IV=0.43
IV=0.08
IV=0.49
MODEL SUMMARY
Day of max cover = 78.1
Max cover(%) = 2.7
Cross-r2 = -0.009
Tolerance = 9.634
0
1
2
3
4
5
6
0
20
40
60
80
Summer days with soil warmer than 10 degrees C
0
20
40
60
80
Summer days with soil warmer than 10 degrees C


Lupinus argenteus
F
C
W
H
IV=0.75
IV=0.25
IV=0.19
IV=0.01
MODEL SUMMARY
Day of max cover = 0*
Max cover(%) = 5.5
Cross-r2 = 0.082
Tolerance = 5.379
% Cover
0
5
10
15
Luzula spicata
IV=0.64
IV=0.54
IV=0.08
IV=0.14
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = 1.6
Cross-r2 = -0.041
Tolerance = 26.498
0
2
4
6
8
Mertensia alpina
IV=0.57
IV=0.22
IV=0.03
IV=0.05
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = 1.1
Cross-r2 = -0.059
Tolerance = 34.328
Myosotis alpestris
IV=0
IV=0.39
IV=0.01
IV=0.01
MODEL SUMMARY
Day of max cover = 25.8
Max cover(%) = 4.6
Cross-r2 = 0.027
Tolerance = 5.379
10
Oxytropis borealis
IV=0.3
IV=0
IV=0
IV=0.1
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = 1
Cross-r2 = -0.04
Tolerance = 22.328
Oxytropis lagopus
IV=0
IV=0.02
IV=0.52
IV=0.04
MODEL SUMMARY
Day of max cover = 55.5
Max cover(%) = 2
Cross-r2 = 0.051
Tolerance = 5.379
1
3
5
20
40
60
80
Summer days with soil warmer than 10 degrees C
Summer days with soil warmer than 10 degrees C


Pedicularis cystopteridifolia
F
C
W
H
IV=0.28
IV=0
IV=0.06
IV=0
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = <0.1
Cross-r2 = -0.042
Tolerance = 30.657
% Cover
0.00
0.05
0.10
0.15
0.20
0.25
0.30
Penstemon procerus
F
C
W
H
IV=0.37
IV=0.27
IV=0.07
IV=0
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = 0.4
Cross-r2 = -0.021
Tolerance = 28.121
0.0
0.5
1.0
1.5
2.0
2.5
Phlox multiflora
F
C
W
H
IV=0
IV=0.48
IV=0.01
IV=0.2
MODEL SUMMARY
Day of max cover = 25.8
Max cover(%) = 2.6
Cross-r2 = 0.126
Tolerance = 5.379
% Cover
0
1
2
3
4
Phlox pulvinata
F
C
W
H
IV=0.17
IV=0.39
IV=0.43
IV=0.1
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = 3.7
Cross-r2 = -0.053
Tolerance = 34.328
0
2
4
6
8
10
12
14
Poa alpina
F
C
W
H
IV=0.36
IV=0.39
IV=0
IV=0.05
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = 0.5
Cross-r2 = 0.003
Tolerance = 24.582
% Cover
0.0
0.5
1.0
1.5
2.0
0
20
40
60
80
Summer days with soil warmer than 10 degrees C
Poa cusickii
F
C
W
H
IV=0.12
IV=0.16
IV=0.64
IV=0
MODEL SUMMARY
Day of max cover = 42.2
Max cover(%) = 2.5
Cross-r2 = -0.011
Tolerance = 9.634
0
2
4
6
8
0
20
40
60
80
Summer days with soil warmer than 10 degrees C


Poa pattersonii
F
C
W
H
IV=0
IV=0.02
IV=0.17
IV=0.44
MODEL SUMMARY
Day of max cover = 78.1
Max cover(%) = 2.9
Cross-r2 = 0.384
Tolerance = 5.379
Poa rupicola
IV=0.22
IV=0.59
IV=0.26
IV=0.13
MODEL SUMMARY
Day of max cover = 34.4
Max cover(%) = 7.9
Cross-r2 = 0.039
Tolerance = 5.379
Polemonium viscosum
IV=0.4
IV=0.11
IV=0.05
IV=0.19
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = 1.4
Cross-r2 = -0.057
Tolerance = 34.328
Polygonum bistortoides
IV=0.73
IV=0.21
IV=0.06
IV=0.01
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = 2.3
Cross-r2 = 0.208
Tolerance = 16.684
Potentilla diversifolia
IV=0.66
IV=0.67
IV=0.2
IV=0.04
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = 8
Cross-r2 = 0.064
Tolerance = 16.684
Potentilla ovina
IV=0.24
IV=0.19
IV=0.2
IV=0.02
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = 1
Cross-r2 = -0.045
Tolerance = 31.642
% Cover
0
2
4
6
5
10
15
20
1
3
0
20
40
60
80
Summer days with soil warmer than 10 degrees C


Ranunculus eschscholtzii
F
C
W
H
IV=0.15
IV=0
IV=0.01
IV=0.04
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = <0.1
Cross-r2 = -0.053
Tolerance = 34.328
% Cover
0.0
0.2
0.4
0.6
0.8
Salix arctica
F
C
W
H
IV=0.07
IV=0.19
IV=0
IV=0
MODEL SUMMARY
Day of max cover = 21.1
Max cover(%) = 1
Cross-r2 = 0.054
Tolerance = 5.379
0
1
2
3
4
Saxifraga rhomboidea
F
C
W
H
IV=0.63
IV=0.17
IV=0
IV=0.01
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = 1
Cross-r2 = 0.247
Tolerance = 16.684
% Cover
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Sedum lanceolatum
F
C
W
H
IV=0.02
IV=0.62
IV=0.59
IV=0.25
MODEL SUMMARY
Day of max cover = 31.2
Max cover(%) = 2.1
Cross-r2 = 0.038
Tolerance = 13.341
0
2
4
6
8
10
Selaginella densa
F
C
W
H
IV=0
IV=0.3
IV=0.52
IV=0.07
MODEL SUMMARY
Day of max cover = 53.1
Max cover(%) = 20.8
Cross-r2 = 0.462
Tolerance = 5.379
% Cover
0
10
20
30
0
20
40
60
80
Summer days with soil warmer than 10 degrees C
Senecio canus
F
C
W
H
IV=0
IV=0
IV=0.14
IV=0.27
MODEL SUMMARY
Day of max cover = 78.1
Max cover(%) = 1.3
Cross-r2 = 0.207
Tolerance = 5.379
0
1
2
3
4
0
20
40
60
80
Summer days with soil warmer than 10 degrees C


Sibbaldia procumbens
F
C
W
H
IV=0.33
IV=0
IV=0.04
IV=0
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = 2.3
Cross-r2 = 0.047
Tolerance = 22.328
% Cover
0
2
4
6
8
10
12
Smelowskia calycina
F
C
W
H
IV=0
IV=0.04
IV=0.43
IV=0.12
MODEL SUMMARY
Day of max cover = 42.2
Max cover(%) = 1.3
Cross-r2 = 0.014
Tolerance = 5.379
0
1
2
3
4
Stellaria monantha
F
C
W
H
IV=0.61
IV=0.13
IV=0.01
IV=0.02
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = 0.6
Cross-r2 = 0.265
Tolerance = 16.684
% Cover
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
Trisetum spicatum
F
C
W
H
IV=0.49
IV=0.15
IV=0.04
IV=0.19
MODEL SUMMARY
Day of max cover = 78.1
Max cover(%) = 2.2
Cross-r2 = -0.051
Tolerance = 24.582
0
1
2
3
4
5
Veronica wormskjoldii
F
C
W
H
IV=0.33
IV=0.02
IV=0
IV=0
MODEL SUMMARY
Day of max cover = 0
Max cover(%) = 0.7
Cross-r2 = 0.059
Tolerance = 22.328
% Cover
0
1
2
3
4
0
20
40
60
80
Summer days with soil warmer than 10 degrees C

APPENDIX B

APPENDICES PERTAINING TO CHAPTER 3--

ALPINE COMMUNITIES, ECOLOGY, AND FLORA OF MOUNT WASHBURN

Appendix B.1: Mount Washburn Alpine Species Checklist

Annotations in this appendix describe distribution, moisture, habitat, and collection numbers.

Distribution: **Rare** = rare, **Infr** = infrequent, **Freq** = frequent, **Wide** = widespread.
Moisture: wet = wet, moi = moist, dry = dry.
Habitat: *sm* = late melt, *t* = talus and extremely rocky sites, *tr* = treeline, *rt* = ridgetop, *d* = disturbed, *tu* = turf, *l* = ledges, *all* = all habitats.
Collections: AHO-YELLO = vouchers from dissertation research deposited in the YNP herbarium in Gardiner MT, AHO = Aho private collection not deposited in YNP herbarium, YELLO = existing vouchers in YNP herbarium.

LYCOPHYTA

Selaginellaceae

Selaginella densa Rydb.	**Freq,** dry, *tu, rt,* AHO-303 (YELLO)

ANTHOPHYTA-MONCOTYLEDONEAE

Cyperaceae

Carex albonigra Mack.	**Infr,** wet, *ta* YELLO-4702
Carex elynoides Holm	**Wide,** dry, *tu, rt* AHO-152, 381 (YELLO)
Carex haydeniana Olney	**Infr,** wet, *sm* YELLO-4653
Carex obtusata Lilj.	**Freq,** dry, *tu* AHO-146, 335 (YELLO)
Carex paysonis Clokey	**Wide,** wet, *sm* AHO-145, 380 (YELLO)
Carex petasata Dewey	YELLO-4662

Carex phaeocephala Piper	**Freq,** wet to moi, *sm, d* AHO-144 (YELLO)

Juncaceae

Juncus drummondii Meyer	**Infr,** wet, *sm* AHO-544
Luzula spicata L. DC.	**Wide,** wet to dry, *all* AHO-564

Liliaceae

Allium cernuum Roth	**Infr,** dry to moi, *d, tr* AHO-108 (YELLO)
Allium brevistylum Wats.	**Infr**, *tr* YELLO-565
Fritillaria pudica (Pursh) Spreng.	**Infr,** wet, *tr* YELLO-630

Poaceae

Bromus inermis Leyss. var. *inermis*	**Infr,** dry to moi, *d* AHO-94 (YELLO)
Elymus scribneri Vasey Jones	**Freq,** dry to wet, *ta, rt* AHO-557
Elymus trachycaulus Link Gould ex Shinners var. *andinus* (Scribn. & SM.) Dorn	**Freq,** dry to wet, *d* AHO-88 (YELLO)
Festuca brachyphylla Schultes & Schultes	**Wide,** dry to wet, *all* AHO-SWC3
Phleum alpinum L.	**Infr,** wet to moi, *tr, d* AHO-567
Poa alpina L.	**Freq,** dry to wet, *tu, sm* AHO-541
Poa arctica R. Br. var. *grayana* (Vasey) Dorn	**Infr,** dry to moi, *tu* noted, **no voucher**
Poa cusickii Vasey var. *cusickii*	**Wide,** dry to wet, *all* AHO-360, 85(YELLO)
Poa cusickii Vasey var. *epilis* (Scribn.) Hitchc.	**Wide,** dry to wet, *all* AHO-80 (YELLO)
Poa interior Rydb.	**Infr,** wet to moi, *ta, sm* AHO-379 (YELLO)
Poa pattersonii Vasey	**Wide,** dry to wet, *tu* AHO-77 (YELLO)
Poa reflexa Vasey & Scrib. ex Vasey	**Infr,** wet, *sm* AHO-549
Poa rupicola Nash ex Rydb.	**Freq,** dry to wet, *tu* AHO-75, 382 (YELLO)
Poa secunda Presl var. *incurva* (Scrib. & Wms. ex Scribn.) Beetle	**Infr,** dry to moi, *tu, ta* AHO-72,73 (YELLO)

Stipa nelsonii Scribn.	**Infr,** dry to moi, *tr* AHO-554
Trisetum spicatum (L.) Richt.	**Wide,** dry to wet, *all* YELLO-4588

ANTHOPHYTA-DICOTYLEDONEAE

Apiaceae

Lomatium cous (Wats.) Coult. & Rose	**Wide,** dry to wet, *all* AHO-559

Asteraceae

Achillea millefolium L. var. *lanulosa* (Nutt.) Piper	**Wide,** wet to dry, *all* AHO-271 (YELLO)
Agoseris glauca (Pursh) Raf. var. *dasycephala* (T. & G.) Jeps.	**Wide,** dry to wet, *all* AHO-268 (YELLO)
Antennaria anaphaloides Rydb.	**Infr,** moi, *tr* AHO-322 (YELLO)
Antennaria media Greene	**Freq,** wet, *sm* AHO-548
Antennaria microphylla Rydb.	**Wide,** dry to wet, *all* AHO-SWC6
Antennaria umbrinella Rydb.	**Wide,** dry to wet, *all* AHO-565
Antennaria rosea Greene	**Infr,** moi, *tr* AHO-572
Arnica latifolia Bong.	**Infr,** wet, *sm, tu* AHO-259 (YELLO)
Arnica longifolia Eaton	**Freq,** *tr* YELLO-2688
Arnica rydbergii Greene	**Freq,** wet, *ta, l, d* AHO-558
Artemisia frigida Willd.	**Infr,** dry to moi, *tr, d* AHO-252 (YELLO)
Artemisia scopulorum Gray	**Freq,** wet, *sm* AHO-257 YELLO
Aster alpigenus (T. & G.) Gray var. *haydenii* Porter Cronq.	**Infq,** dry to moi, *sm, tu* AHO-249 (YELLO)
Aster engelmannii Eaton Gray	**Infr,** dry, *tu, tr* YELLO-2984
Aster foliaceus Lindl. ex DC. var. *apricus* Gray	**Freq,** wet, *sm* AHO-248 (YELLO)
Aster integrifolius Nutt.	YELLO-2811
Chaenactis alpina (Gray) Jones var. *alpina*	**Infr,** dry to moi, *ta, d* AHO-244 (YELLO)
Chrysothamnus viscidiflorus Hook. (Nutt.)	**Infr,** dry to moi, *d, tr* AHO-372 (YELLO)
Cirsium eatonii (Gray) Robins.	**Infr,** dry to moi, *ta, l, d* AHO-243 (YELLO)
Erigeron compositus Pursh var. *discoideus* Gray	**Freq,** dry, *rt, ta* AHO-556

Erigeron eatonii Gray	**Rare,** dry, *tr, d* AHO-238 (YELLO)
Erigeron peregrinus (Banks ex Pursh) Greene	**Infr,** moi, *tu, tr* YELLO-2947
Erigeron rydbergii Cronq.	**Freq,** dry, *tu, rt* AHO-234, 378 (YELLO)
Erigeron simplex Greene	**Freq,** dry to wet, *sm, tu* AHO-233 (YELLO)
Erigeron speciosus (Lindl.) DC.	YELLO-4265
Erigeron ursinus Eaton	YELLO-2933
Eriophyllum lanatum (Pursh) Forbes	**Infr,** dry, *tr, tu* AHO-223 (YELLO)
Haplopappus acaulis (Nutt.) Gray	**Infr,** dry to moi, *ta, d* noted, **no voucher**
Haplopappus suffruticosus (Nutt.) Gray	**Infr,** dry to moi, *ta, rt, d* AHO-228 (YELLO)
Hieracium gracile Hook.	**Infr,** dry to moi, *d* noted, **no voucher**
Senecio canus Hook.	**Freq,** dry to moi, *ta, rt* AHO-224 (YELLO)
Senecio cymbalarioides Buek	YELLO-4402
Senecio fremontii T. & G.	**Freq,** dry to moi, *ta, rt, tu* AHO-220 (YELLO)
Senecio integerrimus Nutt.	**Infr,** moi to wet, *sm, tr* AHO-218 (YELLO)
Senecio lugens Richardson	YELLO-3106
Solidago multiradiata Ait.	**Freq,** dry to moi, *ta d,* AHO-212 (YELLO)
Taraxacum ceratophorum (Ledeb.) DC.	**Freq,** dry to moi, *all* YELLO-3193
Taraxacum eriophorum Rydb.	**Rare,** moi, ta AHO-210 (YELLO)
Taraxacum officinale Weber	**Freq,** moi to wet**,** *d* AHO-208 (YELLO)
Townsendia parryi Eaton	**Infr,** dry to moi**,** *tr* AHO-207 (YELLO)
Boraginaceae	
Mertensia alpina (Torrey) G. Don	**Freq,** dry to moi, *tu, sm* AHO-205 (YELLO)
Mertensia ciliata (James ex Torrey) G. Don	**Infr,** dry to moi, *tr, tu* YELLO-2215
Myosotis alpestris Schmidt	**Freq,** dry to moi, *tu, sm* AHO-204 (YELLO)
Brassicaceae	
Arabis drummondii Gray	**Infr,** dry to moi, *ta, d,* YELLO-1203
Arabis lemmonii Wats.	**Infr,** dry to moi, *ta, d,* YELLO-4363

Arabis lyallii Wats.	**Infr,** dry to moi, *tu* AHO-547
Arabis microphylla Nutt.	**Infr,** dry to moi, *ta, d,* AHO-568
Arabis pendulocarpa A. Nels. var. *pendulocarpa*	**Infr,** dry to moi, *ta, d,* AHO-199 (YELLO)
Arabis pendulocarpa A. Nels. var. *saximontana* Rollins Dorn	**Infr,** dry to moi, *ta, d,* AHO-190 (YELLO)
Descurainia sophia (L.) Webb ex Prantl	**Infr,** dry to moi, *d,* AHO-562
Draba cana Rydb.	**Infr,** dry to moi, *ta* AHO-189 (YELLO)
Draba crassifolia Grah.	**Freq,** moi to wet, *sm* AHO-324 (YELLO)
Draba densifolia Nutt.	**Infr,** dry, *rt,* YELLO-1266
Draba incerta Payson	**Freq,** dry to moi, *ta, rt* AHO-326 (YELLO)
Draba paysonii Macbr. var. *treleassii* (Schulz) Hitchc.	**Rare,** dry to moi, *ta, rt* AHO-186 (YELLO)
Lepidium sp.	**Infr,** dry to moi, *d, tr* AHO-178 (YELLO)
Smelowskia calycina (Steph. ex Willd.) Meyer var. *americana* (Regel & Herder) Drury & Rollins	**Freq,** dry to moi, *all* YELLO-1317
Thlaspi parviflorum A. Nels.	**Infr,** dry to moi, *tr, tu* AHO-176 (YELLO)

Caryophyllaceae

Arenaria congesta Nutt.	**Freq,** moi to wet, *sm, tu, ta* AHO-174 (YELLO)
Arenaria obtusiloba (Rydb.) Fern	**Freq,** moi to wet, *sm, tu, ta* AHO-363 (YELLO)
Arenaria rubella (Wahl.) Smith	**Wide,** dry to wet, *sm, tu, ta* AHO-170 (YELLO)
Cerastium arvense L.	**Freq,** moi to wet, *sm, tu, ta* AHO-546
Lychnis apetala L.	**Freq,** moi to wet, *sm, tu* AHO-165 (YELLO)
Stellaria monantha Hulten	**Freq,** moi to wet, *sm, tu* AHO-161 (YELLO)
Stellaria umbellata Turcz. ex Kar. & Kir.	**Freq,** wet, *sm* YELLO-1026

Chenopodiaceae

Chenopodium rubrum L.	**Rare,** *d* AHO-551

Crassulaceae

Sedum lanceolatum Torrey	**Wide,** dry to wet, *all* AHO-159 (YELLO)
Ericaceae	
Vaccinium scoparium Leiberg ex Cov.	**Infr,** wet, *sm* AHO-560
Vaccinium membranaceum Dougl. ex Torrey	*tr,* wet YELLO-3323
Fabaceae	
Astragalus alpinus L.	**Freq,** dry to wet, *sm, tu* YELLO-1596, 4263
Astragalus australis (L.) Lam.	**Freq,** *tr* YELLO-1587
Astragalus kentrophyta Gray var. *tegetarius* (Wats.) Dorn	**Freq,** dry to moi, *rt, ta* AHO-SWC9
Astragalus miser Dougl.	**Infr,** dry to moi, *tr, tu* AHO-333 (YELLO)
Lupinus argenteus Pursh	**Wide,** dry to moi, *tu, sm* AHO-129 (YELLO)
Oxytropis borealis DC. var. *viscida* (Nutt.) Welsh	**Rare,** dry, *rt* AHO-127 (YELLO)
Oxytropis lagopus Nutt.	**Freq,** dry, *tu, rt* AHO-126 (YELLO)
Oxytropis parryi Gray	**Rare,** dry to moi, *tu* AHO-125 (YELLO)
Fumariaceae	
Corydalis aurea Willd.	**Infr,** dry to moi, *tr* AHO-123 (YELLO)
Gentianiaceae	
Swertia radiata (Kell.) Kutze	**Freq,** dry to moi, *tu, tr* AHO-535
Geraniaceae	
Geranium viscosissimum Fisch. & Meyer ex Meyer	**Infr,** *tr* YELLO-1733
Grossulariaceae	

Ribes montigenum McClatchie		**Infr,** moi, *tr, sm* AHO-118 (YELLO)
	Hydrophyllaceae	
Phacelia hastata Dougl. ex Lehm.		**Freq,** dry to moi, *ta* AHO-SWC-10
Phacelia sericea (Grah. ex Hook.) Gray		**Freq,** dry to moi, *ta* AHO-116 (YELLO)
	Linaceae	
Linum lewisii Pursh		**Freq,** dry to moi, *ta, tu* AHO-561
	Onagraceae	
Epilobium angustifolium L.		**Freq,** dry to moi, *tr* AHO-99 (YELLO)
Epilobium clavatum Trel.		**Infr,** wet, *ta, sm* AHO-540
Epilobium halleanum Hausskn.		**Rare,** wet, *sm* AHO_YELLO-101
	Polemoniaceae	
Phlox multiflora A. Nels.		**Wide,** dry to moi, *tr,* AHO-SWC-11
Phlox pulvinata (Wherry) Cronq.		**Freq,** dry, *rt, tu* AHO-168, 398, 399 (YELLO)
Polemonium pulcherrimum Hook.		**Infr,** dry to moi, rocky *tu, ta* AHO-555
Polemonium viscosum Nutt.		**Infr,** dry to moi, *tu, ta* YELLO-2129
	Polygonaceae	
Eriogonum flavum Nutt.		**Infr,** dry, *rt, tu, tr* YELLO-776
Eriogonum ovalifolium Nutt.		**Infr,** dry, *rt, tu* AHO-65 (YELLO)
Eriogonum umbellatum Torrey		**Freq,** dry to moi, *tr, tu* AHO-64 (YELLO)
Oxyria digyna (L.) Hill		**Infr,** moi, *ta* AHO-552

Polygonum aviculare L.		**Infr,** dry to moi, *d* AHO-62 (YELLO)
Polygonum bistortoides Pursh		**Freq,** dry to moi, *tu,* AHO-SWC12
Polygonum douglasii Greene		**Infr,** dry to moi, *ta, d* AHO-539
Rumex paucifolius Nutt.		**Infr,** dry to moi, *tu* noted, **no voucher**
Rumex salicifolius Weinm.		**Freq,** dry to moi, *d, tr* AHO-58 (YELLO)
	Portulacaceae	
Claytonia lanceolata Pursh		**Infr,** dry to moi, *tu* AHO-553
Lewisia pygmaea (Gray) Robins.		**Freq,** wet to moi, *tu, sm* AHO-368 (YELLO)
Spraguea umbellata Torrey var. *caudicifera* Gray		**Infr,** moi, *ta, d* AHO-545
	Primulaceae	
Androsace septentrionalis L. var. *subulifera* Gray		**Wide,** dry to moi, *all* AHO-542
Dodecatheon conjugens Greene		**Infr,** *tu* YELLO-2017
Dodecatheon pulchellum (Raf.) Merr.		**Freq,** moi to wet, *tu, sm* AHO-51 (YELLO)
	Ranunculaceae	
Aquilegia flavescens Wats.		**Infr,** moi to wet, *tr* YELLO-1062
Delphinium bicolor Nutt.		**Freq,** moi, *tu, tr* AHO-330, 369 (YELLO)
Delphinium nutallianum Pritzel ex Walpers		**Infr,** moi to wet, *tu, tr* AHO-570
Ranunculus eschscholtzii Schlecht.		**Freq,** moi to wet, *ta, sm* AHO-43 (YELLO)
Ranunculus glaberrimus Hook.		**Infr,** *tr* YELLO-1148
	Rosaceae	
Geum triflorum Pursh		**Freq,** dry to moi, *tu, tr* AHO-329, 394 (YELLO)
Potentilla arguta Pursh		**Infr,** dry to moi, *tr* AHO-574
Potentilla diversifolia Lehm.		**Freq,** dry to moi, *tu,* AHO-35, 36 (YELLO)
Potentilla gracilis Dougl. ex Hook.		**Infr,** dry to moi, *tu,* AHO-534
Potentilla ovina Macoun.		**Freq,** dry, *tu, rt* AHO-32 (YELLO)

Sibbaldia procumbens L.	**Freq,** moi to wet, *sm, tu* AHO-74 (YELLO)

Salicaceae

Salix arctica Pallas var. *petraea* Anderss.	**Freq,** wet, *sm* AHO-543
Salix glauca L.	**Rare,** wet, *sm, tr* YELLO-748
Salix reticulata L. var. *nana* Anderss.	**Freq,** wet, *sm* noted, **no voucher**

Saxifragaceae

Heuchera parvifolia Nutt. ex T. & G.	**Infr,** moi, *d, tr* AHO_YELLO-26
Parnassia fimbriata Konig	**Rare,** wet, *tr* YELLO-1385
Saxifraga cespitosa L.	**Rare,** wet, sm YELLO-1565
Saxifraga rhomboidea Greene	**Infr,** dry to moi, *tu* AHO-400, 401, (YELLO)

Scrophulariaceae

Besseya wyomingensis (A. Nels.) Rydb.	**Infr,** dry to moi, *tu* AHO-SWC-14
Castilleja pallescens (Gray) Greenm.	**Infr,** dry to moi, *tu, tr* AHO 323 (YELLO)
Castilleja rhexifolia Rydb.	**Rare,** moi to wet, *tr* YELLO-2301
Mimulus lewisii Pursh	**Rare,** wet, *tr* YELLO-2490
Pedicularis cystopteridifolia Rydb.	**Infr,** wet, *sm* AHO-10 (YELLO)
Penstemon attenuatus Dougl. ex Lindl.	**Infr,** dry to moi, *tu, tr* AHO-6 (YELLO)
Penstemon cyaneus Pennell	**Infr,** *tr* YELLO-2374
Penstemon procerus Dougl. ex Grah.	**Infr,** dry to moi, *tu* AHO-SWC-15
Veronica wormskjoldii R. & S.	**Infr,** wet, *sm* AHO-538 (YELLO)

CONIFEROPHYTA

Cupressaceae

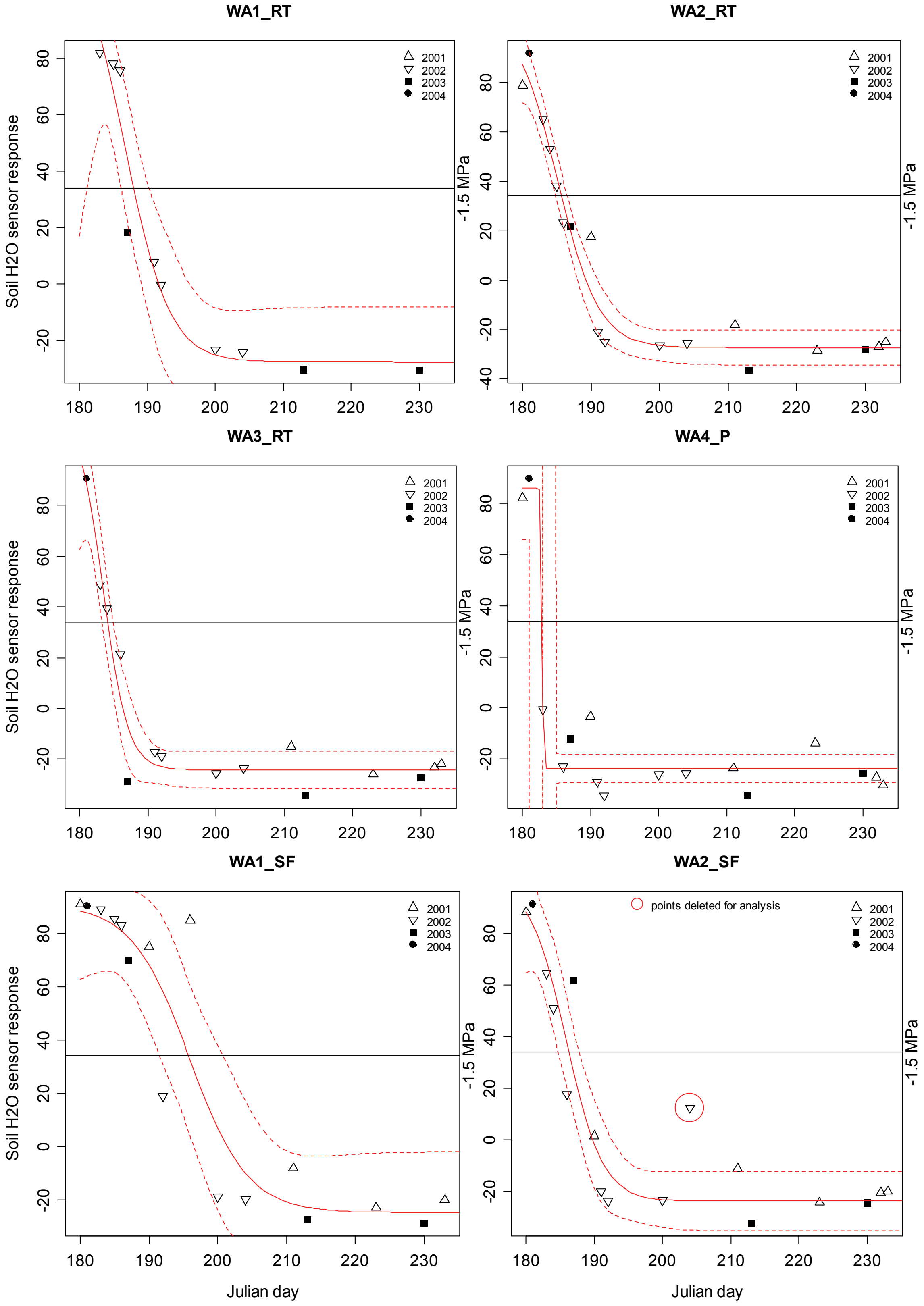
Juniperus communis L. var. *depressa* Pursh	**Infr,** dry to moi, *tr* noted, **no voucher**

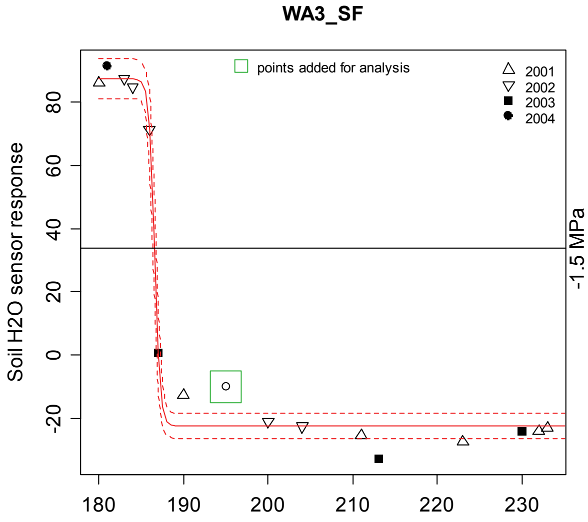
Pinaceae

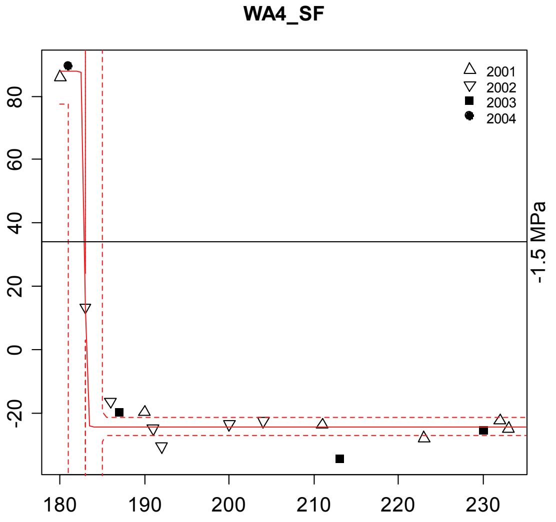
Abies lasiocarpa (Hook.) Nutt.	**Infr,** dry to moi, *tr* YELLO-49
Picea engelmannii Parry ex Engelm.	**Infr,** dry to moi, *tr* AHO-537
Pinus albicaulis Engelm.	**Infr,** dry to moi, *tr* YELLO-56

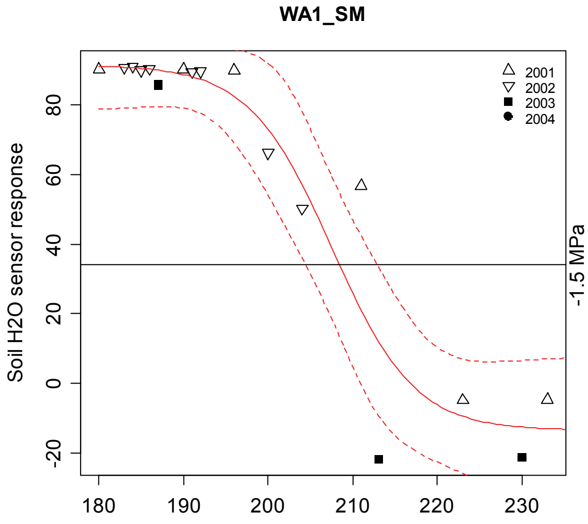
Appendix B.2: Sigmoidal Fits to Soil Water Data at Mt. Washburn Sites

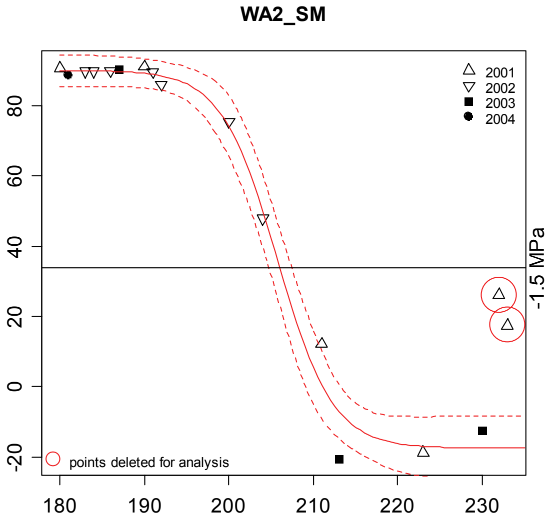
Dotted lines on either side of predicted responses are 95% confidence intervals. Models represent Julian day 175-235. Deleted and extrapolated points are also noted.

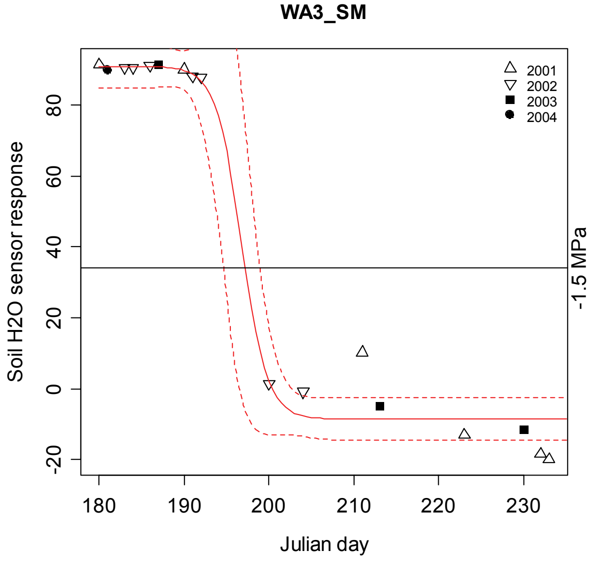

WA1_RT
WA2_RT
WA3_RT
WA4_P
WA1_SF
WA2_SF
Soil H2O sensor response
-1.5 MPa
△ 2001
▽ 2002
■ 2003
● 2004
○ points deleted for analysis
80
60
40
20
0
-20
-40
180
190
200
210
220
230
Julian day

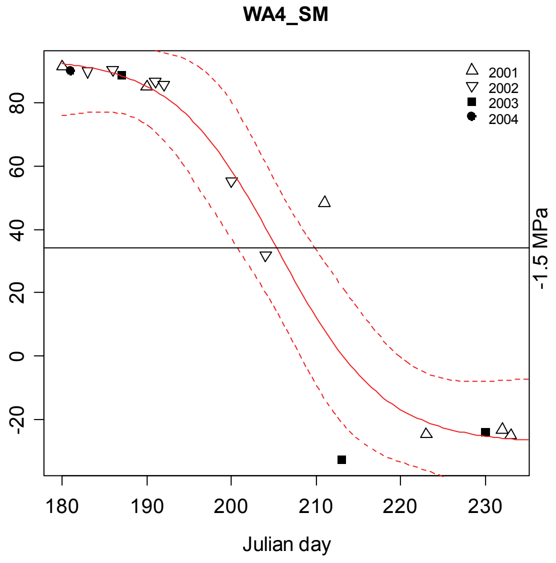

WA3_SF
Soil H2O sensor response
-1.5 MPa
points added for analysis
2001
2002
2003
2004
-20
0
20
40
60
80
180
190
200
210
220
230

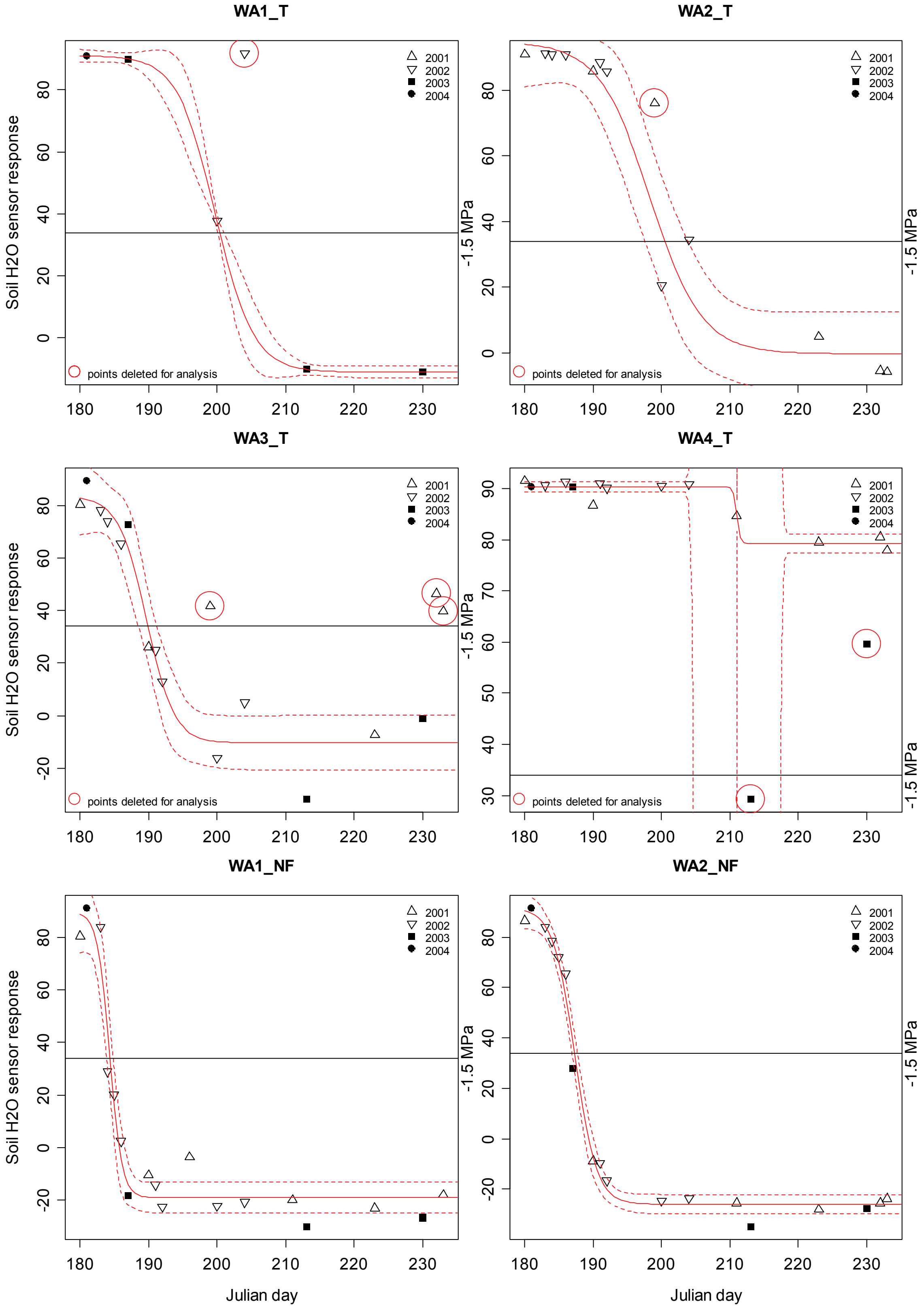

WA4_SF
-1.5 MPa
2001
2002
2003
2004
-20
0
20
40
60
80
180
190
200
210
220
230


WA1_SM
Soil H2O sensor response
-1.5 MPa
2001
2002
2003
2004
-20
0
20
40
60
80
180
190
200
210
220
230


WA2_SM
-1.5 MPa
2001
2002
2003
2004
points deleted for analysis
-20
0
20
40
60
80
180
190
200
210
220
230


WA3_SM
Soil H2O sensor response
-1.5 MPa
2001
2002
2003
2004
-20
0
20
40
60
80
180
190
200
210
220
230
Julian day


WA4_SM
-1.5 MPa
2001
2002
2003
2004
-20
0
20
40
60
80
180
190
200
210
220
230
Julian day


WA1_T
WA2_T
WA3_T
WA4_T
WA1_NF
WA2_NF
Soil H2O sensor response
-1.5 MPa
Julian day
2001
2002
2003
2004
points deleted for analysis
180
190
200
210
220
230
-20
0
20
40
60
80
30
50
70
90

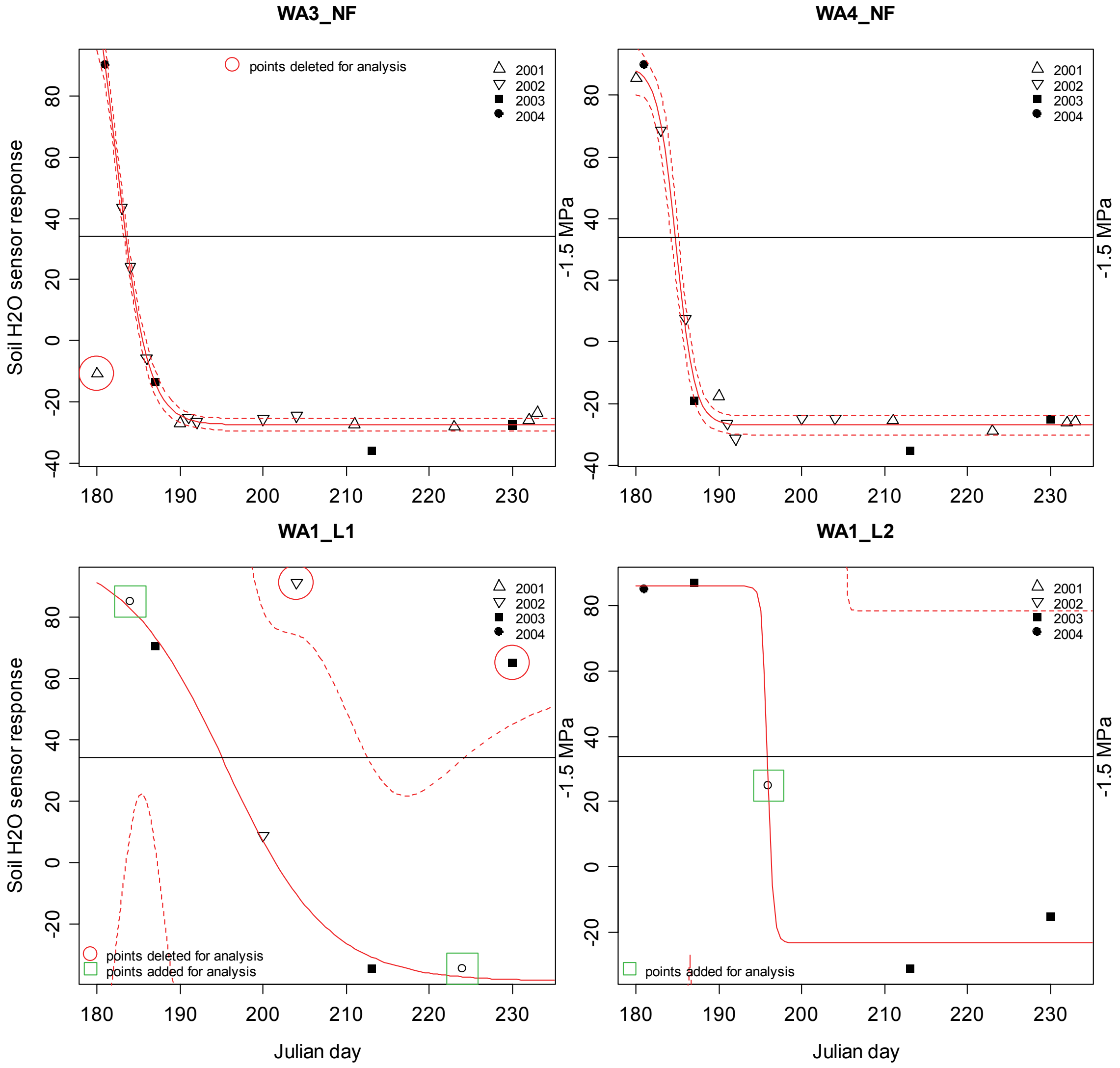

WA3_NF
WA4_NF
WA1_L1
WA1_L2
Soil H2O sensor response
-1.5 MPa
Julian day
points deleted for analysis
points added for analysis
2001
2002
2003
2004
-40
-20
0
20
40
60
80
180
190
200
210
220
230

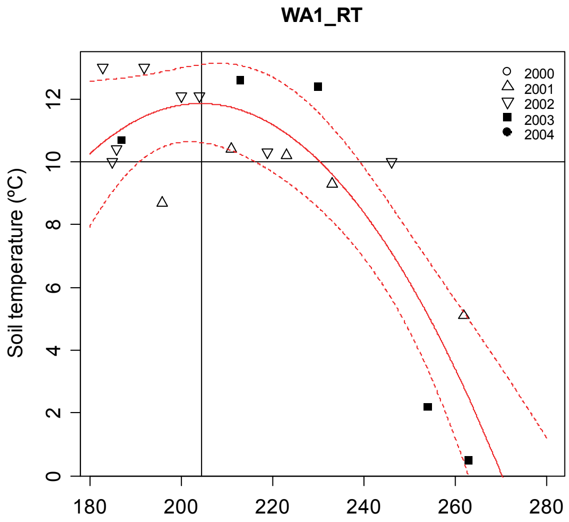
Table B.2.1 Moisture model summary

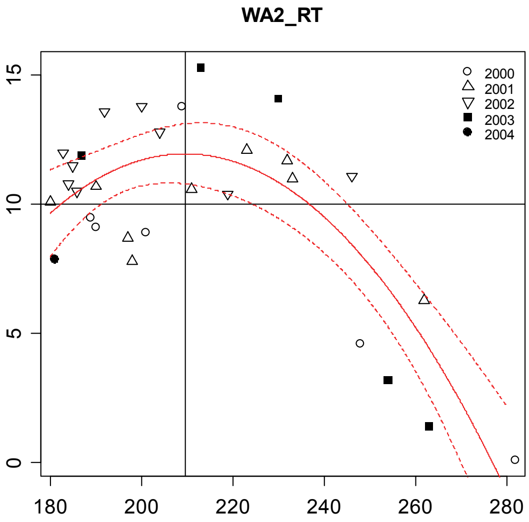
	Julian day that indicated ψ is reached (adjusted model with outliers deleted)				Adjusted model evaluation (with deleted or added points)			Unadjusted model evaluation (without deleted or added points)		
	-0.12Mpa	-0.25Mpa	-1.5Mpa	-2.5Mpa	r^2	Adj. r^2	Model *p*-val.	r^2	Adj. r^2	Model *p*-val.
WA1_RT	183.9	184.9	187.9	188.9	0.94	0.88	<0.001	0.94	0.88	<0.001
WA2_RT	181.1	182.4	185.7	186.6	0.96	0.95	<0.001	0.96	0.95	<0.001
WA3_RT	181.6	182.3	184.1	184.6	0.94	0.92	<0.001	0.94	0.92	<0.001
WA4_P	182.7	182.8	182.9	182.9	0.95	0.94	<0.001	0.95	0.94	<0.001
WA1_SF	186.3	189.7	195.8	197.2	0.87	0.82	<0.001	0.87	0.82	<0.001
WA2_SF	181.6*	183*	186.3*	187.1*	0.92*	0.89*	<0.001*	0.88	0.84	<0.001
WA3_SF	185.7†	186.1†	186.6†	186.7†	0.99†	0.99†	<0.001†	0.66	0.52	0.006
WA4_SF	182.7	182.8	182.9	183	0.99	0.98	<0.001	0.99	0.98	<0.001
WA1_SM	197.3	201.2	208.4	210.3	0.91	0.88	<0.001	0.91	0.88	<0.001
WA2_SM	198.3*	201.1*	206*	207.3*	0.99*	0.98*	<0.001*	0.93	0.91	<0.001
WA3_SM	193.6	194.8	197.2	197.9	0.98	0.98	<0.001	0.98	0.98	<0.001
WA4_SM	193	197.2	205.4	207.4	0.93	0.9	<0.001	0.93	0.9	<0.001
WA1_T	193.9*	196.2*	200.4*	201.6*	1*	1*	<0.001*	0.83	0.13	0.249
WA2_T	191.9*	194.6*	200.5*	202.4*	0.96*	0.94*	<0.001*	0.81	0.72	0.001
WA3_T	183.1*	186.2*	189.9*	190.8*	0.95*	0.93*	<0.001*	0.72	0.63	<0.001
WA4_T	211.7*	NA*	NA*	NA*	0.94*	0.91*	<0.001*	NA	NA	NA
WA1_NF	182.2	183	184.4	184.7	0.96	0.94	<0.001	0.96	0.94	<0.001
WA2_NF	183.8	185.1	187.3	187.8	0.99	0.99	<0.001	0.99	0.99	<0.001
WA3_NF	181.5*	181.9*	183.5*	184*	0.99*	0.99*	<0.001*	0.69	0.59	0.001
WA4_NF	182.1	183.1	184.7	185.1	0.99	0.99	<0.001	0.99	0.99	<0.001
WA1_L1	185*†	188.1*†	195*†	196.8*†	1*†	0.99*†	0.004*†	NA	NA	NA
WA1_L2	194.9†	195.3†	195.9†	196†	0.99†	0.96†	0.016†	NA	NA	NA
Average	**188.1**	**188.7**	**191.9**	**192.8**	**0.96**	**0.94**	**<0.001**	**0.89**	**0.82**	**0.014**

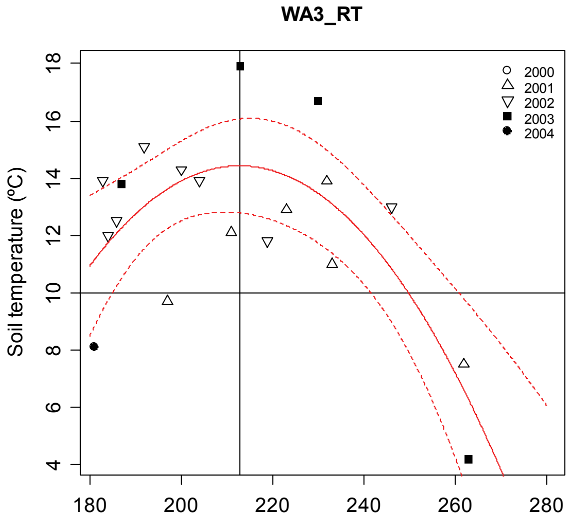
*Outlier points deleted from model, †Points added to model at data gaps

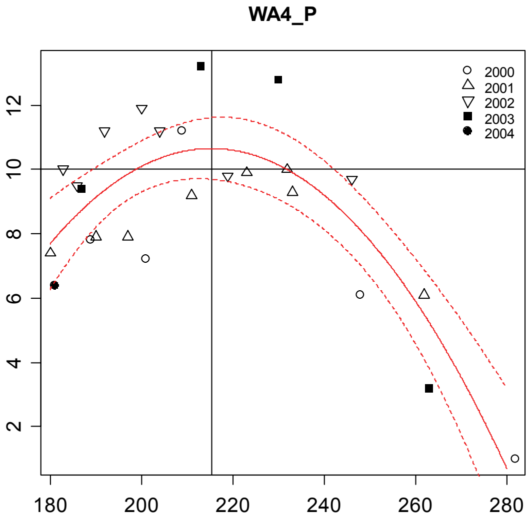
Appendix B.3: Quadratic Fits to Soil Temperature Data at Mt. Washburn Sites

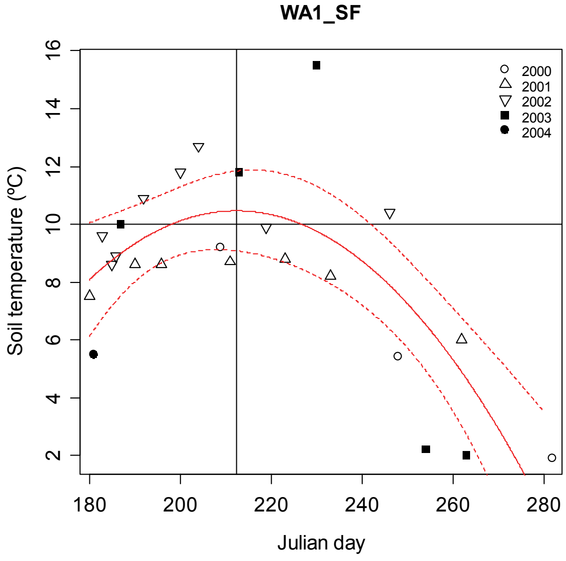
Dotted lines on either side of predicted responses are 95% confidence intervals. Models represent Julian day 180-280.

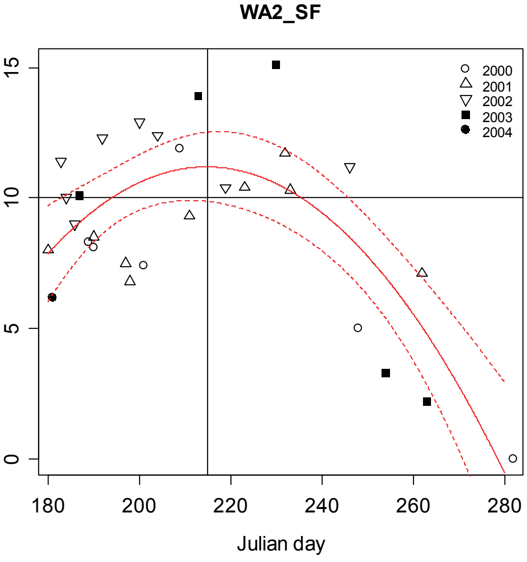

WA1_RT
Soil temperature (ºC)
0
2
4
6
8
10
12
180
200
220
240
260
280
2000
2001
2002
2003
2004

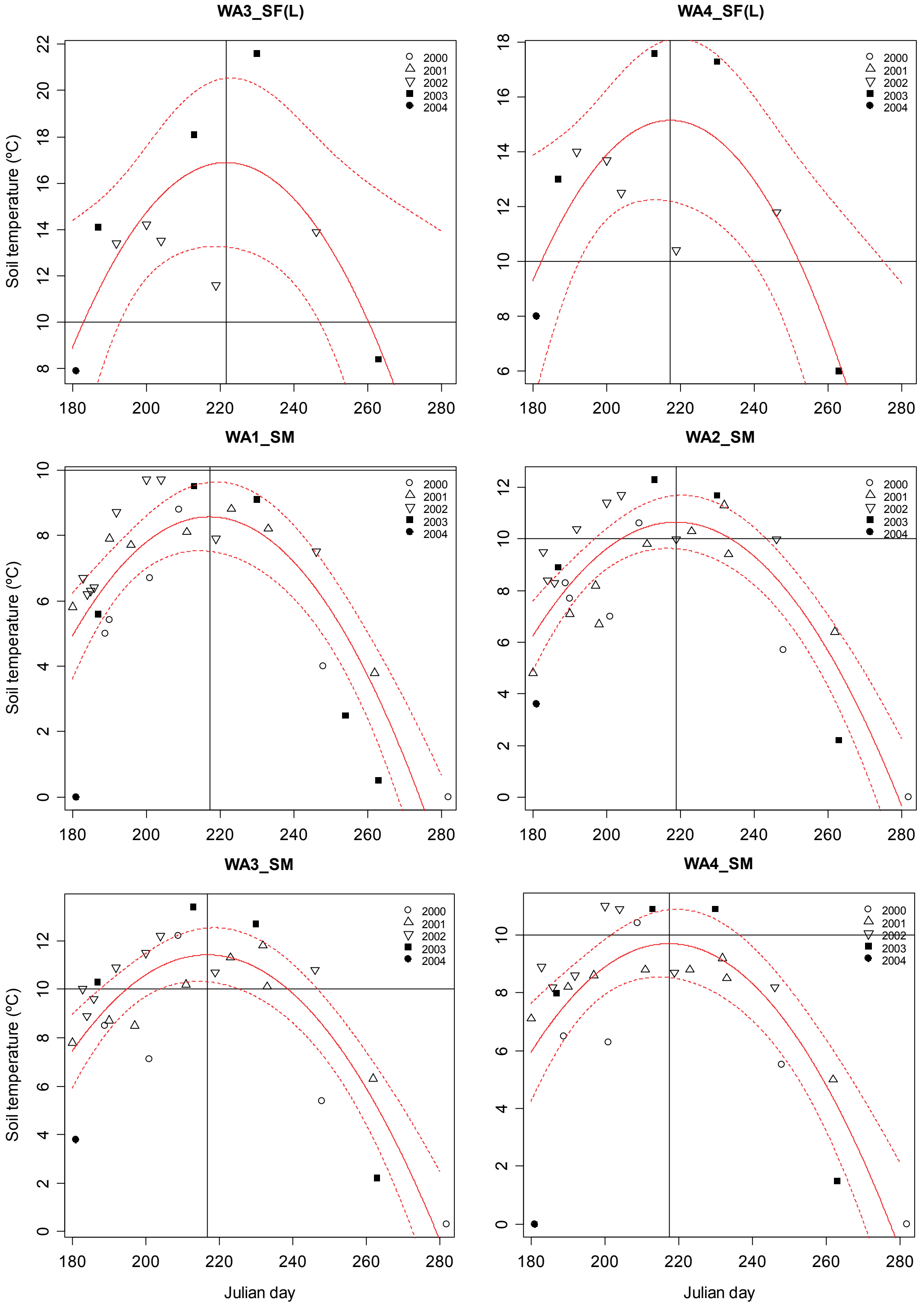

WA2_RT
0
5
10
15
180
200
220
240
260
280
2000
2001
2002
2003
2004

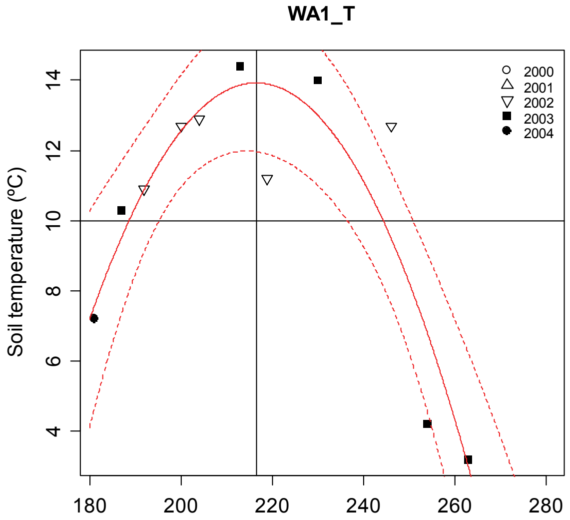

WA3_RT
Soil temperature (ºC)
4
6
8
10
12
14
16
18
180
200
220
240
260
280
2000
2001
2002
2003
2004

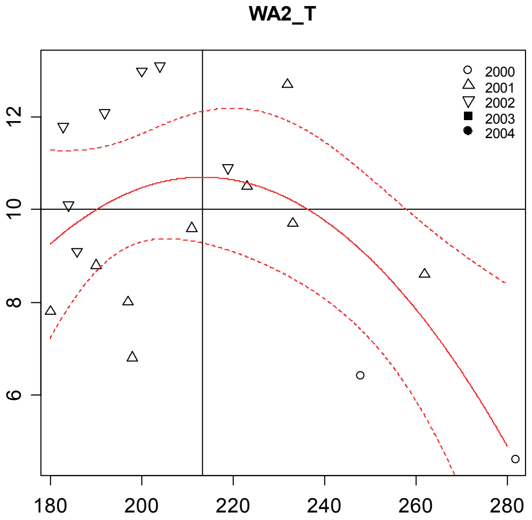

WA4_P
2
4
6
8
10
12
180
200
220
240
260
280
2000
2001
2002
2003
2004

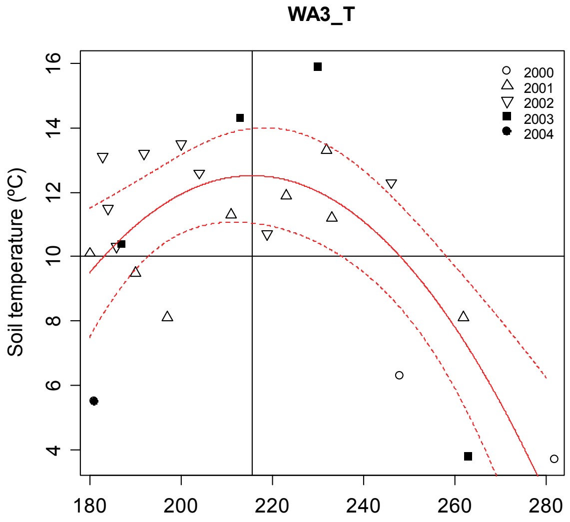

WA1_SF
Soil temperature (ºC)
2
4
6
8
10
12
14
16
180
200
220
240
260
280
Julian day
2000
2001
2002
2003
2004

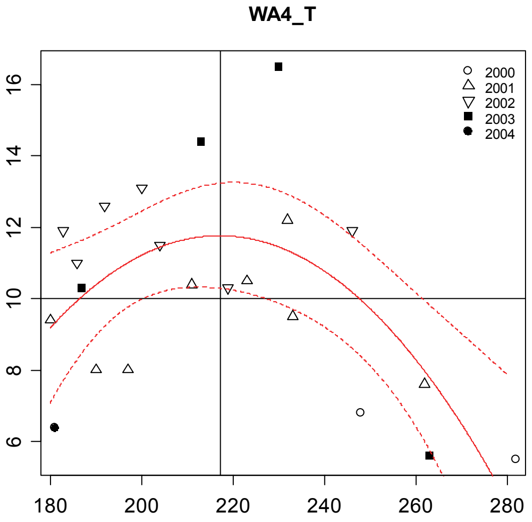

WA2_SF
0
5
10
15
180
200
220
240
260
280
Julian day
2000
2001
2002
2003
2004

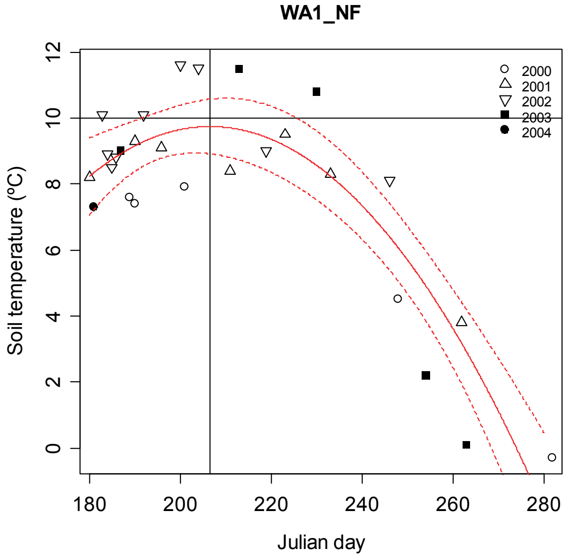

WA3_SF(L)
WA4_SF(L)
WA1_SM
WA2_SM
WA3_SM
WA4_SM
Soil temperature (ºC)
Julian day
180
200
220
240
260
280
2000
2001
2002
2003
2004

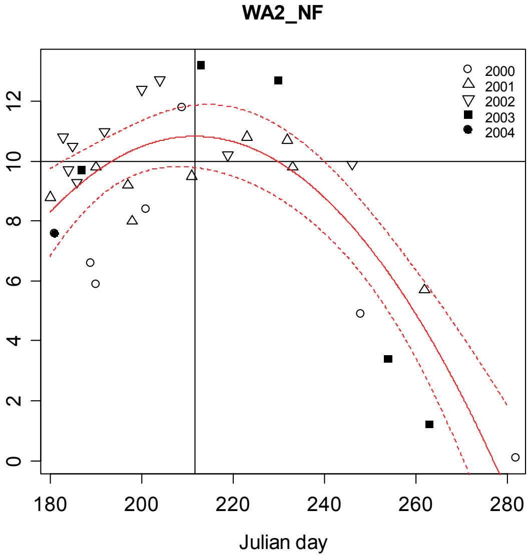

WA1_T
Soil temperature (°C)
4
6
8
10
12
14
180
200
220
240
260
280
2000
2001
2002
2003
2004


WA2_T
6
8
10
12
180
200
220
240
260
280
2000
2001
2002
2003
2004


WA3_T
Soil temperature (°C)
4
6
8
10
12
14
16
180
200
220
240
260
280
2000
2001
2002
2003
2004


WA4_T
6
8
10
12
14
16
180
200
220
240
260
280
2000
2001
2002
2003
2004


WA1_NF
Soil temperature (°C)
0
2
4
6
8
10
12
180
200
220
240
260
280
Julian day
2000
2001
2002
2003
2004


WA2_NF
0
2
4
6
8
10
12
180
200
220
240
260
280
Julian day
2000
2001
2002
2003
2004

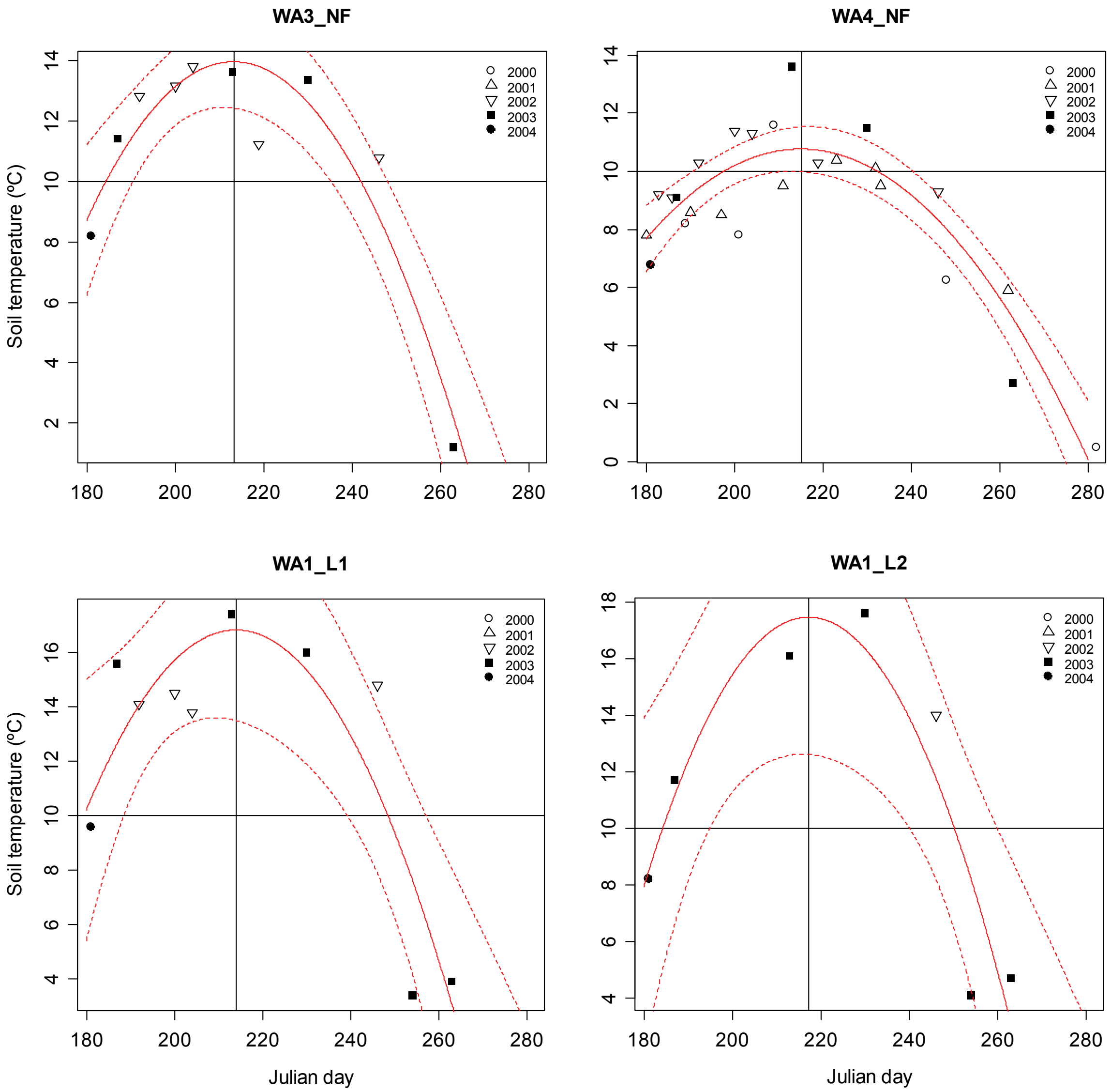

WA3_NF
WA4_NF
WA1_L1
WA1_L2
Soil temperature (ºC)
Julian day
○ 2000
△ 2001
▽ 2002
■ 2003
● 2004
180
200
220
240
260
280
0
2
4
6
8
10
12
14
16
18

Table B.3.1. Summary of temperature fit models.

	Obs. maximum temp.	Pred. maximum temp. ± 95%ci	Pred. max. day (Julian)	Heatsum	Days above 10ºC	r^2	Model *p*-val.
WA1_RT	13.0	11.9 ± 2.5	204.4	64.5	51.4	0.75	<0.001
WA2_RT	15.3	12 ± 2.3	209.7	71.4	55.4	0.65	<0.001
WA3_RT	17.9	14.4 ± 3.3	212.9	216.5	70.7	0.54	<0.001
WA4_P	13.2	10.7 ± 1.9	215.4	14.4	34.0	0.69	<0.001
WA1_SF	15.5	10.5 ± 2.8	212.5	8.8	29.5	0.57	<0.001
WA2_SF	15.1	11.2 ± 2.6	214.9	32.9	42.5	0.57	<0.001
WA3_SF	21.6	16.9 ± 7.3	221.8	354.7	78.1	0.53	0.017
WA4_SF	17.6	15.2 ± 5.9	217.4	240.0	70.8	0.60	0.009
WA1_SM	9.7	8.6 ± 2.1	217.3	0.0	0.0	0.66	<0.001
WA2_SM	12.3	10.7 ± 2.1	218.9	13.1	30.8	0.69	<0.001
WA3_SM	13.4	11.4 ± 2.2	216.9	41.5	44.8	0.70	<0.001
WA4_SM	11.0	9.7 ± 2.3	217.5	0.0	0.0	0.64	<0.001
WA1_T	14.4	13.9 ± 3.9	216.6	145.7	56.6	0.82	<0.001
WA2_T	13.1	10.7 ± 2.8	213.4	21.7	47.2	0.38	0.006
WA3_T	15.9	12.5 ± 2.9	215.7	109.0	65.8	0.53	<0.001
WA4_T	16.5	11.8 ± 2.9	217.2	72.1	62.1	0.41	0.001
WA1_NF	11.6	9.7 ± 1.7	206.7	0.0	0.0	0.78	<0.001
WA2_NF	13.2	10.8 ± 2.1	211.8	20.0	37.1	0.67	<0.001
WA3_NF	13.8	14 ± 3.1	213.3	152.6	58.6	0.89	<0.001
WA4_NF	13.6	10.8 ± 1.5	215.1	17.8	35.8	0.80	<0.001
WA1_L1	17.4	16.8 ± 6.7	214.1	314.4	69.4	0.77	<0.001
WA1_L2	17.6	17.5 ± 9.7	217.4	328.4	66.9	0.84	0.004
Average	**14.7**	**12.4 ± 3.4**	**214.6**	**101.8**	**45.8**	**0.66**	**0.002**

Appendix B.4: Classification Pruning Analysis for Chapter 3

Seven evaluators were used for pruning analysis of classification solutions: Average silhouette width (ASW, Rousseeuw 1987)[*], C-index (Hubert and Levin 1975), Gamma (Goodman and Kruskal 1954), Indicator species analysis (ISA) average p-value, and number of ISA significant indicators at α = 0.05 (Dufrêne and Legendre 1997), Partition analysis ratio (PARTANA, Roberts 2005), and point-biserial correlation (PBC, Brogden 1949). These classification validation measures are described in Chapter 7. Their uses in pruning analysis are described in Aho (2006). Evaluator responses were expressed as the residuals of linear regressions of evaluator responses vs. number of clusters (see Aho 2006), i.e. standardized responses were detrended with respect to a linear regression.

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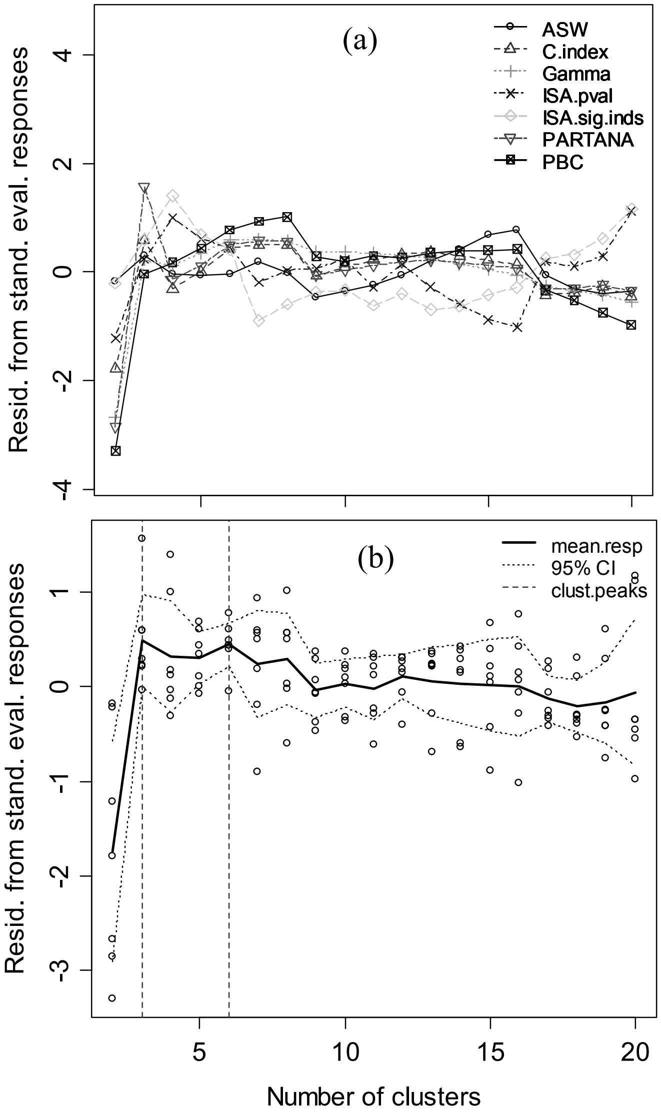
[*] For bibliographic information on Appendix B see the Chapter 3 literature cited section.



Residuals from standardized responses

	Max cluster	Min cluster
ASW	16	5
ISAMIC	3	3
C.index	6	2
Gamma	6	2
ISA.pval	20	3
ISA.sig.inds	4	30
PARTANA	3	3
PBC	8	2
AVERAGE	3, 6	2

Figure B.4.1. Pruning analysis. (a) Individual evaluator responses. (b) Average evaluator response. Average optima across all evaluators are suggested by vertical dashed lines. Best (maximum) and worst (minimum) pruning levels for the seven evaluators are noted in the table below the figure.

APPENDIX C

APPENDICES PERTAINING TO CHAPTER 4--
ALPINE COMMUNITIES OF THE ABSAROKA VOLCANICS

Appendix C.1: Classification Pruning Analysis for Chapter 4

Six evaluators were used for pruning analysis of classification solutions: Average silhouette width (ASW, Rousseeuw 1987)[*], C-index (Hubert and Levin 1975), Indicator species analysis (ISA) average *p*-value, and number of ISA significant indicators at α =0.05 (Dufrêne and Legendre 1997), Partition analysis ratio (PARTANA, Roberts 2005), and point-biserial correlation (PBC, Brogden 1949). These classification validation measures are well described in Chapter 7. In Figs C.1.1- C.1.4 evaluator responses were expressed as the residuals of linear regressions of evaluator responses vs. number of clusters (see Aho 2006), i.e. standardized responses were detrended with respect to a linear regression. Average optima across all evaluators are suggested by vertical dashed lines. Best (maximum) and worst (minimum) pruning levels for six evaluators are noted in tables to the right of figures. ISA evaluators (particularly ISA *p*-value) were emphasized over other methods since we desired effective indicator species over compact clusters (see Aho et al. 2006). Raw (non-standardized and non-detrended) ISA responses are listed in Table 4.A1.

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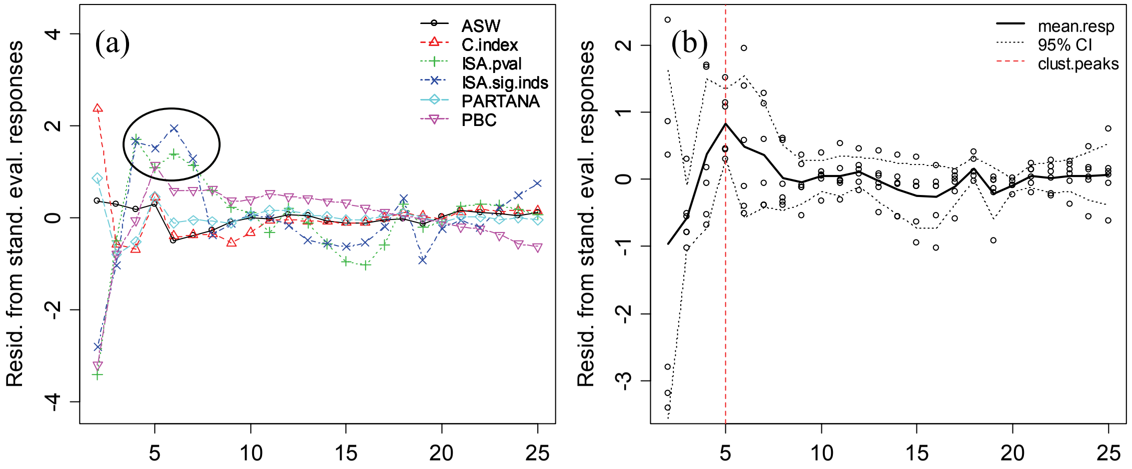
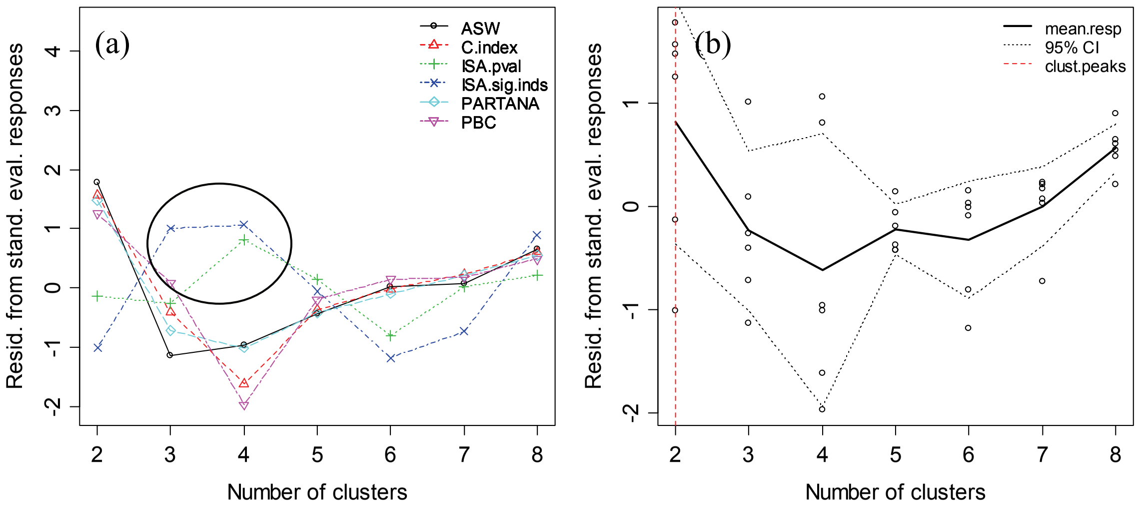
[*] For Appendix C bibliographic information see the Chapter 4 literature cited section.



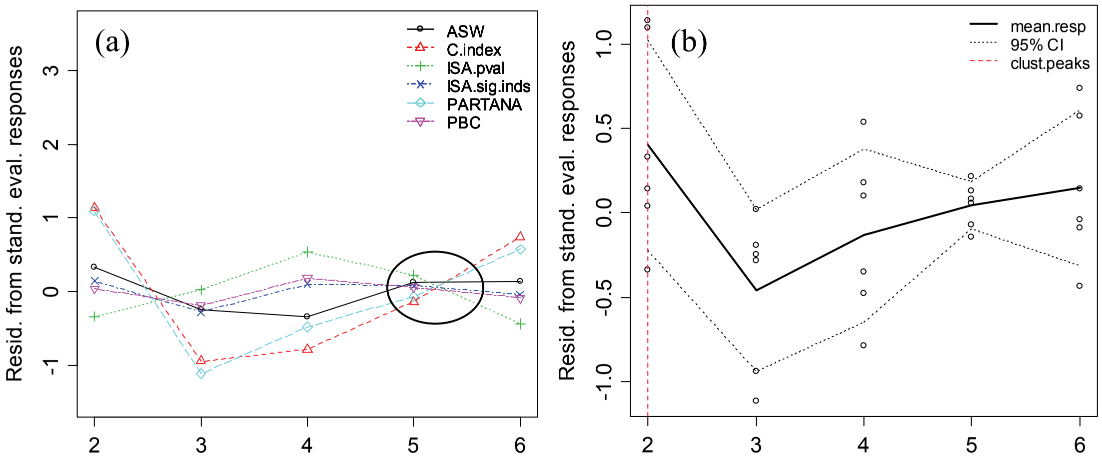
	Max.clust	Min.clust
ASW	2	6
C.index	2	4
ISA.pval	4	2
ISA.sig.inds	6	2
PARTANA	2	3
PBC	5	2
AVG.	5	2

Figure C.1.1. All sites. (a) Individual evaluator responses. (b) Average evaluator response. Four clusters was chosen as the optimal solution. Most evaluators favored solutions in the 4-6 cluster range. ISA p-values best at four clusters.



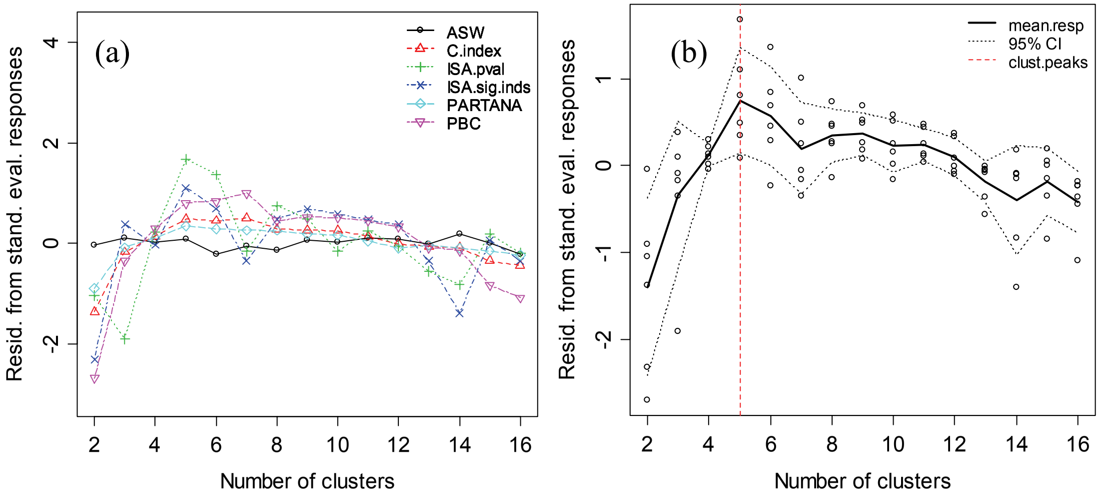
	Max.clust	Min.clust
ASW	2	3
C.index	2	4
ISA.pval	4	6
ISA.sig.inds	4	6
PARTANA	2	4
PBC	2	4
AVG.	2	4

Figure C.1.2. Talus. (a) Individual evaluator responses. (b) Average evaluator response Four classes chosen as optimum. Note ISA evaluators are being favored over other strategies.



	Max.clust	Min.clust
ASW	2	4
C.index	2	3
ISA.pval	4	6
ISA.sig.inds	2	3
PARTANA	2	3
PBC	4	3
AVG.	2	3

Figure C.1.3. Snowmelt sites. (a) Individual evaluator responses. (b) Average evaluator response. A five cluster solution was chosen as the optimal solution. No evaluator disliked this solution. Non-detrended ISA-*p*-values were best at this solution (Table 4.A1).



	Max.clust	Min.clust
ASW	14	6
C.index	7	2
ISA.pval	5	3
ISA.sig.inds	5	2
PARTANA	5	2
PBC	7	2
AVG.	5	2

Figure C.1.4. Turf. Optimum five classes. (a) Individual evaluator responses. (b) Average evaluator response

Table C.1.1. Indicator species analysis results for optimal pruning of classification (Dufrêne and Legendre 1997). Bold numbers indicate optimal solutions.

All data			Talus data			Snowmelt data			Turf/ ridgetop data		
# of classes	avg. P-val	# of significant ind. spp.	# of classes	avg. P-val	# of significant ind. spp.	# of classes	avg. p-val	# of significant ind. spp.	# of classes	avg. p-val	# of significant ind. spp.
2	0.67	8	2	0.58	5	2	0.76	7	2	0.38	15
3	0.31	27	3	0.46	9	3	0.63	9	3	0.30	29
4	**0.18**	**59**	**4**	**0.42**	**11**	4	0.49	16	4	0.30	30
5	0.22	52	5	0.45	11	**5**	**0.40**	**23**	**5**	**0.24**	**32**
6	0.19	56	6	0.49	10	6	0.41	24	6	0.25	31
7	0.20	53	7	0.47	10	7	group with 1 member		7	0.27	31

Appendix C.2: North Absaroka Indicator Species Analysis

Table C.2.1. Indicator species analysis results (Dufrêne and Legendre 1997). Significant results ($\alpha = 0.05$) are indicated with asterisks[1]. P-values are the result of tests of the hypothesis of no association between indicator value for a particular and its "maximum group".

	4 groups			**15 groups**		
species	Max grp	indicator value (IV)	p - value	Max grp	indicator value (IV)	p - value
Achillea millefolium	TURF	21.9	0.002**	CAEL_PHMU	19.3	0.145
Agoseris aurantiaca	SNOWMELT	11.1	0.29	CAPA_AGVA	33.3	0.042*
Agoseris glauca v. *dasy.*	SNOWMELT	12	0.067	CAPA_AGVA	19.7	0.157
Agoseris glauca v. *laciniata*	LEDGE	7.3	0.002**	ELSC_CIEA	10.1	0.501
Agrostis variabilis	SNOWMELT	66.4	0.052*	CAPA_AGVA	58.6	0.004**
All mosses	SNOWMELT	74.6	0.119	CAPA_ARSC	43.5	0.008**
Androsace septentrionalis	TURF	35	0.011*	RAES_ASFO	34.1	0.016*
Anemone tetonensis	TALUS	2.3	0.002**	ELSC_CIEA	14.3	0.374
Antennaria lanata	SNOWMELT	5.6	0.042*	CAPA_AGVA	16.7	0.317
Antennaria media	SNOWMELT	41.6	0.204	CAPA_AGVA	37.9	0.02*
Antennaria microphylla	TURF	10.7	0.225	CASC_CAPH	23.7	0.183
Antennaria umbrinella	TURF	20.8	0.2	CAEL_PHMU	28.7	0.048*
Arabis spp. (all)	TALUS	24.3	1	EPCL_ARABIS	13.9	0.28
Arenaria congesta	TURF	22.4	0.014*	CAEL_PHMU	34.7	0.03*
Arenaria obtusiloba	TURF	53.2	0.06	CASC_CAPH	31.9	0.036*
Arenaria rubella	TURF	2	<0.001***	ERCO_ASKE	5.2	0.907
Arnica sp. (*diversifolia*?)	LEDGE	6.9	0.002**	ELSC_CIEA	10.6	0.509
Arnica latifolia	SNOWMELT	5.6	0.034*	CAPA_AGVA	16.7	0.319
Arnica rydbergii	LEDGE	98.7	0.025*	ARRY_EPCL	93.4	<0.001***
Artemisia scopulorum	SNOWMELT	45.3	0.268	CAPA_ARSC	57.8	0.007**
Aster alpigenus	SNOWMELT	38.9	0.58	ASAL_SIPR	59.7	0.002**
Aster foliaceus v. *apricus*	TURF	12.2	<0.001***	RAES_ASFO	49.9	0.009**
Astragalus alpinus	TURF	10.4	0.05*	CAAL	72.8	<0.001***
Astragalus kentrophyta	TURF	82.4	0.245	ERCO_ASKE	29.8	0.004**
Besseya wyomingensis	TURF	9	0.006**	CASC_CAPH	13.4	0.317
Botrychium sp.	TALUS	2.3	0.268	ELSC_ERCO	7.1	1
Carex albonigra	TURF	10.5	0.34	CAAL	100	<0.001***
Carex atrata v. erecta	SNOWMELT	5.6	0.115	CAPA_AGVA	16.7	0.319
Carex elynoides	TURF	10.5	0.004**	CAEL_PHMU	50	0.002**
Carex haydeniana	SNOWMELT	39.3	0.465	RAPY_CAHA	63.8	0.005**
Carex paysonis	SNOWMELT	66.1	0.183	CAPA_ARSC	47.9	0.014*
Carex phaeocephala	TURF	24.5	0.795	CASC_CAPH	63.2	0.002**
Carex pyrenaica	SNOWMELT	22.2	0.006**	CAPA_AGVA	37.7	0.035*
Carex scirpoidea	TURF	5.3	0.034*	CASC_CAPH	33.3	0.064
Castilleja pulchella	TURF	10.5	<0.001***	CAAL	100	<0.001***
Cerastium arvense	TURF	48.8	0.361	ERCO_ASKE	26.8	0.06
Cirsium eatonii	LEDGE	18.4	0.321	ELSC_CIEA	82.1	<0.001***
Claytonia megarhiza	TALUS	9.1	0.248	ELSC_ERCO	9.9	0.523
Cystopteris fragilis	LEDGE	20	0.002**	ARRY_EPCL	20	0.159
Deschampsia cespitosa	SNOWMELT	35.3	0.29	CAPA_AGVA	64.9	0.009**
Dodecatheon pulchellum	SNOWMELT	11.1	0.067	CAPA_ARSC	23.8	0.168
Draba crassifolia	SNOWMELT	9.4	0.002**	EPCL_ARABIS	8.2	0.631
Draba globosa	TURF	5.3	0.052*	CAEL_PHMU	10.9	0.522
Draba incerta	TURF	10.6	0.119	CASC_CAPH	36.1	0.018*
Draba lonchocarpa	TALUS	2.3	0.011*	SABR_POVI	7.1	1
Elymus scribneri	TALUS	36.2	0.002**	ELSC_CIEA	27.2	0.004**

Table C.2.1 cont.

species	Max grp	indicator value (IV)	p - value	Max grp	indicator value (IV)	p - value
Epilobium anagallidifolium	SNOWMELT	14.5	0.042*	CAPA_AGVA	39.7	0.016*
Epilobium clavatum	LEDGE	47.6	0.204	ARRY_EPCL	18.9	0.175
Erigeron compositus	TURF	41.1	0.225	ERCO_ASKE	52.7	<0.001***
Erigeron humilis	SNOWMELT	14.3	0.2	RAPY_CAHA	87.9	<0.001***
Erigeron simplex	TURF	33.6	1	CAPA_ARSC	27.6	0.037*
Erigeron ursinus	SNOWMELT	5.6	0.014*	CAPA_AGVA	16.7	0.319
Eriogonum ovalifolium	TURF	2.6	0.06	ERCO_ASKE	7.1	1
Festuca brachyphylla	SNOWMELT	48.6	<0.001***	RAPY_CAHA	33.1	0.002**
Geum rossii	SNOWMELT	9.9	0.002**	GERO_SAAR	39.8	0.019*
Hieracium gracile	SNOWMELT	5.6	0.034*	GERO_SAAR	25	0.135
Juncus drummondii	SNOWMELT	19.4	0.025*	CAPA_AGVA	34.1	0.04*
Juncus mertensianus	SNOWMELT	5.6	0.268	CAPA_AGVA	16.7	0.319
Juncus parryi	SNOWMELT	5.2	0.58	CAPA_AGVA	15.8	0.297
lichen	SNOWMELT	8.6	<0.001***	ASAL_SIPR	83.2	<0.001***
Lewisia pygmaea	SNOWMELT	22.2	0.05*	CAPA_AGVA	46.8	0.002**
Lloydia serotina	SNOWMELT	7.3	0.245	CAAL	35.2	0.07
Lomatium cous	TURF	17.5	0.006**	CAAL	29	0.032*
Lupinus argenteus	SNOWMELT	3.3	0.268	CAPA_AGVA	10.1	0.481
Luzula spicata	SNOWMELT	36.2	0.34	CAPA_ARSC	19.5	0.134
Luzula wahlenbergii	SNOWMELT	11.1	0.115	CAPA_AGVA	33.3	0.087
Mertensia alpina	TURF	39.3	0.004**	CAAL	29.5	0.042*
Myosotis alpestris	TURF	5.9	0.465	CAAL	37.8	0.046*
Oxyria digyna	SNOWMELT	7.7	0.183	RAPY_CAHA	81.1	<0.001***
Penstemon montanus	SNOWMELT	5.6	0.795	CAPA_AGVA	16.7	0.325
Penstemon procerus	TURF	4.3	0.714	CAEL_PHMU	20	0.16
Phacelia hastata	TALUS	5.3	0.488	ELSC_CIEA	10.4	0.48
Phacelia sericea	TURF	2.6	0.608	ERCO_ASKE	7.1	1
Phleum alpinum	SNOWMELT	11.1	0.043*	CAPA_AGVA	33.3	0.091
Phlox multiflora	TURF	21.5	0.014*	CAEL_PHMU	49.6	0.009**
Phlox pulvinata	TURF	7.9	0.161	ERCO_ASKE	21.4	0.118
Phyllodoce glanduliflora	SNOWMELT	16.7	0.019*	CAPA_AGVA	50	0.002**
Pinus albicaulis	SNOWMELT	3.3	0.68	CAPA_ARSC	13	0.379
Poa alpina	TURF	29.5	0.038*	CAAL	29.5	0.04*
Poa cusickii	SNOWMELT	14.9	0.071	GERO_SAAR	38.9	0.053*
Poa interior	TALUS	3.2	0.735	ELSC_CIEA	8.2	0.662
Poa leptocoma	SNOWMELT	16.7	0.017*	RAPY_CAHA	91.2	<0.001***
Poa pattersonii	TURF	30.6	0.073	CAEL_PHMU	17.9	0.167
Poa reflexa	SNOWMELT	18	0.02*	CAPA_ARSC	36	0.019*
Poa rupicola	TURF	23.6	0.01*	CAAL	26.8	0.097
Poa secunda	TURF	28.4	0.023*	ERCO_ASKE	27.2	0.06
Polemonium pulcherrimum	TALUS	2.3	1	ELSC_ERCO	7.1	1
Polemonium viscosum	TALUS	20.5	0.025*	SABR_POVI	15.8	0.306
Polygonum bistortoides	TURF	9.6	0.261	ASAL_SIPR	45.3	0.011*
Polygonum douglasii	TURF	5.3	0.312	ERCO_ASKE	14.3	0.332
Polygonum viviparum	SNOWMELT	11.1	0.023*	CAPA_AGVA	33.3	0.084
Potentilla diversifolia	SNOWMELT	22.4	0.046*	CAPA_ARSC	18.9	0.224
Potentilla ovina	TURF	13.2	0.064	CAAL	41.6	0.055
Potentilla rubricaulis	TURF	2.6	0.609	CAEL_PHMU	12.5	0.435
Ranunculus pygmaeus	SNOWMELT	11.1	0.035*	RAPY_CAHA	100	<0.001***
Ranunculus eschscholtzii	SNOWMELT	16	0.114	CAPA_ARSC	14.8	0.32
Sagina saginoides	SNOWMELT	11.1	0.039*	CAPA_ARSC	50	0.008**
Salix arctica	SNOWMELT	65.2	<0.001***	GERO_SAAR	85.8	<0.001***
Salix reticulata	SNOWMELT	13.5	0.053*	ASAL_SIPR	83.8	0.002**

Table C.2.1 cont.

species	Max grp	indicator value (IV)	p - value	Max grp	indicator value (IV)	p - value
Saxifraga adscendens	SNOWMELT	5.6	0.244	CAPA_ARSC	25	0.152
Saxifraga bronchialis	TALUS	9.6	0.287	SABR_POVI	16.4	0.284
Saxifraga cespitosa	TURF	2.6	0.615	CAAL	25	0.147
Saxifraga occidentalis	SNOWMELT	21	0.015*	CAPA_ARSC	17.4	0.326
Saxifraga oppositifolia	TURF	2.6	0.588	CAAL	25	0.142
Saxifraga rhomboidea	TURF	10.5	0.048*	CAEL_PHMU	50	0.002**
Saxifraga rivularis	SNOWMELT	11.1	0.035*	RAPY_CAHA	100	<0.001***
Sedum integrifolium	SNOWMELT	11.1	0.041*	CAPA_ARSC	50	0.007**
Sedum lanceolatum	TURF	68.3	<0.001***	CAEL_PHMU	28.1	0.044*
Selaginella densa	TURF	23.8	0.016*	CASC_CAPH	29.7	0.037*
Senecio canus	TURF	20.2	0.02*	ERCO_ASKE	30.5	0.039*
Senecio fremontii	TALUS	15.7	0.082	RAES_ASFO	19.2	0.147
Senecio werneriifolius	TURF	15.6	0.037*	ERCO_ASKE	13.3	0.334
Sibbaldia procumbens	SNOWMELT	63.4	<0.001***	CAPA_AGVA	36	0.015*
Silene acaulis	TURF	39.6	0.002**	CASC_CAPH	38.9	0.021*
Smelowskia calycina	TURF	31.5	0.003**	CAEL_PHMU	28.1	0.058
Stellaria monantha	SNOWMELT	36.3	0.002**	RAPY_CAHA	27.9	0.052*
Stellaria umbellata	SNOWMELT	14.3	0.032*	CAPA_AGVA	23.6	0.08
Taraxacum ceratophorum	SNOWMELT	3	0.727	CAPA_AGVA	9.4	0.604
Taraxacum laevigatum	TURF	3.5	0.75	CAPA_ARSC	11.2	0.41
Trisetum spicatum	TURF	59	<0.001***	CAEL_PHMU	26.5	0.058
Veronica wormskjoldii	SNOWMELT	38.1	0.002**	CAPA_AGVA	96.1	<0.001***
Viola adunca	SNOWMELT	5.6	0.268	CAPA_AGVA	16.7	0.319
Viola spp.	SNOWMELT	5.6	0.253	CAPA_AGVA	16.7	0.293

[1] Signif. codes: "***"≤ 0.001 "**"≤ 0.01 "*"< 0.05. P values based on 1000 permutations.

APPENDIX D

APPENDICES PERTAINING TO CHAPTER 5:

LOCAL AND REGIONAL VARIATION IN ALPINE VEGETATION

Appendix D.1: Code names for plant species found in plots in the study area. The first 4 letters of the code refer to the family name while the next 4 letters refer to the genus and species, e.g. ApiaLOCO = Apiaceae *Lomatium cous*.

#	code	Species name	#	code	Species name	#	code	Species name	#	code	Species name
1	AsteACMI	*Achillea millefolium*	46	CyprCARU	*Carex rupestris*	91	ApiaLOCO	*Lomatium cous*	136	RosePORU	*Potentilla rubricaulis*
2	AsteAGAR	*Agoseris aurantiaca*	47	CyprCASC	*Carex scirpoidea.*	92	FabaLUAR	*Lupinus argenteus*	137	RannRAPY	*Ranunculus pygmaeus*
3	AsteAGGL	*Agoseris glauca* v. *dasycephala*	48	ScroCAPU	*Castilleja pulchella*	93	JuncLUSP	*Luzula spicata*	138	RannRAES	*Ranunculus eschscholtzii*
4	PoacAGVA	*Agrostis variabilis*	49	CaryCEAR	*Cerastium arvense*	94	JuncLUWA	*Luzula wahlenbergii*	139	CarySASA	*Sagina saginoides*
5	BryALMSS	All mosses	50	AsteCIET	*Cirsium eatonii*	95	CaryLYAP	*Lychnis apetala*	140	SaliSAAR	*Salix arctica*
6	PrimANSE	*Androsace septentrionalis*	51	PortCLLA	*Claytonia lanceolata*	96	BoraMEAL	*Mertensia alpina*	141	SaliSAGL	*Salix glauca*
7	RannANPA	*Anemone multifida*	52	PortCLME	*Claytonia megarhiza*	97	BoraMECI	*Mertensia ciliata*	142	SaliSARE	*Salix reticulata*
8	RannANTE	*Anemone tetonensis*	53	AsplCYFR	*Cystopteris fragilis*	98	BoraMYAL	*Myosotis alpestris*	143	SaliSARO	*Salix rotundifolia*
9	AsteANAN	*Antennaria anaphaloides*	54	RannDEOC	*Delphinium occidentale*	99	PolyOXDI	*Oxyria digyna*	144	SaxiSAAD	*Saxifraga adscendens*
10	AsteANLA	*Antennaria lanata*	55	PoacDECE	*Deschampsia cespitosa*	100	FabaOXBO	*Oxytropis borealis*	145	SaxiSABR	*Saxifraga bronchialis*
11	AsteANME	*Antennaria media*	56	PrimDOPU	*Dodecatheon pulchellum*	101	FabaOXLA	*Oxytropis lagopus*	146	SaxiSACE	*Saxifraga cespitosa*
12	AsteANMI	*Antennaria microphylla*	57	BrasDRCA	*Draba cana*	102	FabaOXPA	*Oxytropis parryi*	147	SaxiSAOC	*Saxifraga occidentalis*
13	AsteANUM	*Antennaria umbrinella*	58	BrasDRCR	*Draba crassifolia*	103	FabaOXSE	*Oxytropis sericea*	148	SaxiSAOP	*Saxifraga oppositifolia*
14	RannAQFL	*Aquilegia flavescens*	59	BrasDRDE	*Draba densifolia*	104	ScroPEBR	*Pedicularis bracteosa*	149	SaxiSARH	*Saxifraga rhomboidea*
15	BraALLAR	Arabis species (all)	60	BrasDRGL	*Draba globosa*	105	ScroPECY	*Pedicularis cystopteridifolia*	150	SaxiSASU	*Saxifraga subapetala*
16	CaryARCO	*Arenaria congesta*	61	BrasDRIN	*Draba incerta*	106	ScroPEGR	*Pedicularis groenlandica*	151	CrasSEIN	*Sedum integrifolium*
17	CaryAROB	*Arenaria obtusiloba*	62	BrasDRLO	*Draba lonchocarpa*	107	ScroPEOE	*Pedicularis oederi*	152	CrasSELA	*Sedum lanceolatum*
18	CaryARRU	*Arenaria rubella*	63	BrasDROL	*Draba oligosperma*	108	ScroPEMO	*Penstemon montanus*	153	SelaSEDE	*Selaginella densa*
19	AsteARFU	*Arnica fulgens*	64	BrasDRPR	*Draba praelta*	109	ScroPEPR	*Penstemon procerus*	154	AsteSECA	*Senecio canus*
20	AsteARLA	*Arnica latifolia*	65	RoseDROC	*Dryas octopetala*	110	HydrPHHA	*Phacelia hastata*	155	AsteSECR	*Senecio crassulus*
21	AsteARRY	*Arnica rydbergii*	66	PoacELSC	*Elymus scribneri*	111	HydrPHSE	*Phacelia sericea*	156	AsteSEFR	*Senecio fremontii*
22	AsteARSC	*Artemisia scopulorum*	67	PoacELTR	*Elymus trachycaulus*	112	PoacPHAL	*Phleum alpinum*	157	AsteSEFU	*Senecio fuscatus*
23	AsteASAL	*Aster alpigenus*	68	OnagEPAN	*Epilobium anagallidifolium*	113	PolePHMU	*Phlox multiflora*	158	AsteSEIN	*Senecio integerrimus*
24	AsteASFO	*Aster foliaceus* v. *apricus*	69	OnagEPCL	*Epilobium clavatum*	114	PolePHPU	*Phlox pulvinata*	159	AsteSEWE	*Senecio werneriifolius*
25	FabaASAL	*Astragalus alpinus*	70	OnagEPHA	*Epilobium halleanum*	115	EricPHGL	*Phyllodoce glanduliflora*	160	RoseSIPR	*Sibbaldia procumbens*
26	FabaASKE	*Astragalus kentrophyta*	71	AsteERCO	*Erigeron compositus*	116	PinePIAL	*Pinus albicaulis*	161	CarySIAC	*Silene acaulis*
27	ScroBEWY	*Besseya wyomingensis*	72	AsteERHU	*Erigeron humilis*	117	PoacPOAL	*Poa alpina*	162	BrasSMCA	*Smelowskia calycina*
28	OphiBOMI	*Botrychium species*	73	AsteERRY	*Erigeron rydbergii*	118	PoacPOAR	*Poa arctica* v. *grayana*	163	AsteSOMU	*Solidago multiradiata*
29	PoacBRI2	*Bromus inermis* v. *purpurescens*	74	AsteERSI	*Erigeron simplex*	119	PoacPOCU	*Poa cusickii*	164	CarySTMO	*Stellaria monantha*
30	ApiaBUAM	*Bupleurum americanum*	75	AsteERUR	*Erigeron ursinus*	120	PoacPOIN	*Poa interior*	165	CarySTUM	*Stellaria umbellata*
31	PoacCAPU	*Calamagrostis purpurascens*	76	PolyEROV	*Eriogonum ovalifolium*	121	PoacPOLE	*Poa leptocoma*	166	PoacSTLE	*Stipa lettermanii*
32	RannCALE	*Caltha leptosepala*	77	BoraERNA	*Eritrichium nanum*	122	PoacPOPA	*Poa pattersonii*	167	AsteTACE	*Taraxacum ceratophorum*
33	CampCAUN	*Campanula uniflora*	78	PoacFEBR	*Festuca brachyphylla*	123	PoacPOPR	*Poa pratensis*	168	AsteTALA	*Taraxacum laevigatum*
34	CyprCAAL	*Carex albonigra*	79	PoacFEID	*Festuca idahoensis*	124	PoacPORE	*Poa reflexa*	169	AsteTAOF	*Taraxacum officianale*
35	CyprCAAT	*Carex atrata* v. *erecta*	80	GentGEAL	*Gentian algida*	125	PoacPORU	*Poa rupicola*	170	AsteTASP	*Taraxacum species*
36	CyprCAEL	*Carex elynoides*	81	GentGEAM	*Gentianella amarella*	126	PoacPOSE	*Poa secunda*	171	FabaTRNA	*Trifolium nanum*
37	CyprCAGY	*Carex gynocrates?*	82	GentGESP	*Gentianella detonsa*	127	PolePOPU	*Polemonium pulcherrimum*	172	FabaTRPA	*Trifolium parryi*
38	CyprCAHA	*Carex haydeniana*	83	RoseGERO	*Geum rossii*	128	PolePOVI	*Polemonium viscosum*	173	PoacTRSP	*Trisetum spicatum*
39	CyprCAMS	*Carex misandra*	84	RoseGETR	*Geum triflorum*	129	PolyPOBI	*Polygonum bistortoides*	174	RannTRLA	*Trollius laxus*
40	CyprCANA	*Carex nardina*	85	JuncJUDR	*Juncus drummondii*	130	PolyPODO	*Polygonum douglasii*	175	EricVASC	*Vaccinium scoparium*
41	CyprCANO	*Carex nova*	86	JuncJUME	*Juncus mertensianus*	131	PolyPOVI	*Polygonum viviparum*	176	ValeVAED	*Valeriana edulis*
42	CyprCAOB	*Carex obtusata*	87	JuncJUPA	*Juncus parryi*	132	RosePOT1	*Potentilla* sp.	177	ScroVEWO	*Veronica wormskioldii*
43	CyprCAPA	*Carex paysonis*	88	PortLEPY	*Lewisia pygmaea*	133	RosePODI	*Potentilla diversifolia*	178	ViolVIAD	*Viola adunca*
44	CyprCAPH	*Carex phaeocephala*	89	LinaLILE	*Linum lewisii*	134	RosePONI	*Potentilla nivea*	179	ViolVISP	*Viola species*
45	CyprCAPY	*Carex pyrenaica*	90	LiliLLSE	*Lloydia serotina*	135	RosePOOV	*Potentilla ovina*	180	LiliZIEL	*Zigadenus elegans*

Appendix D.2: Complete Murdoch analyses for Chapter 5

Table D.2.1. Murdoch analysis results for topographic types. Eighty-six species which occurred in at least 5% of the 178 plots across the 4 alpine regions were analyzed. Species are sorted with respect to Murdoch scores (M) from good (top of table) to poor indicators of particular topographic types.

Talus			Ridge			S. face			N. face			snowmelt		
Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val
AsteANMI	1.372	0.00	BoraERNA	2.876	<0.001	CyprCASC	2.065	<0.001	SaxiSABR	1.710	0.001	ScroVEWO	3.820	<0.001
OnagEPCL	0.967	0.03	FabaOXLA	1.778	0.001	AsteSECA	1.277	<0.001	ScroBEWY	1.512	<0.001	PoacAGVA	3.715	<0.001
PolePOVI	0.736	0.01	CarySASA	1.372	0.002	AsteSOMU	1.218	0.005	FabaASAL	1.304	<0.001	CyprCAPA	2.574	<0.001
BraALLAR	0.507	0.06	FabaOXSE	1.239	0.003	CyprCAAL	1.190	0.010	AsteSEFR	1.304	0.002	SaliSAAR	2.547	<0.001
PoacELSC	0.478	0.01	AsteERRY	1.218	0.005	PolePHMU	1.085	0.002	AsteERRY	1.150	0.008	RoseSIPR	2.516	<0.001
AsteSEFR	0.456	0.12	FabaTRNA	1.218	0.005	ApiaBUAM	1.036	0.017	PolePOVI	1.150	<0.001	PoacPORE	2.365	<0.001
ApiaLOCO	0.302	0.10	BrasDRIN	1.085	0.002	AsteANUM	1.024	0.001	CyprCAEL	1.137	0.001	AsteANME	2.272	<0.001
AsteERCO	0.176	0.19	ApiaBUAM	1.036	0.017	AsteAGGL	0.998	0.002	PoacPOIN	1.081	0.023	RannCALE	2.211	<0.001
AsteCIET	-0.014	0.36	CyprCAOB	1.036	0.002	AsteASAL	0.967	0.015	PolyPOVI	1.081	0.023	JuncJUDR	2.211	<0.001
OnagEPAN	-0.237	0.25	FabaASKE	0.995	<0.001	AsteSEFU	0.967	0.030	FabaTRPA	0.986	0.007	PoacPHAL	2.211	<0.001
PoacPOPA	-0.357	0.05	AsteCIET	0.967	0.030	PrimDOPU	0.902	0.026	CyprCAOB	0.968	0.003	CyprCAHA	1.923	<0.001
PoacPOSE	-0.452	0.09	AsteERCO	0.937	<0.001	FabaTRNA	0.902	0.026	PoacPOAL	0.947	<0.001	OnagEPAN	1.854	<0.001
ScroCAPU	-0.499	0.15	BrasSMCA	0.937	<0.001	CaryARCO	0.766	0.032	AsteSEFU	0.899	0.038	BrasDRCR	1.769	<0.001
PoacTRSP	-0.517	0.00	PolePHPU	0.934	<0.001	PoacELTR	0.766	0.032	AsteSOMU	0.834	0.035	PrimDOPU	1.672	<0.001
AsteACMI	-0.574	0.01	SelaSEDE	0.893	0.001	SelaSEDE	0.766	0.005	RosePOOV	0.793	0.030	AsteASAL	1.651	<0.001
BrasDRCR	-0.574	0.12	AsteSECA	0.887	0.010	FabaASKE	0.704	<0.001	BoraMEAL	0.776	<0.001	OnagEPCL	1.518	0.003
BrasSMCA	-0.574	0.02	PoacELSC	0.844	<0.001	CyprCAEL	0.679	0.028	BraALLAR	0.773	0.011	CarySTMO	1.469	<0.001
CaryCEAR	-0.637	0.00	PoacPORU	0.813	0.004	ScroCAPU	0.679	0.056	PoacPOCU	0.765	0.026	ScroPEPR	1.384	0.001
AsteANUM	-0.787	0.03	PoacPOSE	0.802	0.003	FabaOXSE	0.679	0.056	BoraMYAL	0.716	0.051	AsteAGGL	1.295	<0.001
PoacPORE	-0.825	0.09	PrimANSE	0.546	0.015	RosePOOV	0.584	0.076	JuncLUSP	0.694	<0.001	PolyPOVI	1.295	0.010
SaxiSABR	-0.825	0.09	CrasSELA	0.541	<0.001	CarySIAC	0.584	0.029	RannCALE	0.611	0.084	RannRAES	1.295	<0.001
PolePHPU	-0.847	0.00	PoacPOPA	0.466	0.006	ApiaLOCO	0.515	0.020	CyprCAHA	0.611	0.071	AsteARSC	1.260	<0.001
BryALMSS	-0.930	<0.0	AsteANUM	0.407	0.095	AsteACMI	0.510	0.006	ScroPEPR	0.611	0.071	CyprCAPH	1.025	0.001
CaryAROB	-0.999	<0.0	PoacFEBR	0.407	<0.001	FabaLUAR	0.497	0.047	SaxiSAOC	0.611	0.099	FabaTRPA	0.979	0.008
FabaASKE	-1.007	0.00	ScroCAPU	0.361	0.161	CaryAROB	0.490	0.001	AsteASFO	0.506	0.055	PoacDECE	0.938	<0.001
RoseSIPR	-1.113	0.01	CarySIAC	0.274	0.162	BoraMEAL	0.478	0.011	PoacPORU	0.471	0.056	PolyPOBI	0.879	<0.001
RoseGERO	-1.153	0.01	CaryAROB	0.174	0.138	BrasDRIN	0.456	0.100	CaryCEAR	0.462	0.001	PoacPOIN	0.825	0.056
RannRAES	-1.153	0.01	CyprCASC	0.120	0.265	CarySASA	0.456	0.126	FabaOXLA	0.457	0.140	PoacPOAL	0.735	0.001
BoraMYAL	-1.193	0.03	RoseGERO	0.120	0.286	PoacTRSP	0.442	0.001	RoseGERO	0.439	0.085	AsteASFO	0.719	0.015
AsteASFO	-1.230	0.00	AsteERSI	0.080	0.297	PoacDECE	0.438	0.055	CaryARCO	0.429	0.124	AsteERSI	0.707	<0.001
CyprCAPH	-1.230	0.00	BryALMSS	0.060	0.291	JuncLUSP	0.436	0.010	PoacELTR	0.429	0.124	RosePODI	0.646	<0.001
CrasSELA	-1.255	<0.0	PoacPOCU	0.051	0.331	FabaASAL	0.434	0.074	FabaLUAR	0.429	0.069	PoacELTR	0.642	0.059
CyprCAHA	-1.267	0.02	CyprCAEL	0.037	0.349	ScroBEWY	0.407	0.095	CarySTMO	0.422	0.055	FabaLUAR	0.642	0.018
CyprCAPA	-1.302	0.00	SaxiSABR	-0.014	0.362	PoacPORU	0.391	0.090	PrimANSE	0.372	0.065	BryALMSS	0.537	<0.001
PoacFEBR	-1.373	<0.0	AsteSEFU	-0.014	0.362	PolyPOBI	0.391	0.041	PoacDECE	0.370	0.083	CyprCAAL	0.537	0.113
PoacPOCU	-1.518	0.01	CaryCEAR	-0.055	0.312	CrasSELA	0.376	0.007	RosePODI	0.370	0.016	SaxiSARH	0.537	0.113

Table D.2.1 cont.

Talus			Ridge			S. face			N. face			Snowbank		
Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val
PoacDECE	-1.545	0.00	RosePOOV	-0.094	0.332	BrasSMCA	0.367	0.049	PoacPOSE	0.349	0.102	JuncLUSP	0.511	0.004
BrasDRIN	-1.623	0.00	BraALLAR	-0.109	0.319	CaryCEAR	0.259	0.039	PolePHPU	0.332	0.074	AsteACMI	0.245	0.112
AsteSECA	-1.623	0.00	BoraMEAL	-0.162	0.214	AsteERSI	0.253	0.098	BryALMSS	0.323	0.009	BoraMYAL	0.219	0.228
PrimANSE	-1.719	<0.0	CaryARCO	-0.168	0.289	RosePODI	0.239	0.081	SelaSEDE	0.282	0.149	PoacFEBR	0.174	0.065
PoacPOAL	-1.826	<0.0	AsteANMI	-0.237	0.259	AsteASFO	0.227	0.201	SaliSAAR	0.274	0.193	PoacTRSP	0.144	0.144
ScroBEWY	-1.960	0.00	RosePODI	-0.332	0.053	PoacFEBR	0.227	0.022	AsteARSC	0.239	0.168	CaryAROB	0.101	0.245
CarySIAC	-2.062	<0.0	BoraMYAL	-0.419	0.181	PolePHPU	0.194	0.183	PolyPOBI	0.230	0.138	PolePHMU	0.071	0.316
AsteERSI	-2.078	<0.0	PolePHMU	-0.419	0.156	PoacPOPA	0.180	0.150	OnagEPAN	0.205	0.237	RoseGERO	0.036	0.350
FabaLUAR	-2.124	<0.0	AsteSEFR	-0.419	0.181	AsteERCO	0.176	0.190	CarySIAC	0.205	0.210	CaryARCO	-0.023	0.377
JuncLUSP	-2.169	<0.0	PoacTRSP	-0.431	0.007	RoseGERO	0.120	0.286	PoacTRSP	0.165	0.107	PrimANSE	-0.040	0.374
AsteARSC	-2.265	<0.0	AsteACMI	-0.438	0.039	PoacPOIN	0.120	0.265	CyprCAPH	0.159	0.253	PoacPOCU	-0.156	0.295
RosePODI	-2.265	<0.0	AsteARSC	-0.545	0.058	RannRAES	0.120	0.286	BrasDRIN	0.141	0.273	FabaASAL	-0.169	0.270
PolyPOBI	-2.617	<0.0	ApiaLOCO	-0.550	0.040	BoraMYAL	0.073	0.306	PolePHMU	0.141	0.273	CarySIAC	-0.169	0.270
BoraMEAL	-2.739	<0.0	PolyPOVI	-0.707	0.124	PoacPOCU	0.051	0.331	CrasSELA	0.066	0.292	ApiaLOCO	-0.225	0.196
AsteAGGL	-Inf	<0.0	PolyPOBI	-0.728	0.009	CyprCAPH	0.029	0.363	JuncJUDR	0.051	0.296	BoraMEAL	-0.255	0.139
PoacAGVA	-Inf	<0.0	FabaTRPA	-0.768	0.068	AsteCIET	-0.014	0.362	RannRAES	0.051	0.343	CarySASA	-0.274	0.242
AsteANME	-Inf	<0.0	CyprCAPH	-0.787	0.036	ScroPEPR	-0.014	0.381	PoacPOPA	0.034	0.365	CaryCEAR	-0.299	0.049
CaryARCO	-Inf	<0.0	CyprCAAL	-0.930	0.077	PrimANSE	-0.041	0.373	AsteACMI	0.031	0.371	CrasSELA	-0.341	0.039
AsteASAL	-Inf	<0.0	FabaLUAR	-0.963	0.013	PoacPOSE	-0.049	0.368	PoacFEBR	0.012	0.393	ScroCAPU	-0.354	0.207
FabaASAL	-Inf	<0.0	PoacPOAL	-1.092	0.001	BoraERNA	-0.132	0.307	AsteANME	-0.082	0.341	RosePOOV	-0.428	0.176
ApiaBUAM	-Inf	<0.0	AsteSOMU	-1.113	0.047	PoacELSC	-0.162	0.214	AsteERSI	-0.082	0.303	CyprCASC	-0.562	0.160
RannCALE	-Inf	<0.0	JuncLUSP	-1.208	<0.001	CarySTMO	-0.208	0.216	FabaOXSE	-0.082	0.339	PoacPOPA	-0.577	0.011
CyprCAAL	-Inf	<0.0	AsteASFO	-1.230	0.007	CyprCAOB	-0.237	0.236	CaryAROB	-0.113	0.231	AsteANUM	-0.642	0.068
CyprCAEL	-Inf	<0.0	ScroBEWY	-1.230	0.007	PoacPHAL	-0.237	0.259	CyprCAAL	-0.200	0.275	AsteCIET	-0.679	0.130
CyprCAOB	-Inf	<0.0	FabaASAL	-1.336	0.004	PoacPOAL	-0.309	0.121	BrasSMCA	-0.222	0.167	AsteANMI	-0.880	0.085
CyprCASC	-Inf	<0.0	BrasDRCR	-1.336	0.022	AsteARSC	-0.332	0.140	ApiaLOCO	-0.280	0.146	AsteSOMU	-0.967	0.069
PrimDOPU	-Inf	<0.0	PoacELTR	-1.400	0.017	RoseSIPR	-0.332	0.178	AsteANMI	-0.305	0.229	AsteSEFR	-1.047	0.055
PoacELTR	-Inf	<0.0	CarySTMO	-1.598	<0.001	BryALMSS	-0.350	0.019	ApiaBUAM	-0.305	0.229	ScroBEWY	-1.085	0.016
AsteERRY	-Inf	<0.0	AsteANME	-1.806	0.002	BrasDRCR	-0.574	0.124	PoacPHAL	-0.305	0.229	PoacPORU	-1.223	0.007
BoraERNA	-Inf	<0.0	PolePOVI	-1.847	0.002	PolePOVI	-0.665	0.065	PoacELSC	-0.345	0.074	PolePOVI	-1.701	0.004
JuncJUDR	-Inf	<0.0	RoseSIPR	-1.847	0.002	BraALLAR	-0.707	0.054	FabaTRNA	-0.401	0.189	BraALLAR	-1.740	0.003
FabaOXLA	-Inf	<0.0	RannRAES	-1.886	0.001	JuncJUDR	-0.707	0.124	FabaASKE	-0.411	0.053	BrasSMCA	-1.778	<0.001
FabaOXSE	-Inf	<0.0	CyprCAPA	-2.029	<0.001	SaxiSAOC	-0.707	0.124	AsteAGGL	-0.445	0.121	PoacPOSE	-2.037	<0.001
ScroPEPR	-Inf	<0.0	PoacDECE	-2.265	<0.001	FabaTRPA	-0.768	0.068	AsteERCO	-0.488	0.036	FabaASKE	-2.543	<0.001
PoacPHAL	-Inf	<0.0	AsteAGGL	-Inf	<0.001	PoacAGVA	-0.825	0.098	ScroCAPU	-0.568	0.127	ApiaBUAM	-Inf	<0.001
PolePHMU	-Inf	<0.0	PoacAGVA	-Inf	<0.001	FabaOXLA	-0.825	0.098	BrasDRCR	-0.642	0.103	CyprCAEL	-Inf	<0.001
PoacPOIN	-Inf	<0.0	AsteASAL	-Inf	<0.001	PoacPORE	-0.825	0.098	AsteANUM	-0.855	0.026	CyprCAOB	-Inf	<0.001

Table D.2.1 cont.

Talus			Ridge			S. face			N. face			Snowbank		
Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val
PoacPORU	-Inf	<0.0	RannCALE	-Inf	<0.001	SaxiSABR	-0.825	0.098	AsteCIET	-0.893	0.084	BrasDRIN	-Inf	<0.001
PolyPOVI	-Inf	<0.0	CyprCAHA	-Inf	<0.001	AsteANMI	-1.026	0.060	OnagEPCL	-0.893	0.084	PoacELSC	-Inf	<0.001
RosePOOV	-Inf	<0.0	PrimDOPU	-Inf	<0.001	AsteANME	-1.070	0.019	PoacPORE	-0.893	0.084	AsteERCO	-Inf	<0.001
CarySASA	-Inf	<0.0	OnagEPAN	-Inf	<0.001	AsteERRY	-1.113	0.047	CyprCAPA	-0.930	0.017	AsteERRY	-Inf	<0.001
SaliSAAR	-Inf	<0.0	OnagEPCL	-Inf	<0.001	CyprCAPA	-1.302	0.005	AsteSECA	-0.947	0.035	BoraERNA	-Inf	<0.001
SaxiSAOC	-Inf	<0.0	JuncJUDR	-Inf	<0.001	RannCALE	-Inf	<0.001	ScroVEWO	-0.999	0.065	FabaOXLA	-Inf	<0.001
SelaSEDE	-Inf	<0.0	ScroPEPR	-Inf	<0.001	CyprCAHA	-Inf	<0.001	PrimDOPU	-1.181	0.039	FabaOXSE	-Inf	<0.001
AsteSEFU	-Inf	<0.0	PoacPHAL	-Inf	<0.001	OnagEPAN	-Inf	<0.001	CarySASA	-1.261	0.030	PolePHPU	-Inf	<0.001
AsteSOMU	-Inf	<0.0	PoacPOIN	-Inf	<0.001	OnagEPCL	-Inf	<0.001	AsteASAL	-1.335	0.023	SaxiSABR	-Inf	<0.001
CarySTMO	-Inf	<0.0	PoacPORE	-Inf	<0.001	PolyPOVI	-Inf	<0.001	PoacAGVA	-Inf	<0.001	SelaSEDE	-Inf	<0.001
FabaTRNA	-Inf	<0.0	SaliSAAR	-Inf	<0.001	SaliSAAR	-Inf	<0.001	CyprCASC	-Inf	<0.001	AsteSECA	-Inf	<0.001
FabaTRPA	-Inf	<0.0	SaxiSAOC	-Inf	<0.001	AsteSEFR	-Inf	<0.001	BoraERNA	-Inf	<0.001	AsteSEFU	-Inf	<0.001
ScroVEWO	-Inf	<0.0	ScroVEWO	-Inf	<0.001	ScroVEWO	-Inf	<0.001	RoseSIPR	-Inf	<0.001	FabaTRNA	-Inf	<0.001

Table D.2.2 Murdoch analysis results for alpine regions. Eighty-six species which occurred in at least 5% of the 178 plots across the 4 alpine regions were analyzed. Species are sorted with respect to Murdoch scores from good (top of table) to poor indicators of particular alpine regions.

Washburn Range			N. Absarokas			Beartooth Plateau			Beartooth Butte		
Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val
AsteERRY	+Inf	<0.001	AsteSEFR	+Inf	<0.001	ApiaBUAM	+Inf	<0.001	PoacELTR	+Inf	<0.001
FabaOXLA	+Inf	<0.001	PoacAGVA	2.355	<0.001	AsteSEFU	+Inf	<0.001	AsteSOMU	+Inf	<0.001
PoacPOCU	3.046	<0.001	SaxiSABR	2.355	<0.001	FabaTRNA	+Inf	<0.001	PrimDOPU	3.301	<0.001
SaxiSARH	2.876	<0.001	BraALLAR	1.907	<0.001	RoseGERO	3.675	<0.001	PoacPHAL	3.205	<0.001
RosePOOV	2.471	<0.001	PrimANSE	1.875	<0.001	RannCALE	2.289	<0.001	FabaOXSE	2.608	<0.001
PoacPORU	2.065	<0.001	PoacELSC	1.585	<0.001	FabaTRPA	2.135	<0.001	CyprCASC	1.819	0.001
ScroPEPR	1.778	<0.001	AsteCIET	1.544	0.004	CarySASA	1.884	<0.001	PoacPOIN	1.819	0.001
PolePHMU	1.660	<0.001	FabaASKE	1.325	<0.001	AsteARSC	1.647	<0.001	BoraERNA	1.778	<0.001
CyprCAOB	1.539	<0.001	AsteANMI	1.256	0.008	CyprCAOB	1.429	<0.001	ScroCAPU	1.73	<0.001
PolePOVI	1.526	<0.001	CyprCAHA	1.169	0.006	CyprCAAL	1.414	0.004	ScroBEWY	1.527	<0.001
CyprCAEL	1.372	<0.001	OnagEPCL	1.005	0.028	BoraERNA	1.414	0.004	AsteAGGL	1.522	<0.001
FabaLUAR	1.372	<0.001	AsteERCO	0.988	<0.001	JuncJUDR	1.373	0.008	AsteASFO	1.388	<0.001
SelaSEDE	1.255	<0.001	PoacPOSE	0.979	<0.001	PolyPOVI	1.373	0.008	RannRAES	1.065	0.001
FabaASAL	1.247	<0.001	OnagEPAN	0.851	0.037	PoacDECE	1.338	<0.001	FabaTRPA	1.057	0.005
BoraMYAL	1.085	0.009	AsteANUM	0.799	0.006	PolyPOBI	1.114	<0.001	FabaLUAR	0.99	0.001
ScroBEWY	1.024	<0.001	PoacPOPA	0.75	<0.001	CarySIAC	1.085	<0.001	RannCALE	0.903	0.033
PolePHPU	1.016	<0.001	AsteANME	0.733	0.015	PolePHPU	0.721	0.002	PolyPOVI	0.903	0.045
ApiaLOCO	0.895	<0.001	ScroVEWO	0.717	0.064	BrasDRIN	0.68	0.04	PolyPOBI	0.875	<0.001
AsteSECA	0.887	0.010	CarySIAC	0.668	0.012	RoseSIPR	0.597	0.044	OnagEPCL	0.749	0.066
CaryAROB	0.874	<0.001	AsteASAL	0.563	0.08	BrasSMCA	0.59	0.005	RosePODI	0.724	<0.001
CaryCEAR	0.821	<0.001	PoacPORE	0.563	0.108	FabaOXSE	0.584	0.084	BoraMYAL	0.68	0.064
CyprCAPA	0.774	0.007	AsteERSI	0.436	0.009	SaliSAAR	0.566	0.074	CarySASA	0.68	0.064
CaryARCO	0.766	0.032	PoacPOAL	0.434	0.023	CyprCAPA	0.54	0.047	PoacDECE	0.662	0.011
CrasSELA	0.746	<0.001	SaxiSAOC	0.381	0.177	CarySTMO	0.465	0.048	AsteANUM	0.631	0.03
OnagEPAN	0.679	0.069	ApiaLOCO	0.371	0.049	RosePODI	0.463	0.005	CyprCAHA	0.584	0.084
AsteAGGL	0.507	0.062	CyprCAPH	0.365	0.101	BryALMSS	0.457	0.001	AsteACMI	0.579	0.003
JuncLUSP	0.505	0.003	RoseSIPR	0.312	0.141	BoraMEAL	0.454	0.018	CyprCAEL	0.497	0.08
RosePODI	0.438	0.006	CaryARCO	0.275	0.197	JuncLUSP	0.44	0.012	PolePHPU	0.417	0.045
AsteACMI	0.434	0.016	SaliSAAR	0.263	0.197	CyprCASC	0.343	0.178	PoacTRSP	0.343	0.008
CyprCAPH	0.407	0.095	PoacFEBR	0.261	0.005	AsteERSI	0.303	0.072	FabaASAL	0.323	0.137
ScroVEWO	0.391	0.160	RannRAES	0.084	0.327	PoacFEBR	0.252	0.016	AsteCIET	0.21	0.226
AsteASAL	0.361	0.161	AsteSECA	0.062	0.349	SelaSEDE	0.246	0.182	PoacPOAL	0.185	0.198
AsteANMI	0.274	0.205	CrasSELA	0.045	0.326	AsteANME	0.21	0.223	CarySTMO	0.179	0.221
BrasDRCR	0.274	0.200	PoacTRSP	0.016	0.394	ScroCAPU	0.21	0.231	BoraMEAL	0.169	0.193
AsteERCO	0.274	0.102	CyprCAAL	-0.025	0.365	PoacPORE	0.21	0.226	BrasDRCR	0.13	0.272
PolyPOBI	0.200	0.168	AsteACMI	-0.03	0.379	CaryAROB	0.179	0.141	BrasSMCA	0.07	0.319

Table D.2.2 cont.

Washburn Range			N. Absarokas			Beartooth Plateau			Beartooth Butte		
Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val
BrasSMCA	0.176	0.190	JuncJUDR	-0.066	0.333	PoacPOSE	0.175	0.233	CyprCAPH	0.027	0.357
PoacPOIN	0.120	0.265	BrasDRCR	-0.094	0.326	PoacTRSP	0.092	0.233	BryALMSS	0.023	0.373
CarySTMO	0.104	0.291	BrasDRIN	-0.13	0.294	CyprCAEL	-0.013	0.392	PoacPOPA	-0.03	0.375
FabaASKE	0.007	0.406	PolePHMU	-0.13	0.294	BrasDRCR	-0.35	0.208	BraALLAR	-0.153	0.29
BryALMSS	-0.001	0.421	JuncLUSP	-0.155	0.162	CaryCEAR	-0.413	0.019	BrasDRIN	-0.196	0.271
PoacPORE	-0.014	0.362	CyprCAPA	-0.302	0.135	PoacPOIN	-0.483	0.182	AsteSECA	-0.196	0.271
PoacFEBR	-0.025	0.350	BoraMEAL	-0.302	0.055	SaxiSAOC	-0.483	0.182	CaryCEAR	-0.221	0.102
PoacPOAL	-0.039	0.375	BryALMSS	-0.316	0.007	CrasSELA	-0.589	0.004	AsteASAL	-0.276	0.241
RoseSIPR	-0.063	0.357	AsteASFO	-0.335	0.122	PoacAGVA	-0.601	0.15	ScroPEPR	-0.276	0.241
PoacPOPA	-0.066	0.318	CaryCEAR	-0.347	0.006	PoacPORU	-0.707	0.049	CaryARCO	-0.419	0.179
BoraMEAL	-0.162	0.214	PolePOVI	-0.478	0.068	PolePOVI	-0.889	0.04	PoacPOCU	-0.544	0.131
AsteANME	-0.286	0.205	CarySTMO	-0.499	0.026	BoraMYAL	-0.969	0.068	SaxiSABR	-0.601	0.15
SaliSAAR	-0.302	0.214	AsteARSC	-0.536	0.023	ScroPEPR	-1.043	0.055	CaryAROB	-0.629	0.005
AsteARSC	-0.332	0.140	CaryAROB	-0.554	<0.001	PoacPOAL	-1.603	<0.001	AsteERSI	-0.69	0.009
PoacELSC	-0.401	0.054	SelaSEDE	-0.58	0.023	RannRAES	-1.662	0.004	CyprCAAL	-0.707	0.123
BrasDRIN	-0.419	0.156	BrasSMCA	-0.59	0.003	AsteASFO	-1.736	0.003	ScroVEWO	-0.707	0.123
AsteASFO	-0.460	0.112	FabaASAL	-0.631	0.019	PoacELSC	-1.805	<0.001	PoacPOSE	-0.802	0.03
PoacTRSP	-0.517	0.002	PoacDECE	-0.777	0.003	AsteACMI	-Inf	<0.001	CrasSELA	-0.865	<0.001
AsteERSI	-0.591	0.012	ScroCAPU	-0.854	0.03	AsteAGGL	-Inf	<0.001	PoacFEBR	-1.007	<0.001
JuncJUDR	-0.707	0.124	RosePOOV	-0.941	0.018	PrimANSE	-Inf	<0.001	ApiaLOCO	-1.09	0.004
RannRAES	-0.707	0.054	PoacPORU	-0.982	0.001	AsteANMI	-Inf	<0.001	AsteERCO	-1.276	0.001
PrimANSE	-0.732	0.016	AsteAGGL	-1.095	0.001	AsteANUM	-Inf	<0.001	SaliSAAR	-1.294	0.024
PrimDOPU	-1.113	0.047	CyprCASC	-1.095	0.03	BraALLAR	-Inf	<0.001	PrimANSE	-1.495	0.001
AsteANUM	-1.230	0.007	PolyPOVI	-1.095	0.03	CaryARCO	-Inf	<0.001	JuncLUSP	-1.525	<0.001
PoacPOSE	-2.183	<0.001	BoraMYAL	-1.142	0.011	AsteASAL	-Inf	<0.001	PolePOVI	-1.623	0.005
PoacAGVA	-Inf	<0.001	ScroPEPR	-1.229	0.007	FabaASAL	-Inf	<0.001	FabaASKE	-1.754	<0.001
BraALLAR	-Inf	<0.001	RosePODI	-1.362	<0.001	FabaASKE	-Inf	<0.001	PoacELSC	-2.515	<0.001
ApiaBUAM	-Inf	<0.001	PoacPHAL	-1.452	0.005	ScroBEWY	-Inf	<0.001	PoacAGVA	-Inf	<0.001
RannCALE	-Inf	<0.001	FabaLUAR	-1.6	<0.001	CyprCAHA	-Inf	<0.001	AsteANME	-Inf	<0.001
CyprCAAL	-Inf	<0.001	CarySASA	-1.634	0.002	CyprCAPH	-Inf	<0.001	AsteANMI	-Inf	<0.001
CyprCAHA	-Inf	<0.001	RoseGERO	-1.922	<0.001	AsteCIET	-Inf	<0.001	AsteARSC	-Inf	<0.001
CyprCASC	-Inf	<0.001	PoacPOIN	-1.922	0.003	PrimDOPU	-Inf	<0.001	ApiaBUAM	-Inf	<0.001
ScroCAPU	-Inf	<0.001	ScroBEWY	-2.002	<0.001	PoacELTR	-Inf	<0.001	CyprCAOB	-Inf	<0.001
AsteCIET	-Inf	<0.001	CyprCAEL	-2.24	<0.001	OnagEPAN	-Inf	<0.001	CyprCAPA	-Inf	<0.001
PoacDECE	-Inf	<0.001	PrimDOPU	-2.327	<0.001	OnagEPCL	-Inf	<0.001	OnagEPAN	-Inf	<0.001
PoacELTR	-Inf	<0.001	PolePHPU	-2.615	<0.001	AsteERCO	-Inf	<0.001	AsteERRY	-Inf	<0.001
OnagEPCL	-Inf	<0.001	PolyPOBI	-2.695	<0.001	AsteERRY	-Inf	<0.001	RoseGERO	-Inf	<0.001
BoraERNA	-Inf	<0.001	PoacPOCU	-2.733	<0.001	ApiaLOCO	-Inf	<0.001	JuncJUDR	-Inf	<0.001

Table D.2.2 cont.

Washburn Range			N. Absarokas			Beartooth Plateau			Beartooth Butte		
Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val
RoseGERO	-Inf	<0.001	ApiaBUAM	-Inf	<0.001	FabaLUAR	-Inf	<0.001	FabaOXLA	-Inf	<0.001
FabaOXSE	-Inf	<0.001	RannCALE	-Inf	<0.001	FabaOXLA	-Inf	<0.001	PolePHMU	-Inf	<0.001
PoacPHAL	-Inf	<0.001	CyprCAOB	-Inf	<0.001	PoacPHAL	-Inf	<0.001	PoacPORE	-Inf	<0.001
PolyPOVI	-Inf	<0.001	PoacELTR	-Inf	<0.001	PolePHMU	-Inf	<0.001	PoacPORU	-Inf	<0.001
CarySASA	-Inf	<0.001	AsteERRY	-Inf	<0.001	PoacPOCU	-Inf	<0.001	RosePOOV	-Inf	<0.001
SaxiSABR	-Inf	<0.001	BoraERNA	-Inf	<0.001	PoacPOPA	-Inf	<0.001	SaxiSAOC	-Inf	<0.001
AsteSEFR	-Inf	<0.001	FabaOXLA	-Inf	<0.001	RosePOOV	-Inf	<0.001	SelaSEDE	-Inf	<0.001
AsteSEFU	-Inf	<0.001	FabaOXSE	-Inf	<0.001	SaxiSABR	-Inf	<0.001	AsteSEFR	-Inf	<0.001
CarySIAC	-Inf	<0.001	AsteSEFU	-Inf	<0.001	AsteSECA	-Inf	<0.001	AsteSEFU	-Inf	<0.001
AsteSOMU	-Inf	<0.001	AsteSOMU	-Inf	<0.001	AsteSEFR	-Inf	<0.001	RoseSIPR	-Inf	<0.001
FabaTRNA	-Inf	<0.001	FabaTRNA	-Inf	<0.001	AsteSOMU	-Inf	<0.001	CarySIAC	-Inf	<0.001
FabaTRPA	-Inf	<0.001	FabaTRPA	-Inf	<0.001	ScroVEWO	-Inf	<0.001	FabaTRNA	-Inf	<0.001

Table D.2.3. Murdoch analysis results for talus. Forty-five species which occurred in at least 5% of the 36 talus plots across the 4 alpine regions were analyzed. Species sorted with respect to Murdoch scores from good (top of table) to poor indicators of alpine regions within the talus topographic type.

Washburn Range			N. Absarokas			Beartooth Plateau			Beartooth Butte		
Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val
CrasSELA	2.303	<0.001	PrimANSE	+Inf	<0.001	PoacDECE	+Inf	<0.001	ScroCAPU	+Inf	<0.001
PolePHPU	2.015	0.001	BraALLAR	+Inf	<0.001	RoseGERO	+Inf	<0.001	BrasDROL	+Inf	<0.001
JuncLUSP	1.609	0.024	AsteARRY	+Inf	<0.001	RoseSIPR	+Inf	<0.001	RoseDROC	+Inf	<0.001
PoacPOAL	1.609	0.024	AsteASFO	+Inf	<0.001	CyprCAPA	1.609	0.024	PoacPOAR	+Inf	<0.001
RannRAES	1.609	0.024	CyprCAPH	+Inf	<0.001	AsteERSI	1.609	0.024	RosePODI	+Inf	<0.001
CaryCEAR	1.427	0.001	BrasDRCR	+Inf	<0.001	PolyOXDI	1.609	0.024	SaxiSAOP	+Inf	<0.001
PolePOVI	1.386	0.002	OnagEPAN	+Inf	<0.001	BryALMSS	0.916	0.024	AsteTACE	+Inf	<0.001
CaryAROB	1.322	0.008	OnagEPCL	+Inf	<0.001	PoacFEBR	0.693	0.073	BrasSMCA	1.897	0.001
AsteERCO	1.139	0.002	AsteSEFR	+Inf	<0.001	PoacPOSE	0.223	0.186	AsteCIET	1.609	0.024
AsteACMI	1.099	0.014	FabaASKE	1.387	0.023	PoacTRSP	-0.875	0.052	CaryAROB	1.322	0.008
PoacPOPA	1.050	0.006	PoacELSC	0.956	0.001	AsteACMI	-Inf	<0.001	PortCLME	1.204	0.024
AsteANMI	0.916	0.045	AsteANMI	0.693	0.089	PrimANSE	-Inf	<0.001	PolePHPU	1.204	0.024
AsteANUM	0.916	0.066	AsteANUM	0.693	0.114	AsteANMI	-Inf	<0.001	BryALMSS	0.916	0.024
ApiaLOCO	0.916	0.010	ApiaLOCO	0.693	0.038	AsteANUM	-Inf	<0.001	PoacTRSP	0.799	0.016
PoacELSC	0.654	0.010	AsteACMI	0.511	0.114	BraALLAR	-Inf	<0.001	PoacPOPA	0.629	0.057
PoacTRSP	0.405	0.109	AsteERCO	0.470	0.082	CaryAROB	-Inf	<0.001	PoacPOSE	0.223	0.186
FabaASKE	0.223	0.186	PortCLME	0.405	0.169	AsteARRY	-Inf	<0.001	CaryCEAR	0.105	0.252
PoacPOSE	0.223	0.186	CyprCAPA	0.000	0.243	AsteASFO	-Inf	<0.001	CrasSELA	0.000	0.256
PoacFEBR	-0.182	0.244	AsteCIET	0.000	0.243	FabaASKE	-Inf	<0.001	PoacFEBR	-0.182	0.244
BrasSMCA	-0.182	0.244	AsteERSI	0.000	0.243	CyprCAPH	-Inf	<0.001	PolePOVI	-0.470	0.152
BryALMSS	-Inf	<0.001	JuncLUSP	0.000	0.243	ScroCAPU	-Inf	<0.001	AsteACMI	-Inf	<0.001
PrimANSE	-Inf	<0.001	PolyOXDI	0.000	0.243	CaryCEAR	-Inf	<0.001	PrimANSE	-Inf	<0.001
BraALLAR	-Inf	<0.001	PoacPOAL	0.000	0.243	AsteCIET	-Inf	<0.001	AsteANMI	-Inf	<0.001
AsteARRY	-Inf	<0.001	RannRAES	0.000	0.243	PortCLME	-Inf	<0.001	AsteANUM	-Inf	<0.001
AsteASFO	-Inf	<0.001	PolePOVI	-0.223	0.222	BrasDRCR	-Inf	<0.001	BraALLAR	-Inf	<0.001
CyprCAPA	-Inf	<0.001	PoacFEBR	-0.288	0.201	BrasDROL	-Inf	<0.001	AsteARRY	-Inf	<0.001
CyprCAPH	-Inf	<0.001	PoacPOSE	-0.405	0.169	RoseDROC	-Inf	<0.001	AsteASFO	-Inf	<0.001
ScroCAPU	-Inf	<0.001	PoacTRSP	-0.470	0.082	PoacELSC	-Inf	<0.001	FabaASKE	-Inf	<0.001
AsteCIET	-Inf	<0.001	CaryCEAR	-0.560	0.073	OnagEPAN	-Inf	<0.001	CyprCAPA	-Inf	<0.001
PortCLME	-Inf	<0.001	PoacPOPA	-0.560	0.073	OnagEPCL	-Inf	<0.001	CyprCAPH	-Inf	<0.001
PoacDECE	-Inf	<0.001	BryALMSS	-0.693	0.061	AsteERCO	-Inf	<0.001	PoacDECE	-Inf	<0.001
BrasDRCR	-Inf	<0.001	BrasSMCA	-0.916	0.044	ApiaLOCO	-Inf	<0.001	BrasDRCR	-Inf	<0.001
BrasDROL	-Inf	<0.001	CrasSELA	-1.609	0.010	JuncLUSP	-Inf	<0.001	PoacELSC	-Inf	<0.001
RoseDROC	-Inf	<0.001	CaryAROB	-1.792	0.004	PolePHPU	-Inf	<0.001	OnagEPAN	-Inf	<0.001
OnagEPAN	-Inf	<0.001	ScroCAPU	-Inf	<0.001	PoacPOAL	-Inf	<0.001	OnagEPCL	-Inf	<0.001
OnagEPCL	-Inf	<0.001	PoacDECE	-Inf	<0.001	PoacPOAR	-Inf	<0.001	AsteERCO	-Inf	<0.001

Table D.2.3 cont.

Washburn Range			N. Absarokas			Beartooth Plateau			Beartooth Butte		
Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val
AsteERSI	-Inf	<0.001	BrasDROL	-Inf	<0.001	PoacPOPA	-Inf	<0.001	AsteERSI	-Inf	<0.001
RoseGERO	-Inf	<0.001	RoseDROC	-Inf	<0.001	PolePOVI	-Inf	<0.001	RoseGERO	-Inf	<0.001
PolyOXDI	-Inf	<0.001	RoseGERO	-Inf	<0.001	RosePODI	-Inf	<0.001	ApiaLOCO	-Inf	<0.001
PoacPOAR	-Inf	<0.001	PolePHPU	-Inf	<0.001	RannRAES	-Inf	<0.001	JuncLUSP	-Inf	<0.001
RosePODI	-Inf	<0.001	PoacPOAR	-Inf	<0.001	SaxiSAOP	-Inf	<0.001	PolyOXDI	-Inf	<0.001
SaxiSAOP	-Inf	<0.001	RosePODI	-Inf	<0.001	CrasSELA	-Inf	<0.001	PoacPOAL	-Inf	<0.001
AsteSEFR	-Inf	<0.001	SaxiSAOP	-Inf	<0.001	AsteSEFR	-Inf	<0.001	RannRAES	-Inf	<0.001
RoseSIPR	-Inf	<0.001	RoseSIPR	-Inf	<0.001	BrasSMCA	-Inf	<0.001	AsteSEFR	-Inf	<0.001
AsteTACE	-Inf	<0.001	AsteTACE	-Inf	<0.001	AsteTACE	-Inf	<0.001	RoseSIPR	-Inf	<0.001

Table D.2.4. Murdoch analysis results for ridge. Sixty-seven species which occurred in at least 5% of the 36 ridge plots across the 4 alpine region were analyzed. Species sorted with respect to Murdoch scores from good (top of table) to poor (bottom of table) indicators of alpine areas within the ridge topographic type.

Washburn Range			N. Absarokas			Beartooth Plateau			Beartooth Butte		
Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val
AsteERRY	+Inf	<0.001	PrimANSE	+Inf	<0.001	AsteARSC	+Inf	<0.001	RannANPA	+Inf	<0.001
FabaLUAR	+Inf	<0.001	AsteANMI	+Inf	<0.001	ApiaBUAM	+Inf	<0.001	ScroBEWY	+Inf	<0.001
FabaOXLA	+Inf	<0.001	BraALLAR	+Inf	<0.001	RoseGERO	+Inf	<0.001	CyprCANA	+Inf	<0.001
RosePOOV	+Inf	<0.001	CaryARCO	+Inf	<0.001	RosePONI	+Inf	<0.001	CyprCASC	+Inf	<0.001
PolyEROV	2.996	<0.001	AsteASFO	+Inf	<0.001	AsteSEFU	+Inf	<0.001	BrasDROL	+Inf	<0.001
PoacPOCU	2.708	<0.001	FabaASAL	+Inf	<0.001	FabaTRNA	+Inf	<0.001	BoraMYAL	+Inf	<0.001
PoacPORU	1.609	<0.001	CyprCAPH	+Inf	<0.001	FabaTRPA	+Inf	<0.001	FabaOXSE	3.401	<0.001
SelaSEDE	1.455	<0.001	AsteCIET	+Inf	<0.001	ScroCAPU	2.708	<0.001	PoacCAPU	2.303	0.003
CyprCAEL	1.204	0.024	HydrPHHA	+Inf	<0.001	PolyPOBI	2.303	<0.001	BoraERNA	2.303	<0.001
CyprCAOB	1.204	0.003	SaxiSABR	+Inf	<0.001	CarySIAC	2.120	<0.001	CyprCAEL	2.015	0.001
PolePHMU	0.916	0.066	AsteSEFR	+Inf	<0.001	CyprCAOB	2.015	<0.001	CarySASA	1.897	<0.001
CaryAROB	0.836	<0.001	AsteSEWE	+Inf	<0.001	JuncLUSP	2.015	0.001	AsteANUM	1.609	0.001
PolePHPU	0.762	<0.001	AsteACMI	2.079	0.001	CarySTMO	1.609	0.024	RosePODI	1.273	<0.001
CaryCEAR	0.654	0.010	ApiaLOCO	1.609	0.010	BoraMEAL	1.427	<0.001	AsteSECA	1.099	0.014
BrasSMCA	0.629	<0.001	PoacELSC	1.281	<0.001	CarySASA	1.322	0.008	PolePHPU	0.762	<0.001
AsteSECA	0.511	0.109	PoacPOSE	1.204	0.002	AsteERSI	1.022	0.002	BryALMSS	0.693	<0.001
BryALMSS	0.446	0.028	PoacPOAL	1.099	0.052	PoacCAPU	0.916	0.066	AsteERSI	0.693	0.024
PoacPOPA	0.446	0.028	AsteERCO	0.981	<0.001	BoraERNA	0.916	0.024	PoacPOPA	0.693	<0.001
CrasSELA	0.357	<0.001	FabaASKE	0.887	<0.001	RosePODI	0.916	0.010	BrasSMCA	0.629	<0.001
FabaASKE	0.274	0.069	PolePHMU	0.693	0.114	SelaSEDE	0.799	0.016	ScroCAPU	0.511	0.121
ApiaLOCO	<0.001	0.256	PoacTRSP	0.588	0.043	PolePHPU	0.762	<0.001	PoacPOAL	0.511	0.121
PolyPOBI	<0.001	0.256	CrasSELA	0.375	0.009	BrasSMCA	0.629	<0.001	BrasDRIN	0.357	0.151
RosePODI	<0.001	0.309	AsteANUM	<0.001	0.345	CaryAROB	0.580	0.014	BoraMEAL	0.105	0.252
PoacFEBR	-0.077	0.121	CaryCEAR	<0.001	0.370	PoacPOSE	0.405	0.109	PolyPOBI	<0.001	0.256
AsteERCO	-0.236	0.143	PoacFEBR	<0.001	0.301	BrasDRIN	0.357	0.151	CaryAROB	-0.065	0.276
BrasDRIN	-0.470	0.152	CarySTMO	<0.001	0.243	PoacTRSP	0.310	0.143	PoacFEBR	-0.077	0.121
BoraMEAL	-0.693	0.091	PoacPOPA	-0.095	0.250	BryALMSS	0.163	0.185	PoacTRSP	-0.182	0.228
PoacELSC	-0.742	0.016	BrasDRIN	-0.223	0.222	PoacFEBR	0.143	<0.001	AsteERCO	-0.236	0.143
AsteACMI	-Inf	<0.001	JuncLUSP	-0.405	0.169	PoacPORU	<0.001	0.309	AsteACMI	-0.470	0.152
PrimANSE	-Inf	<0.001	AsteSECA	-0.511	0.114	FabaOXSE	-0.182	0.244	CaryCEAR	-0.470	0.089
RannANPA	-Inf	<0.001	CarySIAC	-0.511	0.114	CaryCEAR	-0.470	0.089	FabaASKE	-0.788	0.010
AsteANMI	-Inf	<0.001	AsteERSI	-0.588	0.043	CrasSELA	-0.470	0.024	CrasSELA	-0.916	0.002
AsteANUM	-Inf	<0.001	PoacPORU	-0.693	0.038	PoacELSC	-0.742	0.016	PoacELSC	-1.482	0.001
BraALLAR	-Inf	<0.001	BryALMSS	-0.916	<0.001	AsteACMI	-Inf	<0.001	PrimANSE	-Inf	<0.001
CaryARCO	-Inf	<0.001	BoraMEAL	-0.981	0.014	PrimANSE	-Inf	<0.001	AsteANMI	-Inf	<0.001
AsteARSC	-Inf	<0.001	CaryAROB	-1.030	<0.001	RannANPA	-Inf	<0.001	BraALLAR	-Inf	<0.001

Table D.2.4 cont.

Washburn Range			N. Absarokas			Beartooth Plateau			Beartooth Butte		
Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val
AsteASFO	-Inf	<0.001	PoacPOCU	-1.099	0.052	AsteANMI	-Inf	<0.001	CaryARCO	-Inf	<0.001
FabaASAL	-Inf	<0.001	SelaSEDE	-1.204	0.002	AsteANUM	-Inf	<0.001	AsteARSC	-Inf	<0.001
ScroBEWY	-Inf	<0.001	PolyEROV	-1.386	0.023	BraALLAR	-Inf	<0.001	AsteASFO	-Inf	<0.001
ApiaBUAM	-Inf	<0.001	BrasSMCA	-1.504	<0.001	CaryARCO	-Inf	<0.001	FabaASAL	-Inf	<0.001
PoacCAPU	-Inf	<0.001	PolePHPU	-2.197	<0.001	AsteASFO	-Inf	<0.001	ApiaBUAM	-Inf	<0.001
CyprCANA	-Inf	<0.001	RosePODI	-2.398	<0.001	FabaASAL	-Inf	<0.001	CyprCAOB	-Inf	<0.001
CyprCAPH	-Inf	<0.001	RannANPA	-Inf	<0.001	FabaASKE	-Inf	<0.001	CyprCAPH	-Inf	<0.001
CyprCASC	-Inf	<0.001	AsteARSC	-Inf	<0.001	ScroBEWY	-Inf	<0.001	AsteCIET	-Inf	<0.001
ScroCAPU	-Inf	<0.001	ScroBEWY	-Inf	<0.001	CyprCAEL	-Inf	<0.001	AsteERRY	-Inf	<0.001
AsteCIET	-Inf	<0.001	ApiaBUAM	-Inf	<0.001	CyprCANA	-Inf	<0.001	PolyEROV	-Inf	<0.001
BrasDROL	-Inf	<0.001	PoacCAPU	-Inf	<0.001	CyprCAPH	-Inf	<0.001	RoseGERO	-Inf	<0.001
AsteERSI	-Inf	<0.001	CyprCAEL	-Inf	<0.001	CyprCASC	-Inf	<0.001	ApiaLOCO	-Inf	<0.001
BoraERNA	-Inf	<0.001	CyprCANA	-Inf	<0.001	AsteCIET	-Inf	<0.001	FabaLUAR	-Inf	<0.001
RoseGERO	-Inf	<0.001	CyprCAOB	-Inf	<0.001	BrasDROL	-Inf	<0.001	JuncLUSP	-Inf	<0.001
JuncLUSP	-Inf	<0.001	CyprCASC	-Inf	<0.001	AsteERCO	-Inf	<0.001	FabaOXLA	-Inf	<0.001
BoraMYAL	-Inf	<0.001	ScroCAPU	-Inf	<0.001	AsteERRY	-Inf	<0.001	HydrPHHA	-Inf	<0.001
FabaOXSE	-Inf	<0.001	BrasDROL	-Inf	<0.001	PolyEROV	-Inf	<0.001	PolePHMU	-Inf	<0.001
HydrPHHA	-Inf	<0.001	AsteERRY	-Inf	<0.001	ApiaLOCO	-Inf	<0.001	PoacPOCU	-Inf	<0.001
PoacPOAL	-Inf	<0.001	BoraERNA	-Inf	<0.001	FabaLUAR	-Inf	<0.001	PoacPORU	-Inf	<0.001
PoacPOSE	-Inf	<0.001	RoseGERO	-Inf	<0.001	BoraMYAL	-Inf	<0.001	PoacPOSE	-Inf	<0.001
RosePONI	-Inf	<0.001	FabaLUAR	-Inf	<0.001	FabaOXLA	-Inf	<0.001	RosePONI	-Inf	<0.001
CarySASA	-Inf	<0.001	BoraMYAL	-Inf	<0.001	HydrPHHA	-Inf	<0.001	RosePOOV	-Inf	<0.001
SaxiSABR	-Inf	<0.001	FabaOXLA	-Inf	<0.001	PolePHMU	-Inf	<0.001	SaxiSABR	-Inf	<0.001
AsteSEFR	-Inf	<0.001	FabaOXSE	-Inf	<0.001	PoacPOAL	-Inf	<0.001	SelaSEDE	-Inf	<0.001
AsteSEFU	-Inf	<0.001	PolyPOBI	-Inf	<0.001	PoacPOCU	-Inf	<0.001	AsteSEFR	-Inf	<0.001
AsteSEWE	-Inf	<0.001	RosePONI	-Inf	<0.001	PoacPOPA	-Inf	<0.001	AsteSEFU	-Inf	<0.001
CarySIAC	-Inf	<0.001	RosePOOV	-Inf	<0.001	RosePOOV	-Inf	<0.001	AsteSEWE	-Inf	<0.001
CarySTMO	-Inf	<0.001	CarySASA	-Inf	<0.001	SaxiSABR	-Inf	<0.001	CarySIAC	-Inf	<0.001
FabaTRNA	-Inf	<0.001	AsteSEFU	-Inf	<0.001	AsteSECA	-Inf	<0.001	CarySTMO	-Inf	<0.001
FabaTRPA	-Inf	<0.001	FabaTRNA	-Inf	<0.001	AsteSEFR	-Inf	<0.001	FabaTRNA	-Inf	<0.001
PoacTRSP	-Inf	<0.001	FabaTRPA	-Inf	<0.001	AsteSEWE	-Inf	<0.001	FabaTRPA	-Inf	<0.001

Table D.2.5. Murdoch analysis results for south facing plots. Eighty-five species which occurred in at least 5% of the 36 south-facing plots across in the 4 alpine areas were analyzed. Species sorted with respect to Murdoch scores from good (top of table) to poor (bottom of table) indicators of alpine areas within the south face topographic type.

Washburn Range			N. Absarokas			Beartooth Plateau			Beartooth Butte		
Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val
FabaOXBO	+Inf	<0.001	AsteANME	+Inf	<0.001	ApiaBUAM	+Inf	<0.001	CyprCARU	+Inf	<0.001
PoacPOCU	2.708	<0.001	BraALLAR	+Inf	<0.001	BoraERNA	+Inf	<0.001	PrimDOPU	+Inf	<0.001
PolePOVI	2.303	0.003	CyprCAPH	+Inf	<0.001	GentGEAL	+Inf	<0.001	BrasDRCA	+Inf	<0.001
RosePOOV	2.015	0.001	AsteCIET	+Inf	<0.001	RoseGERO	+Inf	<0.001	BrasDRCR	+Inf	<0.001
CyprCAPA	1.609	0.024	HydrPHHA	+Inf	<0.001	PoacPOAR	+Inf	<0.001	PoacELTR	+Inf	<0.001
PoacPORU	1.386	0.002	PolyPODO	+Inf	<0.001	CarySASA	+Inf	<0.001	AsteERUR	+Inf	<0.001
ApiaLOCO	1.322	<0.001	RosePOT1	+Inf	<0.001	AsteSEFU	+Inf	<0.001	PoacFEID	+Inf	<0.001
AsteSECA	1.204	0.003	RoseSIPR	+Inf	<0.001	FabaTRNA	+Inf	<0.001	RoseGETR	+Inf	<0.001
PortCLLA	0.916	0.066	PoacPOPA	2.015	<0.001	FabaTRPA	+Inf	<0.001	PoacPHAL	+Inf	<0.001
BoraMYAL	0.916	0.066	PoacPOSE	1.792	0.004	CyprCAOB	2.708	<0.001	AsteSOMU	+Inf	<0.001
PolePHMU	0.916	0.024	PoacELSC	1.504	0.001	AsteARSC	2.303	<0.001	ValeVAED	+Inf	<0.001
PolePHPU	0.916	0.010	FabaASKE	1.386	<0.001	CyprCAAL	2.015	0.001	ScroBEWY	2.708	<0.001
SaxiSARH	0.916	0.066	CarySIAC	1.386	0.004	CyprCAEL	1.609	0.001	PortCLLA	2.303	0.003
CaryCEAR	0.568	<0.001	PrimANSE	1.253	0.009	PoacPOIN	1.609	0.024	RannRAES	2.303	<0.001
CaryAROB	0.511	<0.001	AsteERCO	1.204	0.002	PolePHPU	1.273	<0.001	ScroCAPU	2.015	0.001
CyprCAEL	0.511	0.109	AsteANUM	1.099	0.006	FabaOXSE	1.204	0.024	FabaLUAR	2.015	<0.001
CyprCAOB	0.511	0.121	PoacPOAL	1.099	0.020	PolyPOBI	1.204	<0.001	FabaOXSE	2.015	0.001
CrasSELA	0.511	<0.001	AsteERSI	0.788	0.009	PoacDECE	1.050	0.006	AsteASFO	1.897	<0.001
SelaSEDE	0.511	0.080	CaryARCO	0.693	0.089	BryALMSS	0.916	0.003	AsteAGGL	1.792	<0.001
AsteERCO	0.405	0.109	AsteASAL	0.693	0.089	CyprCASC	0.916	0.045	FabaASAL	1.386	0.002
FabaASAL	0.357	0.151	ScroPEPR	0.693	0.114	BrasDRIN	0.916	0.045	PolyPOBI	1.204	<0.001
PoacFEBR	0.310	<0.001	PolePHMU	0.693	0.061	BoraMYAL	0.916	0.066	PoacDECE	1.050	0.006
AsteACMI	0.288	0.115	SaxiSARH	0.693	0.114	ScroPEPR	0.916	0.066	CaryARCO	0.916	0.045
FabaASKE	0.223	0.147	AsteSECA	0.405	0.132	BrasSMCA	0.916	0.003	AsteASAL	0.916	0.045
BrasSMCA	0.223	0.182	ApiaLOCO	0.288	0.153	RosePODI	0.836	<0.001	CyprCASC	0.916	0.045
AsteAGGL	0.105	0.252	BoraMEAL	0.223	0.159	AsteERSI	0.821	0.004	AsteTASP	0.916	0.045
PoacELSC	0.105	0.252	JuncLUSP	0.201	0.157	JuncLUSP	0.762	<0.001	AsteACMI	0.836	<0.001
BrasDRIN	<0.001	0.256	CaryAROB	0.167	0.144	CarySTMO	0.693	0.073	CarySTMO	0.693	0.073
JuncLUSP	-0.125	0.226	CrasSELA	0.167	0.144	BoraMEAL	0.654	0.010	PoacPOCU	0.511	0.121
CarySTMO	-0.182	0.244	PoacFEBR	0.143	0.114	SelaSEDE	0.511	0.080	PrimANSE	0.357	0.151
ScroBEWY	-0.336	0.193	CyprCAPA	<0.001	0.243	CaryAROB	0.274	0.069	PoacTRSP	0.310	<0.001
PoacPOAL	-0.336	0.193	BrasDRIN	<0.001	0.329	CarySIAC	0.223	0.199	RosePODI	0.288	0.115
PoacPOPA	-0.405	0.115	PoacPOIN	<0.001	0.243	PoacFEBR	0.083	0.193	AsteANUM	<0.001	0.309
PoacTRSP	-0.511	0.014	SelaSEDE	<0.001	0.362	PoacTRSP	0.083	0.193	PolePHPU	<0.001	0.309
RosePODI	-0.531	0.067	AsteTASP	<0.001	0.329	CaryCEAR	0.051	0.276	PoacPOSE	-0.182	0.244
FabaLUAR	-0.588	0.118	PoacTRSP	<0.001	0.345	RannRAES	<0.001	0.256	BryALMSS	-0.262	0.185

Table D.2.5 cont.

Washburn Range			N. Absarokas			Beartooth Plateau			Beartooth Butte		
Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val
AsteANUM	-0.788	0.069	AsteACMI	-0.105	0.253	AsteTASP	<0.001	0.256	CaryCEAR	-0.288	0.109
BryALMSS	-1.030	0.028	BryALMSS	-0.134	0.250	AsteASFO	-0.182	0.244	PoacPOAL	-0.336	0.193
PolyPOBI	-1.030	0.028	BrasSMCA	-0.134	0.250	CrasSELA	-0.336	0.080	BoraMEAL	-0.470	0.089
BoraMEAL	-1.224	0.010	PoacPORU	-0.223	0.222	PoacPORU	-0.470	0.152	CrasSELA	-0.788	0.010
PrimANSE	-Inf	<0.001	CaryCEAR	-0.262	0.082	AsteACMI	-Inf	<0.001	PoacFEBR	-0.956	0.001
AsteANME	-Inf	<0.001	CyprCAAL	-0.405	0.169	AsteAGGL	-Inf	<0.001	AsteANME	-Inf	<0.001
BraALLAR	-Inf	<0.001	ScroCAPU	-0.405	0.169	PrimANSE	-Inf	<0.001	BraALLAR	-Inf	<0.001
CaryARCO	-Inf	<0.001	RosePOOV	-0.405	0.169	AsteANME	-Inf	<0.001	CaryAROB	-Inf	<0.001
AsteARSC	-Inf	<0.001	RosePODI	-0.539	0.022	AsteANUM	-Inf	<0.001	AsteARSC	-Inf	<0.001
AsteASAL	-Inf	<0.001	AsteARSC	-0.693	0.089	BraALLAR	-Inf	<0.001	FabaASKE	-Inf	<0.001
AsteASFO	-Inf	<0.001	FabaASAL	-0.693	0.061	CaryARCO	-Inf	<0.001	ApiaBUAM	-Inf	<0.001
ApiaBUAM	-Inf	<0.001	CyprCASC	-0.693	0.089	AsteASAL	-Inf	<0.001	CyprCAAL	-Inf	<0.001
CyprCAAL	-Inf	<0.001	BoraMYAL	-0.693	0.114	FabaASAL	-Inf	<0.001	CyprCAEL	-Inf	<0.001
CyprCAPH	-Inf	<0.001	PolePOVI	-0.693	0.114	FabaASKE	-Inf	<0.001	CyprCAOB	-Inf	<0.001
CyprCARU	-Inf	<0.001	FabaLUAR	-0.847	0.030	ScroBEWY	-Inf	<0.001	CyprCAPA	-Inf	<0.001
CyprCASC	-Inf	<0.001	AsteASFO	-0.916	0.044	CyprCAPA	-Inf	<0.001	CyprCAPH	-Inf	<0.001
ScroCAPU	-Inf	<0.001	CarySTMO	-0.916	0.044	CyprCAPH	-Inf	<0.001	AsteCIET	-Inf	<0.001
AsteCIET	-Inf	<0.001	AsteAGGL	-0.981	0.014	CyprCARU	-Inf	<0.001	BrasDRIN	-Inf	<0.001
PoacDECE	-Inf	<0.001	PoacDECE	-0.981	0.014	ScroCAPU	-Inf	<0.001	PoacELSC	-Inf	<0.001
PrimDOPU	-Inf	<0.001	CyprCAEL	-1.099	0.020	AsteCIET	-Inf	<0.001	AsteERCO	-Inf	<0.001
BrasDRCA	-Inf	<0.001	RannRAES	-1.609	0.010	PortCLLA	-Inf	<0.001	AsteERSI	-Inf	<0.001
BrasDRCR	-Inf	<0.001	PolyPOBI	-1.872	<0.001	PrimDOPU	-Inf	<0.001	BoraERNA	-Inf	<0.001
PoacELTR	-Inf	<0.001	ScroBEWY	-1.946	0.001	BrasDRCA	-Inf	<0.001	GentGEAL	-Inf	<0.001
AsteERSI	-Inf	<0.001	PolePHPU	-2.398	<0.001	BrasDRCR	-Inf	<0.001	RoseGERO	-Inf	<0.001
AsteERUR	-Inf	<0.001	ApiaBUAM	-Inf	<0.001	PoacELSC	-Inf	<0.001	ApiaLOCO	-Inf	<0.001
BoraERNA	-Inf	<0.001	CyprCAOB	-Inf	<0.001	PoacELTR	-Inf	<0.001	JuncLUSP	-Inf	<0.001
PoacFEID	-Inf	<0.001	CyprCARU	-Inf	<0.001	AsteERCO	-Inf	<0.001	BoraMYAL	-Inf	<0.001
GentGEAL	-Inf	<0.001	PortCLLA	-Inf	<0.001	AsteERUR	-Inf	<0.001	FabaOXBO	-Inf	<0.001
RoseGERO	-Inf	<0.001	PrimDOPU	-Inf	<0.001	PoacFEID	-Inf	<0.001	ScroPEPR	-Inf	<0.001
RoseGETR	-Inf	<0.001	BrasDRCA	-Inf	<0.001	RoseGETR	-Inf	<0.001	HydrPHHA	-Inf	<0.001
FabaOXSE	-Inf	<0.001	BrasDRCR	-Inf	<0.001	ApiaLOCO	-Inf	<0.001	PolePHMU	-Inf	<0.001
ScroPEPR	-Inf	<0.001	PoacELTR	-Inf	<0.001	FabaLUAR	-Inf	<0.001	PoacPOAR	-Inf	<0.001
HydrPHHA	-Inf	<0.001	AsteERUR	-Inf	<0.001	FabaOXBO	-Inf	<0.001	PoacPOIN	-Inf	<0.001
PoacPHAL	-Inf	<0.001	BoraERNA	-Inf	<0.001	HydrPHHA	-Inf	<0.001	PoacPOPA	-Inf	<0.001
PoacPOAR	-Inf	<0.001	PoacFEID	-Inf	<0.001	PoacPHAL	-Inf	<0.001	PoacPORU	-Inf	<0.001
PoacPOIN	-Inf	<0.001	GentGEAL	-Inf	<0.001	PolePHMU	-Inf	<0.001	PolePOVI	-Inf	<0.001
PoacPOSE	-Inf	<0.001	RoseGERO	-Inf	<0.001	PoacPOAL	-Inf	<0.001	PolyPODO	-Inf	<0.001
PolyPODO	-Inf	<0.001	RoseGETR	-Inf	<0.001	PoacPOCU	-Inf	<0.001	RosePOT1	-Inf	<0.001

Table D.2.5 cont.

Washburn Range			N. Absarokas			Beartooth Plateau			Beartooth Butte		
Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val
RosePOT1	-Inf	<0.001	FabaOXBO	-Inf	<0.001	PoacPOPA	-Inf	<0.001	RosePOOV	-Inf	<0.001
RannRAES	-Inf	<0.001	FabaOXSE	-Inf	<0.001	PoacPOSE	-Inf	<0.001	CarySASA	-Inf	<0.001
CarySASA	-Inf	<0.001	PoacPHAL	-Inf	<0.001	PolePOVI	-Inf	<0.001	SaxiSARH	-Inf	<0.001
AsteSEFU	-Inf	<0.001	PoacPOAR	-Inf	<0.001	PolyPODO	-Inf	<0.001	SelaSEDE	-Inf	<0.001
RoseSIPR	-Inf	<0.001	PoacPOCU	-Inf	<0.001	RosePOT1	-Inf	<0.001	AsteSECA	-Inf	<0.001
CarySIAC	-Inf	<0.001	CarySASA	-Inf	<0.001	RosePOOV	-Inf	<0.001	AsteSEFU	-Inf	<0.001
AsteSOMU	-Inf	<0.001	AsteSEFU	-Inf	<0.001	SaxiSARH	-Inf	<0.001	RoseSIPR	-Inf	<0.001
AsteTASP	-Inf	<0.001	AsteSOMU	-Inf	<0.001	AsteSECA	-Inf	<0.001	CarySIAC	-Inf	<0.001
FabaTRNA	-Inf	<0.001	FabaTRNA	-Inf	<0.001	RoseSIPR	-Inf	<0.001	BrasSMCA	-Inf	<0.001
FabaTRPA	-Inf	<0.001	FabaTRPA	-Inf	<0.001	AsteSOMU	-Inf	<0.001	FabaTRNA	-Inf	<0.001
ValeVAED	-Inf	<0.001	ValeVAED	-Inf	<0.001	ValeVAED	-Inf	<0.001	FabaTRPA	-Inf	<0.001

Table D.2.6. Murdoch analysis results for north facing plots. Ninety-five species which occurred in at least 5% of the 38 north-facing plots across the 4 alpine regions were analyzed. Species sorted with respect to Murdoch scores from good (top of table) to poor indicators of alpine areas within the north face topographic type.

Washburn Range			N. Absarokas			Beartooth Plateau			Beartooth Butte		
Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val
AsteERRY	+Inf	<0.001	AsteANM	+Inf	<0.001	ApiaBUAM	+Inf	<0.001	AsteAGGL	+Inf	<0.001
PolyEROV	+Inf	<0.001	CyprCAH	+Inf	<0.001	RannCALE	+Inf	<0.001	PoacBRI2	+Inf	<0.001
FabaOXBO	+Inf	<0.001	BrasDRC	+Inf	<0.001	CyprCAAL	+Inf	<0.001	CyprCAAT	+Inf	<0.001
FabaOXLA	+Inf	<0.001	PoacELS	+Inf	<0.001	CyprCAMS	+Inf	<0.001	CyprCARU	+Inf	<0.001
PoacPOCU	+Inf	<0.001	OnagEPA	+Inf	<0.001	CyprCANO	+Inf	<0.001	ScroCAPU	+Inf	<0.001
PoacPORU	+Inf	<0.001	LiliLLSE	+Inf	<0.001	GentGEAL	+Inf	<0.001	BrasDRCA	+Inf	<0.001
SaxiSARH	+Inf	<0.001	PolyOXD	+Inf	<0.001	JuncJUDR	+Inf	<0.001	PoacELTR	+Inf	<0.001
RosePOOV	2.639	<0.001	PinePIAL	+Inf	<0.001	ScroPEOE	+Inf	<0.001	PoacFEID	+Inf	<0.001
CaryARCO	2.416	0.001	SaxiSAB	+Inf	<0.001	PolyPOVI	+Inf	<0.001	LinaLILE	+Inf	<0.001
CyprCAOB	2.416	<0.001	AsteSEFR	+Inf	<0.001	SaliSARE	+Inf	<0.001	PoacPHAL	+Inf	<0.001
PolePHMU	2.416	0.001	PrimANS	2.803	<0.001	CrasSEIN	+Inf	<0.001	AsteSOMU	+Inf	<0.001
SelaSEDE	2.282	<0.001	FabaASK	1.571	0.002	AsteSEFU	+Inf	<0.001	LiliZIEL	+Inf	<0.001
ApiaLOCO	2.128	<0.001	AsteERSI	1.522	<0.001	FabaTRNA	+Inf	<0.001	AsteANUM	2.367	0.002
CyprCAEL	2.010	<0.001	BraALLA	1.166	0.007	RoseGERO	2.773	<0.001	FabaOXSE	2.367	0.002
FabaASAL	1.540	<0.001	PoacPOS	1.166	0.007	FabaTRPA	2.185	<0.001	PoacPOIN	1.674	0.009
FabaLUAR	1.435	0.001	PoacPOP	1.107	0.001	AsteARSC	2.079	<0.001	AsteASFO	1.451	0.001
BoraMYAL	1.435	0.012	RannRAE	1.012	0.038	PoacDECE	1.856	<0.001	AsteACMI	1.386	<0.001
ScroPEPR	1.435	0.012	SaxiSAO	1.012	0.066	PoacPOAR	1.674	0.021	CyprCAPH	1.386	0.006
PolePOVI	1.366	<0.001	PoacFEB	0.894	<0.001	CarySTMO	1.338	<0.001	FabaLUAR	1.269	0.003
PolePHPU	1.317	<0.001	AsteERC	0.829	0.043	BrasDRIN	1.269	0.021	BoraMYAL	1.269	0.021
CaryAROB	1.281	<0.001	CarySIAC	0.829	0.043	SaliSAAR	1.269	0.021	ScroPEPR	1.269	0.021
AsteANMI	1.030	0.064	SaliSAAR	0.724	0.088	BrasSMCA	1.269	0.003	ScroBEWY	1.163	<0.001
ScroBEWY	1.030	0.001	PoacPOA	0.606	0.007	CarySIAC	1.163	0.012	FabaTRPA	1.163	0.012
PoacPOAR	1.030	0.064	AsteASF	0.542	0.094	PolyPOBI	1.086	0.001	PolyPOBI	1.086	0.001
PoacPOIN	1.030	0.048	AsteANM	0.318	0.171	CyprCAPA	0.981	0.059	RannRAES	0.981	0.039
AsteSECA	1.030	0.064	AsteSEC	0.318	0.171	FabaOXSE	0.981	0.059	CarySTMO	0.981	0.008
RosePODI	0.847	<0.001	PoacTRS	0.151	0.171	SaxiSAOC	0.981	0.059	BraALLAR	0.827	0.031
CrasSELA	0.829	<0.001	CyprCAP	0.031	0.317	PoacPOSE	0.827	0.031	CyprCAEL	0.693	0.047
AsteERCO	0.519	0.106	BrasDRIN	-0.087	0.286	PolePHPU	0.758	0.018	RosePODI	0.693	<0.001
JuncLUSP	0.454	0.007	BryALMS	-0.212	0.088	RosePODI	0.450	0.027	BoraMEAL	0.633	<0.001
CaryCEAR	0.442	<0.001	JuncLUSP	-0.257	0.081	BryALMSS	0.421	<0.001	BrasDRIN	0.288	0.169
BryALMSS	0.336	0.018	AsteANU	-0.375	0.183	PoacTRSP	0.339	0.049	PoacPOAL	0.227	0.145
CyprCAPA	0.336	0.164	CyprCAP	-0.375	0.183	CyprCAOB	0.288	0.174	FabaASAL	0.208	0.190
BrasSMCA	0.182	0.230	CaryCEA	-0.429	0.007	PoacFEBR	0.288	0.064	PoacPOPA	0.208	0.190
AsteACMI	0.113	0.264	CaryARO	-0.470	0.067	JuncLUSP	0.288	0.064	PoacDECE	0.170	0.221
BoraMEAL	-0.012	0.335	BoraMEA	-0.508	0.016	BoraMEAL	0.116	0.219	CaryCEAR	0.148	0.136

Table D.2.6 cont.

Washburn Range			N. Absarokas			Beartooth Plateau			Beartooth Butte		
Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val
FabaASKE	-0.223	0.233	AsteARS	-0.529	0.099	PolePOVI	0.065	0.273	PoacTRSP	0.065	0.264
PolyPOBI	-0.270	0.184	CrasSEL	-0.529	0.027	CrasSELA	-0.061	0.279	AsteERSI	-0.031	0.314
PoacPOAL	-0.417	0.067	BrasSMC	-0.529	0.099	CaryCEAR	-0.118	0.174	PolePHPU	-0.118	0.264
PoacTRSP	-0.580	0.017	AsteACM	-0.598	0.050	AsteERSI	-0.811	0.064	CaryAROB	-0.272	0.180
PoacFEBR	-0.629	0.009	PoacDEC	-0.662	0.059	PoacPOAL	-1.322	0.004	CrasSELA	-0.523	0.069
CyprCAPH	-0.762	0.094	RoseGER	-0.780	0.062	AsteACMI	-Inf	<0.001	JuncLUSP	-0.768	0.012
PoacPOPA	-0.916	0.018	ApiaLOC	-0.780	0.062	AsteAGGL	-Inf	<0.001	BryALMSS	-0.852	0.005
AsteARSC	-1.168	0.028	PolePOVI	-0.780	0.033	PrimANSE	-Inf	<0.001	PrimANSE	-Inf	<0.001
CarySTMO	-1.368	0.011	SelaSEDE	-0.934	0.034	AsteANME	-Inf	<0.001	AsteANME	-Inf	<0.001
PrimANSE	-1.455	0.007	CaryARC	-1.068	0.052	AsteANMI	-Inf	<0.001	AsteANMI	-Inf	<0.001
AsteAGGL	-Inf	<0.001	PolePHM	-1.068	0.052	AsteANUM	-Inf	<0.001	CaryARCO	-Inf	<0.001
AsteANME	-Inf	<0.001	FabaASA	-1.148	0.002	BraALLAR	-Inf	<0.001	AsteARSC	-Inf	<0.001
AsteANUM	-Inf	<0.001	RosePOO	-1.291	0.027	CaryARCO	-Inf	<0.001	FabaASKE	-Inf	<0.001
BraALLAR	-Inf	<0.001	CarySTM	-1.291	0.004	CaryAROB	-Inf	<0.001	ApiaBUAM	-Inf	<0.001
AsteASFO	-Inf	<0.001	ScroBEW	-1.627	<0.001	AsteASFO	-Inf	<0.001	RannCALE	-Inf	<0.001
PoacBRI2	-Inf	<0.001	PolyPOBI	-2.246	<0.001	FabaASAL	-Inf	<0.001	CyprCAAL	-Inf	<0.001
ApiaBUAM	-Inf	<0.001	RosePOD	-2.726	<0.001	FabaASKE	-Inf	<0.001	CyprCAHA	-Inf	<0.001
RannCALE	-Inf	<0.001	AsteAGG	-Inf	<0.001	ScroBEWY	-Inf	<0.001	CyprCAMS	-Inf	<0.001
CyprCAAL	-Inf	<0.001	PoacBRI2	-Inf	<0.001	PoacBRI2	-Inf	<0.001	CyprCANO	-Inf	<0.001
CyprCAAT	-Inf	<0.001	ApiaBUA	-Inf	<0.001	CyprCAAT	-Inf	<0.001	CyprCAOB	-Inf	<0.001
CyprCAHA	-Inf	<0.001	RannCAL	-Inf	<0.001	CyprCAEL	-Inf	<0.001	CyprCAPA	-Inf	<0.001
CyprCAMS	-Inf	<0.001	CyprCAA	-Inf	<0.001	CyprCAHA	-Inf	<0.001	BrasDRCR	-Inf	<0.001
CyprCANO	-Inf	<0.001	CyprCAA	-Inf	<0.001	CyprCAPH	-Inf	<0.001	PoacELSC	-Inf	<0.001
CyprCARU	-Inf	<0.001	CyprCAE	-Inf	<0.001	CyprCARU	-Inf	<0.001	OnagEPAN	-Inf	<0.001
ScroCAPU	-Inf	<0.001	CyprCAM	-Inf	<0.001	ScroCAPU	-Inf	<0.001	AsteERCO	-Inf	<0.001
PoacDECE	-Inf	<0.001	CyprCAN	-Inf	<0.001	BrasDRCA	-Inf	<0.001	AsteERRY	-Inf	<0.001
BrasDRCA	-Inf	<0.001	CyprCAO	-Inf	<0.001	BrasDRCR	-Inf	<0.001	PolyEROV	-Inf	<0.001
BrasDRCR	-Inf	<0.001	CyprCAR	-Inf	<0.001	PoacELSC	-Inf	<0.001	PoacFEBR	-Inf	<0.001
BrasDRIN	-Inf	<0.001	ScroCAP	-Inf	<0.001	PoacELTR	-Inf	<0.001	GentGEAL	-Inf	<0.001
PoacELSC	-Inf	<0.001	BrasDRC	-Inf	<0.001	OnagEPAN	-Inf	<0.001	RoseGERO	-Inf	<0.001
PoacELTR	-Inf	<0.001	PoacELT	-Inf	<0.001	AsteERCO	-Inf	<0.001	JuncJUDR	-Inf	<0.001
OnagEPAN	-Inf	<0.001	AsteERR	-Inf	<0.001	AsteERRY	-Inf	<0.001	LiliLLSE	-Inf	<0.001
AsteERSI	-Inf	<0.001	PolyERO	-Inf	<0.001	PolyEROV	-Inf	<0.001	ApiaLOCO	-Inf	<0.001
PoacFEID	-Inf	<0.001	PoacFEID	-Inf	<0.001	PoacFEID	-Inf	<0.001	PolyOXDI	-Inf	<0.001
GentGEAL	-Inf	<0.001	GentGEA	-Inf	<0.001	LinaLILE	-Inf	<0.001	FabaOXBO	-Inf	<0.001
RoseGERO	-Inf	<0.001	JuncJUD	-Inf	<0.001	LiliLLSE	-Inf	<0.001	FabaOXLA	-Inf	<0.001
JuncJUDR	-Inf	<0.001	LinaLILE	-Inf	<0.001	ApiaLOCO	-Inf	<0.001	ScroPEOE	-Inf	<0.001
LinaLILE	-Inf	<0.001	FabaLUA	-Inf	<0.001	FabaLUAR	-Inf	<0.001	PolePHMU	-Inf	<0.001

Table D.2.6 cont.

Washburn Range			N. Absarokas			Beartooth Plateau			Beartooth Butte		
Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val
LiliLLSE	-Inf	<0.001	BoraMYA	-Inf	<0.001	BoraMYAL	-Inf	<0.001	PinePIAL	-Inf	<0.001
PolyOXDI	-Inf	<0.001	FabaOXB	-Inf	<0.001	PolyOXDI	-Inf	<0.001	PoacPOAR	-Inf	<0.001
FabaOXSE	-Inf	<0.001	FabaOXL	-Inf	<0.001	FabaOXBO	-Inf	<0.001	PoacPOCU	-Inf	<0.001
ScroPEOE	-Inf	<0.001	FabaOXS	-Inf	<0.001	FabaOXLA	-Inf	<0.001	PoacPORU	-Inf	<0.001
PoacPHAL	-Inf	<0.001	ScroPEO	-Inf	<0.001	ScroPEPR	-Inf	<0.001	PoacPOSE	-Inf	<0.001
PinePIAL	-Inf	<0.001	ScroPEPR	-Inf	<0.001	PoacPHAL	-Inf	<0.001	PolePOVI	-Inf	<0.001
PoacPOSE	-Inf	<0.001	PoacPHA	-Inf	<0.001	PolePHMU	-Inf	<0.001	PolyPOVI	-Inf	<0.001
PolyPOVI	-Inf	<0.001	PolePHP	-Inf	<0.001	PinePIAL	-Inf	<0.001	RosePOOV	-Inf	<0.001
RannRAES	-Inf	<0.001	PoacPOA	-Inf	<0.001	PoacPOCU	-Inf	<0.001	SaliSAAR	-Inf	<0.001
SaliSAAR	-Inf	<0.001	PoacPOC	-Inf	<0.001	PoacPOIN	-Inf	<0.001	SaliSARE	-Inf	<0.001
SaliSARE	-Inf	<0.001	PoacPOIN	-Inf	<0.001	PoacPOPA	-Inf	<0.001	SaxiSABR	-Inf	<0.001
SaxiSABR	-Inf	<0.001	PoacPOR	-Inf	<0.001	PoacPORU	-Inf	<0.001	SaxiSAOC	-Inf	<0.001
SaxiSAOC	-Inf	<0.001	PolyPOVI	-Inf	<0.001	RosePOOV	-Inf	<0.001	SaxiSARH	-Inf	<0.001
CrasSEIN	-Inf	<0.001	SaliSARE	-Inf	<0.001	RannRAES	-Inf	<0.001	CrasSEIN	-Inf	<0.001
AsteSEFR	-Inf	<0.001	SaxiSAR	-Inf	<0.001	SaxiSABR	-Inf	<0.001	SelaSEDE	-Inf	<0.001
AsteSEFU	-Inf	<0.001	CrasSEIN	-Inf	<0.001	SaxiSARH	-Inf	<0.001	AsteSECA	-Inf	<0.001
CarySIAC	-Inf	<0.001	AsteSEFU	-Inf	<0.001	SelaSEDE	-Inf	<0.001	AsteSEFR	-Inf	<0.001
AsteSOMU	-Inf	<0.001	AsteSOM	-Inf	<0.001	AsteSECA	-Inf	<0.001	AsteSEFU	-Inf	<0.001
FabaTRNA	-Inf	<0.001	FabaTRN	-Inf	<0.001	AsteSEFR	-Inf	<0.001	CarySIAC	-Inf	<0.001
FabaTRPA	-Inf	<0.001	FabaTRP	-Inf	<0.001	AsteSOMU	-Inf	<0.001	BrasSMCA	-Inf	<0.001
LiliZIEL	-Inf	<0.001	LiliZIEL	-Inf	<0.001	LiliZIEL	-Inf	<0.001	FabaTRNA	-Inf	<0.001

Table D.2.7. Murdoch analysis results for late snowmelt plots. Seven-nine species which occurred in at least 5% of the 32 late-melt plots across the 4 alpine regions were analyzed. Species sorted with respect to Murdoch scores from good (top of table) to poor (bottom of table) indicators of alpine areas within the snowbank topographic type.

Washburn Range			N. Absarokas			Beartooth Plateau			Beartooth Butte		
Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val
ScroBEWY	+Inf	<0.001	AsteAGAR	+Inf	<0.001	AsteANLA	2.853	<0.001	PoacELTR	+Inf	<0.001
ScroPECY	+Inf	<0.001	AsteANUM	+Inf	<0.001	RoseGERO	2.853	<0.001	PoacPOIN	+Inf	<0.001
PolePHMU	+Inf	<0.001	ScroCAPU	+Inf	<0.001	CyprCAPY	1.977	<0.001	AsteSECR	+Inf	<0.001
PoacPORU	+Inf	<0.001	LiliLLSE	+Inf	<0.001	RannCALE	1.466	0.002	AsteTAOF	+Inf	<0.001
SaxiSARH	+Inf	<0.001	JuncLUWA	+Inf	<0.001	ScroPEGR	1.466	0.030	RannTRLA	+Inf	<0.001
AsteSEIN	+Inf	<0.001	EricPHGL	+Inf	<0.001	FabaTRPA	1.179	0.012	PoacPHAL	2.565	<0.001
ScroPEPR	2.890	<0.001	CarySASA	+Inf	<0.001	CaryAROB	0.956	<0.001	PrimDOPU	2.383	<0.001
FabaLUAR	1.946	<0.001	BrasSMCA	+Inf	<0.001	JuncJUDR	0.773	0.063	CyprCAAT	2.159	0.004
CaryARCO	1.792	0.011	PoacAGVA	2.590	<0.001	AsteANME	0.591	0.014	AsteERUR	2.159	0.004
PoacPOCU	1.792	0.011	PoacPOPA	2.457	<0.001	AsteARSC	0.591	0.014	OnagEPCL	1.872	0.002
SaliSARE	1.792	0.011	CarySIAC	1.897	0.004	PoacDECE	0.550	0.043	FabaTRPA	1.754	0.001
CyprCAPH	1.658	<0.001	PoacPORE	1.427	0.006	PolyPOBI	0.437	0.030	AsteASFO	1.689	<0.001
CaryCEAR	1.569	<0.001	CyprCAAL	1.204	0.044	RoseSIPR	0.437	0.030	RannCALE	1.466	0.002
FabaASAL	1.504	0.009	BoraMYAL	1.204	0.044	CyprCAPA	0.425	<0.001	ScroPEGR	1.466	0.030
OnagEPAN	1.386	0.005	CarySTUM	1.204	0.044	PoacFEBR	0.368	<0.001	PolyPOVI	1.466	0.015
AsteACMI	1.099	<0.001	ScroVEWO	0.916	0.016	BryALMSS	0.214	<0.001	CrasSEIN	1.466	0.015
AsteAGGL	1.099	0.002	CyprCAHA	0.734	0.043	BrasDRCR	0.214	0.203	CyprCAHA	1.243	0.003
PrimANSE	1.099	0.012	PrimANSE	0.511	0.104	SaliSAAR	0.167	0.212	ApiaLOCO	1.179	0.012
AsteASAL	1.099	0.012	AsteASAL	0.511	0.104	CarySIAC	0.080	0.228	PoacDECE	0.879	0.003
PortLEPY	1.099	0.012	AsteERSI	0.511	0.009	PoacTRSP	0.080	0.248	CyprCAAL	0.773	0.083
RosePOOV	1.099	0.056	JuncJUDR	0.511	0.122	RosePODI	-0.092	0.203	PoacPOCU	0.773	0.083
CrasSELA	1.099	0.002	PolyPOVI	0.511	0.136	JuncLUSP	-0.208	0.164	RannRAES	0.773	0.018
AsteASFO	0.875	0.023	RosePOOV	0.511	0.133	PortLEPY	-0.480	0.149	PolyPOBI	0.693	<0.001
BrasDRCR	0.875	0.023	RannRAES	0.511	0.066	PoacAGVA	-0.613	0.111	PoacTRSP	0.619	<0.001
CaryAROB	0.847	0.001	SaliSAAR	0.511	0.049	BoraMEAL	-0.613	0.111	AsteACMI	0.550	0.043
JuncLUSP	0.780	<0.001	CrasSEIN	0.511	0.136	AsteERSI	-0.731	0.018	RosePODI	0.425	<0.001
PolyPOBI	0.780	<0.001	CrasSELA	0.511	0.066	CarySTMO	-0.731	0.018	AsteAGGL	0.368	0.122
AsteERSI	0.693	<0.001	RoseSIPR	0.405	0.036	CaryCEAR	-1.019	0.030	PoacPOAL	0.368	0.086
CarySTMO	0.480	0.012	AsteANME	0.393	0.059	PoacPOAL	-1.242	0.009	FabaLUAR	0.080	0.264
CyprCAPA	0.470	<0.001	PoacFEBR	0.344	0.012	AsteACMI	-Inf	<0.001	CyprCAPH	-0.038	0.307
RosePODI	0.470	<0.001	CarySTMO	0.310	0.063	AsteAGAR	-Inf	<0.001	BryALMSS	-0.283	0.034
BoraMEAL	0.405	0.129	BryALMSS	0.288	<0.001	AsteAGGL	-Inf	<0.001	BrasDRCR	-0.613	0.111
BoraMYAL	0.405	0.147	BoraMEAL	0.288	0.180	PrimANSE	-Inf	<0.001	BoraMEAL	-0.613	0.111
CarySTUM	0.405	0.147	PoacPOAL	0.260	0.137	AsteANUM	-Inf	<0.001	CarySTMO	-0.731	0.018
ScroVEWO	0.251	0.188	OnagEPAN	0.223	0.218	CaryARCO	-Inf	<0.001	ScroVEWO	-0.731	0.082
AsteARSC	0.223	0.154	ApiaLOCO	0.223	0.218	AsteASAL	-Inf	<0.001	CaryCEAR	-1.019	0.030

Table D.2.7 cont.

Washburn Range			N. Absarokas			Beartooth Plateau			Beartooth Butte		
Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val
PoacFEBR	0.211	0.070	AsteARSC	0.154	0.206	AsteASFO	-Inf	<0.001	SaliSAAR	-1.099	0.020
PoacPORE	0.182	0.224	FabaASAL	0.105	0.261	FabaASAL	-Inf	<0.001	JuncLUSP	-1.424	0.002
RoseSIPR	0.069	0.271	OnagEPCL	0.105	0.261	ScroBEWY	-Inf	<0.001	AsteAGAR	-Inf	<0.001
PoacPOAL	0.000	0.343	SaxiSAOC	0.105	0.261	CyprCAAL	-Inf	<0.001	PoacAGVA	-Inf	<0.001
AsteANME	-0.080	0.270	CyprCAPA	0.069	0.242	CyprCAAT	-Inf	<0.001	PrimANSE	-Inf	<0.001
SaliSAAR	-0.201	0.207	CyprCAPY	<0.001	0.332	CyprCAHA	-Inf	<0.001	AsteANLA	-Inf	<0.001
BryALMSS	-0.383	0.009	PortLEPY	<0.001	0.332	CyprCAPH	-Inf	<0.001	AsteANME	-Inf	<0.001
JuncJUDR	-0.511	0.149	JuncLUSP	-0.028	0.320	ScroCAPU	-Inf	<0.001	AsteANUM	-Inf	<0.001
RannRAES	-0.511	0.100	PoacDECE	-0.077	0.292	PrimDOPU	-Inf	<0.001	CaryARCO	-Inf	<0.001
PoacTRSP	-0.636	0.018	PoacTRSP	-0.108	0.225	PoacELTR	-Inf	<0.001	CaryAROB	-Inf	<0.001
PrimDOPU	-0.693	0.103	CaryARCO	-0.182	0.230	OnagEPAN	-Inf	<0.001	AsteARSC	-Inf	<0.001
ApiaLOCO	-0.693	0.103	CyprCAAT	-0.182	0.230	OnagEPCL	-Inf	<0.001	AsteASAL	-Inf	<0.001
PoacPOPA	-0.847	0.070	AsteERUR	-0.182	0.230	AsteERUR	-Inf	<0.001	FabaASAL	-Inf	<0.001
AsteAGAR	-Inf	<0.001	SaliSARE	-0.182	0.230	LiliLLSE	-Inf	<0.001	ScroBEWY	-Inf	<0.001
PoacAGVA	-Inf	<0.001	AsteAGGL	-0.588	0.063	ApiaLOCO	-Inf	<0.001	CyprCAPA	-Inf	<0.001
AsteANLA	-Inf	<0.001	PoacPHAL	-0.588	0.100	FabaLUAR	-Inf	<0.001	CyprCAPY	-Inf	<0.001
AsteANUM	-Inf	<0.001	CaryCEAR	-0.693	0.036	JuncLUWA	-Inf	<0.001	ScroCAPU	-Inf	<0.001
RannCALE	-Inf	<0.001	BrasDRCR	-0.742	0.060	BoraMYAL	-Inf	<0.001	OnagEPAN	-Inf	<0.001
CyprCAAL	-Inf	<0.001	RosePODI	-0.770	<0.001	ScroPECY	-Inf	<0.001	AsteERSI	-Inf	<0.001
CyprCAAT	-Inf	<0.001	AsteACMI	-0.788	0.020	ScroPEPR	-Inf	<0.001	PoacFEBR	-Inf	<0.001
CyprCAHA	-Inf	<0.001	AsteANLA	-0.875	0.077	PoacPHAL	-Inf	<0.001	RoseGERO	-Inf	<0.001
CyprCAPY	-Inf	<0.001	RoseGERO	-0.875	0.077	PolePHMU	-Inf	<0.001	JuncJUDR	-Inf	<0.001
ScroCAPU	-Inf	<0.001	CaryAROB	-0.956	0.005	EricPHGL	-Inf	<0.001	PortLEPY	-Inf	<0.001
PoacDECE	-Inf	<0.001	PrimDOPU	-1.281	0.023	PoacPOIN	-Inf	<0.001	JuncLUWA	-Inf	<0.001
PoacELTR	-Inf	<0.001	ScroPEPR	-1.281	0.023	PoacPOPA	-Inf	<0.001	BoraMYAL	-Inf	<0.001
OnagEPCL	-Inf	<0.001	FabaLUAR	-1.686	0.003	PoacPORE	-Inf	<0.001	ScroPECY	-Inf	<0.001
AsteERUR	-Inf	<0.001	AsteASFO	-Inf	<0.001	PoacPORU	-Inf	<0.001	ScroPEPR	-Inf	<0.001
RoseGERO	-Inf	<0.001	ScroBEWY	-Inf	<0.001	PolyPOVI	-Inf	<0.001	PolePHMU	-Inf	<0.001
LiliLLSE	-Inf	<0.001	RannCALE	-Inf	<0.001	RosePOOV	-Inf	<0.001	EricPHGL	-Inf	<0.001
JuncLUWA	-Inf	<0.001	PoacELTR	-Inf	<0.001	RannRAES	-Inf	<0.001	PoacPOPA	-Inf	<0.001
ScroPEGR	-Inf	<0.001	ScroPECY	-Inf	<0.001	CarySASA	-Inf	<0.001	PoacPORE	-Inf	<0.001
PoacPHAL	-Inf	<0.001	ScroPEGR	-Inf	<0.001	SaliSARE	-Inf	<0.001	PoacPORU	-Inf	<0.001
EricPHGL	-Inf	<0.001	PolePHMU	-Inf	<0.001	SaxiSAOC	-Inf	<0.001	RosePOOV	-Inf	<0.001
PoacPOIN	-Inf	<0.001	PoacPOCU	-Inf	<0.001	CrasSEIN	-Inf	<0.001	CarySASA	-Inf	<0.001
PolyPOVI	-Inf	<0.001	PoacPOIN	-Inf	<0.001	CrasSELA	-Inf	<0.001	SaliSARE	-Inf	<0.001
CarySASA	-Inf	<0.001	PoacPORU	-Inf	<0.001	AsteSECR	-Inf	<0.001	SaxiSAOC	-Inf	<0.001
SaxiSAOC	-Inf	<0.001	PolyPOBI	-Inf	<0.001	AsteSEIN	-Inf	<0.001	CrasSELA	-Inf	<0.001
CrasSEIN	-Inf	<0.001	AsteSECR	-Inf	<0.001	BrasSMCA	-Inf	<0.001	AsteSEIN	-Inf	<0.001
AsteSECR	-Inf	<0.001	AsteSEIN	-Inf	<0.001	CarySTUM	-Inf	<0.001	RoseSIPR	-Inf	<0.001

Table D.2.7 cont.

Washburn Range			N. Absarokas			Beartooth Plateau			Beartooth Butte		
Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val	Species	*M*	*p*-val
CarySIAC	-Inf	<0.001	AsteTAOF	-Inf	<0.001	AsteTAOF	-Inf	<0.001	CarySIAC	-Inf	<0.001
BrasSMCA	-Inf	<0.001	FabaTRPA	-Inf	<0.001	RannTRLA	-Inf	<0.001	BrasSMCA	-Inf	<0.001
AsteTAOF	-Inf	<0.001	RannTRLA	-Inf	<0.001	ScroVEWO	-Inf	<0.001	CarySTUM	-Inf	<0.001

Appendix D.3: Plant Species Collected and Identified Within the Chapter 5 Study Area

All distinct plants species encountered within alpine regions of the Washburn Range and Northern Absarokas Volcanics over three field seasons were collected and identified. Species were also collected and identified when they occurred within transects on the Beartooth Plateau and on Beartooth Butte. Thus the inventory below provides a comprehensive species list for the volcanic Washburn and Northern Absaroka Mountain Ranges, along with a limited, but comparative list for granitic and calcareous substrates in the Beartooth Mountains. Approximately 300 plant species have been identified within the alpine regions of the study area. Species are listed alphabetically below by division and family. Ciphers indicate mountains and environmental types where species were found. **For the Northern Absaroka Mountains**: **Ab** = Abiathar, **Amp** = Amphitheatre, **B** = Barronette, **Co** = Cutoff, **CB** = Crown Butte, **MB** = Mineral Bowl (between and east of Mineral and Meridian summits), **Me** = Meridian, **Mi** = Miller, **Min** = Mineral, **S** = Sunset, **Wo** = Wolverine. **Wa** = Washburn Range. **Environmental types**: t = talus, r = riparian, sm = late snowmelt, tu = turf, rt = ridgetop, l = ledge, tr = treeline, d = disturbed. **An asterisk (*)** indicates species found only on calcareous substrates in the study area. **A cross (†)** indicates a new report for YNP. New reports among lichens and mosses are currently unknown. Nomenclature for vascular plants follows Dorn (1992).[*] Nomenclature for mosses follows Anderson (1990) and Lawton (1971). Nomenclature follows (Esslinger 2006) for lichens.

Anthophyta

Apiaceae

Bupleurum americanum Coult. & Rose	**Beartooth plateau plots,** rt, tu
Lomatium cous (Wats.) Coult. & Rose	**widespread,** all habitats

Asteraceae

Achillea millefolium L. var. *lanulosa* (Nutt.) Piper	**widespread,** all habitats
Agoseris aurantiaca (Hook.) Greene	**N. Absarokas (Min),** sm
Agoseris glauca (Pursh) Raf. var. *dasycephala* (T. & G.) Jeps.	**widespread,** all habitats
Agoseris glauca (Pursh) Raf. var. *glauca*	**widespread,** all habitats
Agoseris glauca (Pursh) Raf. var. *laciniata* (Eaton) Smiley	**N. Absarokas (Ab),** l
Antennaria anaphaloides Rydb.	**Washburn Range,** tr

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[*] For bibliographic on Appendix D see the Chapter 5 literature cited section.

Antennaria lanata (Hook.) Greene	**N. Absarokas (Mi, CB),** sm
Antennaria media Greene	**widespread,** sm
Antennaria microphylla Rydb.	**widespread,** all habitats
Antennaria rosea Greene	**N. Absarokas (Wo, MB),** t
Antennaria umbrinella Rydb.	**widespread,** t, tu, sm
Arnica diversifolia?	**widespread,** l
**Arnica fulgens* Pursh	**Beartooth Butte plots,** tu
Arnica latifolia Bong.	**N. Absarokas (Co, CB), Wash., Range**, tu, sm
Arnica longifolia Eaton	**N. Absarokas (Mi),** rt
Arnica rydbergii Greene	**widespread,** l
Artemisia frigida Willd.	**Washburn Range,** tu, d
Artemisia michauxiana Bess.	**N. Absarokas (Ba, Min),** l
Artemisia scopulorum Gray	**widespread,** t, tu, sm
Aster alpigenus (T. & G.) Gray var. *haydenii* (Porter) Cronq.	**widespread,** sm
Aster foliaceus Lindl. ex DC. var. *apricus* Gray	**widespread,** sm, tu
Chaenactis alpina (Gray) Jones var. *alpina*	**N. Absarokas (Ba) and Washburn Range,** l, t
Cirsium eatonii (Gray) Robins.	**widespread,** t, l
Crepis nana Richardson	**N. Absarokas (Mi),** rt
Crysothamnus viscidiflorus Hook. (Nutt.)	**N. Absarokas (Co) and Washburn Range,** ta, rt, d
Erigeron compositus Pursh var. *discoideus* Gray	**widespread,** rt, t, tu
Erigeron eatonii Gray	**Washburn Range,** d, tr
Erigeron humulis Grah.	**N. Absarokas (Co, Su)** sm
Erigeron peregrinus (Banks ex Pursh) Greene	**widespread,** tu
Erigeron rydbergii Cronq.	**dominant on Washburn Range,** tu
Erigeron simplex Greene	**widespread,** sm, tu, l
Erigeron ursinus Eaton	**N. Absarokas (Ba, Ab, Co),** l, sm
Eriophyllum lanatum (Pursh) Forbes var. *integrifolium* (Hook.) Smiley	**Washburn Range**, tr
Haplopappus acaulis (Nutt.) Gray	**N. Absarokas (Mi, Co),** rt
Haplopappus suffruticosus (Nutt.) Gray	**N. Absarokas (Co) and Washburn range,** t, d
Hieracium gracile Hook.	**N. Absarokas (Ab),** sm tu
Hulsea algida Gray	**N. Absarokas (Mi),** rt, t
Senecio canus Hook.	**widespread,** t, rt, tu
**Senecio crassulus* Gray	**Beartooth Butte plots,** sm
**Senecio dimorphophyllus* Greene var. *paysonii* Barkley	**N. Absarokas (CB),** t

Senecio fremontii T. & G.	**widespread,** t, l, rt, sm
Senecio fuscatus Hayek	**Beartooth plateau plots,** tu
Senecio integerrimus Nutt. var. *exaltatus* (Nutt.) Cronq.	**Washburn Range,** sm, tr
Senecio triangularis Hook.	**widespread,** tr
Senecio werneriifolius (Gray) Gray var. *alpina* (Gray) Dorn	**N. Absarokas (Amp, Me, Mi),** sm, rt, t
Solidago multiradiata Ait. var. *scopulorum* Gray	**widespread,** tu, rt, l, t, d
Taraxacum ceratophorum (Ledeb.) DC.	**widespread,** sm, l
Taraxacum eriophorum Rydb.	**N. Absarokas (Wo) and Washburn Range,** tu
Taraxacum laevigatum (Gray)	**N. Absarokas (Ab, Mi, Wo),** t, l
Taraxacum officinale Weber	**Washburn Range and Beartooth Butte,** sm, d
Townsendia parryi Eaton	**Washburn Range,** tu, tr
Betulaceae	
Alnus viridis (Vill.) Lam. & DC.	**N. Absarokas (Ba),** tr, r
Boraginaceae	
Eritrichium nanum (Vill.) Schrad. ex Gaudin var. *elongatum* (Rydb.) Cronq.	**Beartooth plateau and Beartooth Butte plots,** rt, tu
Mertensia alpina (Torrey) G. Don	**widespread,** all habitats
**Mertensia ciliata* (James ex Torrey) G. Don	**N. Absarokas (CB),** t
Myosotis alpestris Schmidt	**widespread,** t, tu, sm
Brassicaceae	
Arabis drummondii Gray	**N. Absarokas (Ab, Co),** t, tu, l
Arabis lemonii Wats. var. *lemonii*	**widespread,** t, tu, rt
Arabis lyallii Wats.	**widespread,** t, l
Arabis microphylla Nutt. var. *microphylla*	**widespread,** all habitats
Arabis microphylla Nutt. var. *macouni* (Wats.) Rollins	**widespread,** all habitats
Arabis pendulocarpa A. Nels. var. *pendulocarpa*	**Washburn Range,** t, d
Arabis pendulocarpa A. Nels. var. *saximontana* Rollins (Dorn)	**Washburn Range,** t
Descurainia sophia (L.) Webb ex Prantl	**Washburn Range,** d
Draba cana Rydb.	**Washburn Range,** t
†*Draba crassa* Rydb.	**N. Absarokas (Co),** t
Draba crassifolia Grah.	**widespread,** sm t

Draba densifolia Nutt.	**Washburn Range,** rt
†*Draba globosa* Payson	**N. Absarokas (Me, Co),** rt, tu
Draba incerta Payson	**widespread,** t, rt, tu
Draba lonchocarpa Rydb.	**N. Absarokas (Mi),** rt
Draba oligosperma Hook.	**N. Absarokas (Ba),** rt
Draba paysonii Macbr. var. *treleassii* (Schulz) Hitch.	**Washburn Range,** rt
Draba praelta Greene	**N. Absarokas (Amp),** l
Lepidium sp.	**Washburn Range,** d
Smelowskia calycina (Steph. ex Willd.) Meyer var. *americana* (Regel & Herder) Drury & Rollins	**widespread**, all habitats
Thlaspi parviflorum A. Nels.	**Washburn Range,** tu, tr
<u>Campanulaceae</u>	
**Campanula rotundifolia* L.	**Beartooth Butte plots,** sm, tr
Campanula uniflora L.?	**Beartooth Plateau plots,** rt
<u>Caryophyllaceae</u>	
Arenaria congesta Nutt.	**widespread,** all habitats
Arenaria nuttallii Pax	**N. Absarokas (Mi),** t, rt
Arenaria obtusiloba (Rydb.) Fern.	**widespread,** all habitats
Arenaria rubella (Wahl.) Smith	**N. Absarokas (Me, Su), and Washburn Range,** sm, t
Cerastium arvense L.	**widespread,** all habitats
Lychnis apetala L. (new name?)	**Washburn range,** sm
Sagina saginoides (L.) Karsten	**widespread,** all habitats
Silene acaulis (L.) Jacq.	**widespread,** t, tu, rt
Silene hitchguirei Bocq.	**N. Absarokas (Co),** tu
Stellaria monantha Hulten	**widespread,** sm, t, rt
Stellaria umbellata Turcz. ex Kar. & Kirr.	**widespread,** l, sm
<u>Chenopodiaceae</u>	
Chenopodium rubrum L.	**Washburn Range,** d
<u>Crassulaceae</u>	

Sedum integrifolium (Raf.) A. Nels.	**widespread,** sm
Sedum lanceolatum Torrey	**widespread,** all habitats
Sedum rhodanthum Gray	**N. Absarokas (Amp),** sm
Cyperaceae	
Carex albonigra Mack.	**widespread,** tu, sm
Carex atrata L. var. *erecta* Boott	**N. Absarokas (Ba, Co) and Beartooth Butte**, l, tu, sm
Carex elynoides Holm	**widespread,** tu, rt
Carex haydeniana Olney	**widespread,** sm, t
Carex hoodii Boott	**N. Absarokas (Ba),** l
Carex microptera Mack.	**widespread,** sm
Carex misandra R. Br.	**Beartooth Plateau plots,** tu
**Carex nardina* Fries	**Beartooth Butte plots**
**Carex nigricans* Meyer	**N. Absarokas (CB),** tu
Carex nova Bailey var. *nova*	**Beartooth plateau plots,** tu
Carex obtusata Lilj.	**Washburn Range and Beartooth Butte,** tu
Carex paysonis Clokey	**widespread,** sm, t
Carex phaeocephala Piper	**widespread,** sm, tu, t
Carex pyrenaica Wahl.	**N. Absarokas (Ab, Min) and Beartooth Plateau,** sm
**Carex rupestris* Allioni	**Beartooth Butte plots,** tu
Carex scirpoidea Michx. var. *psuedoscirpoidea* (Rydb.) Cronq.	**widespread,** tu
Eleangnaceae	
Shepherdia Canadensis (L.) Nutt.	**N. Absarokas (Ba),** r, tr
Ericaceae	
Orthilia secunda (L.) House	**N. Absarokas (Ba),** tr
Phyllodoce empetriformis (Sw.) D. Don	**N. Absarokas (Wo, MB),** r, t
Phyllodoce glanduliflora (Hook.) Cov.	**N. Absarokas (Min, Ab),** sm
Vaccinium scoparium Leiberg ex Cov.	**N. Absarokas (Ba, Mi) and Washburn Range** rt, t, sm

Fabaceae	
Astragalus alpinus L.	**widespread,** t, tu, sm
Astragalus kentrophyta Gray var. *tegetarius* (Wats.) Dorn	**widespread,** all habitats,
Astragalus miser Dougl.	**Washburn Range,** tr
Hedysarum sulphurescens Rydb.	**N. Absarokas (CB, Co),** rt, t
Lupinus argenteus Pursh	**widespread,** tu, t
Oxytropis borealis DC. var. *viscida* (Nutt.) Welsh	**N. Absarokas (Mi) and Washburn Range,** rt, tu
Oxytropis lagopus Nutt.	**Washburn Range,** tu
Oxytropis parryi Gray	**Washburn Range,** tu
Oxytropis sericea Nutt. var. *spicata* (Hook.) Barneby	**widespread,** tu
Trifolium parryi Gray var. *montanense* (Rydb.) Welsh	**Beartooth Plateau and Beartooth Butte plots**
Trifolium nanum Torrey	**Beartooth Plateau plots**
Fumariaceae	
Corydalis aurea Willd.	**Washburn Range,** tr
Gentianiaceae	
Gentiana algida Pallas	**Beartooth Plateau plots,** sm
**Gentianella amarella* (L.) Boerner	**Beartooth Butte plots,** tu
Gentianella detonsa (Rottb.) G. Don var. *elegans* (A. Nels.) Dorn	**N. Absarokas (B) Beartooth Butte,** r, sm
Gentianella tenella (Rottb.) Boerner	**N. Absarokas (Mi),** sm
Swertia radiata (Kell.) Kutze	**widespread,** tu, tr
Geraniaceae	
**Geranium viscosissimum* Fisch. & Meyer ex Meyer	**N. Absarokas (CB),** tr
Grossulariaceae	
Ribes montigenum McClatchie	**N. Absarokas (Ba) and Washburn Range**, l, tr
Hydrophyllaceae	
Phacelia hastata Dougl. ex Lehm.	**widespread,** t, l, rt
Phacelia sericea (Grah. ex Hook.) Gray var. *ciliosa* Rydb.	**widespread,** t

Phacelia sericea (Grah. ex Hook.) Gray var. *sericea*	**widespread,** t
Juncaceae	
Juncus drummondii Meyer	**widespread,** sm, tu
Juncus mertensianus Bong.	**N. Absarokas (Amp, Cu),** sm
Juncus parryi Engelm.	**N. Absarokas (Ab, Cu, S),** l, sm
**Luzula parviflora* (Ehrh.) Desv.	**N. Absarokas (Amp),** tu
Luzula spicata (L.) DC.	**widespread,** all habitats
Luzula wahlenbergii Rupr.	**N. Absarokas (Min, CB),** sm
Liliaceae	
Allium cernuum Roth	**Washburn range,** tu, tr
Lloydia serotina (L.) Riechenb.	**N. Absarokas (Mi, Wo) and Washburn range,** sm, t
**Zigadenus elegans* Pursh	**N. Absarokas (CB), and Beartooth Butte,** t tu
Linaceae	
Linum lewisii Pursh	**N. Absarokas (CB), and Washburn Range,** tu, tr
Onagraceae	
Epilobium anagallidifolium Lam.	**widespread,** sm
Epilobium angustifolium L.	**widespread,** tr
Epilobium clavatum Trel.	**widespread,** l, t
Epilobium halleanum Hausskn.	**Washburn Range,** sm
Epilobium latifolium L.	**widespread,** tr
Ophioglossaceae	
Botrychium sp. (minganense)?	**N. Absarokas (Mi, Ba),** rt
Poaceae	
Agrostis scabra Willd.	**N. Absarokas (Ba),** l
Agrostis variabilis Rydb.	**widespread,** sm
Bromus carinatus Hook. & Arn.	**N. Absarokas (MB),** tr, r

Bromus inermis Leyss. var. *inermis*	**Washburn Range,** d, t, tr
**Bromus inermis* Leyss. var. *purpurascens* (Hook.) Wagnon	**Beartooth Butte plots,** tu
Calamagrostis purpurescens R. Br.	**Beartooth Plateau and Beartooth Butte plots,** tu, rt
Danthonia intermedia Vasey	**N. Absarokas (Amp),** sm
Deschampsia cespitosa L. (Beauv.)	**widespread (absent on Washburn Range),** sm, tu
Elymus scribneri (Vasey) Jones	**widespread,** t, rt
Elymus trachycaulus (Link) Gould ex Shinners var. *andinus* (Scribn. & SM.) Dorn	**Washburn Range,** d, t
Elymus trachycaulus (Link) Gould ex Shinners var. *trachycaulus*	**Washburn Range and Beartooth Butte,** d, t, tu
Festuca brachyphylla Schultes & Schultes	**widespread,** all habitats
**Festuca idahoensis* Elmer	**Beartooth Butte plots,** tu
Festuca minutiflora Rydb.	**N. Absarokas (Co),** tu
Phleum alpinum L.	**widespread (abs. from Washburn and B. Butte),** sm, l
Poa alpina L.	**widespread,** all habitats
Poa arctica R. Br.	**widespread,** tu
Poa cusickii Vasey var. *cusickii*	**widespread,** all habitats
Poa cusickii Vasey var. *epilis* (Scribn.) Hitchc.	**widespread,** all habitats
Poa interior Rydb.	**widespread,** d, tu, sm
Poa leptocoma Trin.	**N. Absarokas (Co),** sm
Poa pattersonii Vasey	**widespread,** all habitats
Poa pratensis L.	**widespread** d, l, tu
Poa reflexa Vasey & Scribn. ex Vasey	**widespread,** sm, l
Poa rupicola Nash ex Rydb.	**widespread,** tu, rt
Poa secunda Presl var. *incurva* (Scrib. & Wms. ex Scribn.) Beetle	**widespread,** t, rt, tu
Poa secunda Presl var. *elongata* (Vasey) Dorn	**Beartooth Plateau plots,** tu
**Stipa lettermanii* Vasey	**Beartooth Butte plots,** sm
Stipa nelsonii Scribn.	**Washburn Range,** tr
Trisetum spicatum (L.) Richt.	**widespread,** all habitats
<u>Polemoniaceae</u>	
Phlox multiflora A. Nels.	**widespread,** all habitats

Phlox pulvinata (Wherry) Cronq.	**widespread,** tu, rt
Polemonium pulcherrimum Hook.	**N. Absarokas (Wo, Me) and Washburn Range,** t, sm
Polemonium viscosum Nutt.	**widespread,** t, tu, rt
Polygonaceae	
Eriogonum ovalifolium Nutt.	**N. Absarokas (Ab) and Washburn Range,** rt
Eriogonum umbellatum Torrey	**Washburn Range,** t, tr
Oxyria digyna (L.) Hill	**widespread,** t, sm
Polygonum aviculare L.	**Washburn Range,** d
Polygonum bistortoides Pursh	**widespread,** t, sm
Polygonum douglasii Greene	**N. Absarokas (Mi) and Washburn Ridge**, t
Polygonum viviparum L.	**widespread (absent form Washburn),** sm
Rumex paucifolius Nutt.	**N. Absarokas (CB, Wo) and Washburn Range**, tu, l
Rumex salicifolius Weinm.	**Washburn Range,** d, tr
Portulacaceae	
Claytonia lanceolata Pursh var. *lanceolata*	**widespread,** tu
†*Claytonia megarhiza* (Gray) Parry ex Wats.	**widespread,** t, rt,
Lewisia pygmaea (Gray) Robins.	**widespread,** tu, sm
Spraguea umbellata Torrey var. *caudicifera* Gray	**N. Absarokas (CB, Co),** t, rt
Primulaceae	
Androsace septentrionalis L. var. *subulifera* Gray	**widespread**, t, rt, tu
Dodecatheon pulchellum (Raf.) Merr.	**widespread**, tu, sm
Ranunculaceae	
Anemone multifida Poiret	**N. Absarokas (Su),** l
Anemone tetonensis Porter ex Britt.	**N. Absarokas (Mi),** rt, t
**Aquilegia flavescens* Wats.	**N. Absarokas (CB),** tu, t
Caltha leptosepala DC.	**N. Absarokas (MB) and both Beartooth areas** r, sm
Delphinium bicolor Nutt.	**Washburn Range,** tr
**Delphinium glaucum* Wats.	**N. Absarokas (CB),** t

**Delphinium occidentale* (Wats.) Wats.?	**N. Absarokas (CB),** t
Delphinium nutallianum Pritzel ex Walpers	**Washburn Range,** tr
Ranunculus eschscholtzii Schlect.	**widespread,** t, sm
Ranunculus pygmaeus Wahl.	**N. Absarokas (Cu), Beartooth Plateau,** sm
**Trollius laxus* Salisb. var. *albiflorus* Gray	**Beartooth Butte plots,** sm
<u>Rosaceae</u>	
**Dryas octopetala* L. var. *hookeriana* (Juz.) Breit.	**Beartooth Butte plots,** rt, t
Geum rossii (R. Br.) Ser. var. *turbinatum* (Rydb.) Raup	**N. Absarokas (Ab) dom. on Beartooth Plateau,** tu
Geum triflorum Pursh	**Washburn Range, dom. on Beartooth Butte** tu, tr
Potentilla arguta Pursh	**Washburn Range,** tr
Potentilla diversifolia Lehm. var. *diversifolia*	**widespread,** tu
Potentilla diversifolia Lehm. var. *peridissecta* (Rydb.) Hitchc.	**N. Absarokas (Wo) and Washburn,** tu
Potentilla glandulosa Lindl. var. *psuedorupestris* (Rydb.) Breit.	**N. Absarokas (CB, Mi),** t, rt
Potentilla gracilis Dougl. ex Hook.	**N. Absarokas (Wo)**, tu
Potentilla nivea L.	**Beartooth Plateau plots,** rt
Potentilla ovina Macoun.	**widespread,** tu
Potentilla rubricaulis Lehm.	**N. Absarokas (Ba),** rt
Sibbaldia procumbens L.	**widespread,** sm
<u>Salicaceae</u>	
Salix arctica Pallas var. *petraea* Anderss.	**widespread**, sm, r
**Salix glauca* L. var. *villosa* (Hook.) Anderss.	**Beartooth Butte plots,** tr, t
Salix reticulata L. var. *nana* Anderss.	**widespread**, sm, r
**Salix rotundifolia* Trautv. var. *dodgeana* (Rydb.) Murray	**Beartooth Butte plots** rt, tu
<u>Saxifragaceae</u>	
Heuchera parvifolia Nutt. ex T. & G.	**Washburn range,** d
Lithophragma glabrum Nutt. var. *ramulosum* (Suskd.) *Boivin*	**Absarokas (Co)**, rocky sm
Parnassia fimbriata Konig	**N. Absarokas (Amp),** sm
Saxifraga adscendens L. var. *oregonensis* (Raf.) Breit.	**N. Absarokas (Co, Wo, Su)**, sm, t
Saxifraga bronchialis L. var. *austromontana* (Wieg.) Piper ex Jones	**widespread**, rt, t

Saxifraga cespitosa L. var. *minima* Blank.	**N Absarokas (Wo, Co),** t, sm
Saxifraga occidentalis Wats.	**widespread**, sm
Saxifraga odontoloma Piper	**N. Absarokas (Ba),** l, r
Saxifraga oppositifolia L.	**widespread in N. Abs. and Beartooth Butte** t, rt, sm
**Saxifraga subapetela* E. Nels.	**Beartooth Butte plots**
Saxifraga rhomboidea Greene	**N. Absarokas (Cu), Washburn Range** tu
Saxifraga rivularis L.	**N. Absarokas (Cu, S),** sm
Scrophulariaceae	
Besseya wyomingensis (A. Nels.) Rydb.	**widespread,** tu
Castilleja pallescens (Gray) Greenm.	**Washburn Range,** tu, tr
Castilleja pulchella Rydb.	**widespread,** tu, sm
Castilleja rhexifolia Rydb.	**N. Absarokas (CB, MB),** r
Mimulus guttatus DC.	**N. Absarokas (Ba),** r, tr
Mimulus lewisii Pursh	**N. Absarokas (Ba, CB),** r, tr
**Pedicularis bracteosa* Benth. var. *paysoniana* (Pennel) Cronq.	**N. Absarokas (CB), and Beartooth Butte** sm
Pedicularis cystopteridifolia Rydb.	**Washburn Range,** sm
**Pedicularis groenlandica* Ret z.	**frequent in N. Abs.(CB), and Beartooths,** sm
**Pedicularis oederi* Vahl ex Hornem.	**Beartooth Plateau plots only**
Penstemon attenuatus Dougl. Ex Lindl.	**widespread,** t, tu
Penstemon montanus Greene	**N. Absarokas (CB, Mi)**, t
Penstemon procerus Dougl. ex Grah.	**widespread,** t, tu
Veronica wormskjoldii R. & S.	**widespread,** sm
Urticaceae	
Urtica dioca L.	**N. Absarokas (Ba)**, r, tr
Valerianaceae	
Valeriana dioica L. var. *sylvatica* Wats.	**N. Absarokas (CB) and Washburn Range,** t, tu
**Valeriana edulis* Nutt. ex T. & G.	**N. Absarokas (CB) and Beartooth Butte** tu, t
Violaceae	

Viola adunca Smith	**prob. widespread, voucher from N. Abs. (CB),** t
Viola praemorsa Dougl. ex Lindl. var. *altior* Blank.	**probably widespread, voucher from N. Abs. (CB)**, t
Coniferophyta	
Cupressaceae	
Juniperus communis L. var. *depressa* Pursh	**widespread,** tr
Pinaceae	
Abies lasiocarpa (Hook.) Nutt.	**widespread,** tr
Picea engelmannii Parry ex Engelm.	**widespread,** tr
Pinus albicaulis Engelm.	**widespread,** tr
Lycophyta	
Selaginellaceae	
Selaginella densa Rydb.	**widespread,** tu, rt
Pterophyta	
Aspleniaceae	
Cystopteris fragilis (L.) Bernh.	**widespread,** t, rt
Bryophyta, Hepatophyta (on soil)	
Aulacomnium palustre Schwaegr.	**N. Absarokas (Amp, Co),** sm
Barbilophozia hatchery (Evans) Steph.	**N. Absarokas (Ab),** tu
Brachythecium albicans (Hedw.) B.S.G.	**N. Absarokas (Su, Ba, Amp, Me)** sm, le
Bryum caespiticium Hedw.	**Washburn Range,** sm
Bryum capillare Hedw.	**Washburn Range,** tu

Bryum sp. Hedw.	**N. Absarokas (Ab, Amp, Min),** t, sm
Desmatadon latifolius (Hedw.) Brid.	**N. Absarokas (Co),** sm
Dicranum spp. Hedw.	**N. Absarokas (Min),** sm
Dicranoweisia crispula (Hedw.) Lindb. *ex* Milde	**N. Absarokas (Co),** rt
Drepanocladus spp. (C. Müll.) G. Roth	**N. Absarokas (Wo),** sm
Schistidium spp. Ren. & Card.	**widespread,** rt
Hypnum spp.	**N. Absarokas (Ab),** rt
Hypnum revolutum (Mitt.) Lindb.	**N. Absarokas (Wo),** sm
Philonotis fontana Hedw.	**N. Absarokas (Ab),** t
Pohlia cruda (Hedw.) Lindb.	**N. Absarokas (Ab, Amp),** t
Polytrichium juniperinum Hedw.	**widespread,** tu, sm, rt
Stegonia pilifera (Brid.) Crum & Anderson	**Washburn Range,** tu
Tortula ruralis (Hedw.) Gaertn., Meyer & Scherb.	**widespread,** tu

Lichens (on soil)

Catapyrenium cinereum (Pers.) Körber	**N. Absarokas (Min),** tu
Cladonia pocillum (Ach.) Grognot	**N. Absarokas (Min),** tu
Lepraria cacuminum (A. Massal.) Lohtander	**N. Absarokas (Ab, Min, Amp),** sm, tu
Leprocaulon gracilescens (Nyl.) Lamb & Ward	**N. Absarokas (Min),** sm
Peltigera rufescens (Weiss) Humb.	**N. Absarokas (Min),** tu

APPENDIX E

APPENDICES PERTAINING TO CHAPTER 6:

WATER AND SUBSTRATE CONTROL OF CLIFF COMMUNITIES

Appendix E.1: Complete Indicator Species Analysis Results for Cliff Sites

Treatment levels to which species have the maximum affiliation are indicated with along with p-values. Asterisks indicates $p < 0.05$

		Water			Substrate			Combination		
	LF[1]	Trt[2]	IV[3]	*p*-val[4]	Trt[2]	IV[3]	*p*-val[4]	Trt[2]	IV[3]	*p*-val[4]
Cryptogramma arctostich.	F	WET	5.6	1.000	AND	3.7	1.000	AW	11.1	1.000
Cystopteris fragilis	F	WET	25.0	0.023*	AND	8.9	0.632	AW	16.7	0.238
Acarospora glaucocarpa	L	DRY	13.8	0.323	LIM	14.2	0.193	LD	18	0.230
Aspicilia aliena	L	DRY	4.8	0.756	LIM	5.3	0.768	LI	6.3	1.000
Aspicilia caesiocinerea	L	DRY	52.3	0.001*	AND	46.6	0.001*	AD	73.2	0.001*
Aspicilia calcarea	L	INT	5.6	1.000	AND	3.7	1.000	AI	11.1	1.000
Aspicilia cinerea	L	DRY	11.1	0.313	AND	1.9	1.000	AD	5.6	1.000
Aspicilia contorta	L	DRY	4.7	1.000	AND	7.4	0.495	AD	9.4	1.000
Aspicilia sp.	L	DRY	2.8	1.000	LIM	7.4	0.480	LD	5.6	1.000
Candelariella aurella	L	INT	3.7	1.000	LIM	2.5	1.000	LI	7.4	1.000
Candelariella sp.	L	DRY	70.9	0.001*	AND	34.5	0.069	AD	57.1	0.001*
Candelariella vitellina	L	DRY	4.4	1.000	LIM	7.4	0.487	LD	8.9	1.000
Candelariella (all)	L	DRY	74.5	0.001*	AND	32	0.216	AD	53	0.001*
Catillaria chalybeia	L	DRY	5.6	1.000	LIM	3.7	1.000	LD	11.1	1.000
Caloplaca epithallina	L	DRY	13.8	0.192	AND	10.0	0.383	AD	16.8	0.200
Caloplaca saxicola	L	DRY	16.7	0.106	AND	11.1	0.243	AD	33.3	0.024*
Caloplaca sp.	L	DRY	6.4	0.527	AND	7.2	0.495	AD	6.1	1.000
Collema polycarpon	L	DRY	3.1	1.000	LIM	7.4	0.487	LD	6.2	1.000
Collema sp.	L	DRY	14.4	0.330	LIM	17.9	0.099	LD	13.9	0.400
Collema tenax	L	DRY	9.6	0.344	LIM	6.4	0.592	LD	19.3	0.117
Collema undulatum	L	DRY	13.5	0.462	LIM	19.2	0.187	LD	11.1	0.519
Collema (all)	L	DRY	30.6	0.077	LIM	35.2	0.047	LD	31.6	0.039*
Catapyrenium cinereum	L	DRY	5.6	1.000	LIM	3.7	1.000	LD	11.1	1.000
Catapyrenium norvegicum	L	INT	5.6	1.000	LIM	3.7	1.000	LI	11.1	1.000
Catapyrenium sp.	L	DRY	5.6	1.000	LIM	3.7	1.000	LD	11.1	1.000
Dermatocarpon intestine.	L	WET	14.8	0.304	LIM	16.8	0.222	LW	20.6	0.136
Dermatocarpon miniatum	L	WET	11.7	0.596	LIM	20.0	0.167	LW	23.3	0.134
Endocarpon pulvinatum	L	DRY	16.7	0.104	LIM	6.8	0.471	LD	20.5	0.163
Gyalidea hyalinescens	L	INT	11.1	0.334	AND	2.8	1.000	AI	8.4	1.000
Lecidea atrobrunnea	L	DRY	21.5	0.058	AND	18.5	0.042*	AD	43.1	0.006*
Lecidea sp.	L	DRY	5.6	1.000	AND	3.7	1.000	AD	11.1	1.000
Lecidella stigmatea	L	DRY	35.6	0.003*	AND	13.9	0.517	AD	31.2	0.03*
Lempholemma cladodes	L	DRY	5.6	1.000	LIM	3.7	1.000	LD	11.1	1.000
Lecanora crenulata	L	DRY	20.8	0.072	LIM	9.9	0.474	LD	20.3	0.102
Lecanora dispersa	L	INT	7.2	0.525	LIM	4.8	0.762	LI	14.4	0.274
Lecanora sp.	L	DRY	5.6	1.000	LIM	3.7	1.000	LD	11.1	1.000
Lobothallia alphoplaca	L	DRY	22.2	0.038*	AND	9.3	0.350	AD	27.8	0.052
Leptogium subaridum	L	DRY	15.2	0.095	LIM	8.1	0.497	LD	14.1	0.298
Phaeophyscia decolor	L	DRY	15.4	0.163	AND	10.7	0.234	AD	19.7	0.176
Placynthium nigrum	L	INT	16.8	0.220	LIM	18.0	0.209	LI	19.5	0.131
Psora tuckermanii	L	DRY	5.6	1.000	LIM	3.7	1.000	LD	11.1	1.000
Physcia dubia	L	DRY	22.2	0.022*	AND	10.5	0.392	AD	31.5	0.04*
Physcia sp.	L	DRY	5.6	1.000	AND	3.7	1.000	AD	11.1	1.000

Table E.1.1. cont.

		Water			Substrate			Combination		
	LF[1]	Trt[2]	IV[3]	*p*-val[4]	Trt[2]	IV[3]	*p*-val[4]	Trt[2]	IV[3]	*p*-val[4]
Rhizocarpon geographicum	L	DRY	22.2	0.022*	AND	10.2	0.267	AD	30.6	0.024*
Rhizocarpon geminatum	L	DRY	14.4	0.168	AND	14.8	0.130	AD	28.7	0.04*
Rhizocarpon sp.	L	INT	9.6	0.412	AND	14.8	0.098	AI	19.3	0.165
Rinodina sp.	L	DRY	16.7	0.103	AND	5.9	0.761	AD	17.8	0.277
Rhizoplaca melanopthalma	L	DRY	15.3	0.095	AND	14.8	0.113	AD	30.6	0.025*
Psora himalayana	L	DRY	8.4	0.530	LIM	10.8	0.253	LD	16.8	0.279
Staurothele areolata	L	INT	5.6	1.000	AND	3.7	1.000	AI	11.1	1.000
Staurothele drummondii	L	DRY	62.8	0.001*	LIM	20.7	0.952	LD	30.3	0.062
Staurothele fissa	L	INT	9.3	0.682	LIM	29.6	0.005*	LI	18.5	0.162
Thelidium sp.	L	DRY	2.8	1.000	LIM	7.4	0.487	LD	5.6	1.000
Toninia alutacea	L	DRY	14.3	0.176	LIM	9.5	0.349	LD	15.9	0.201
Toninia candida	L	DRY	14.3	0.402	LIM	18.5	0.041*	LD	28.6	0.108
Verrucaria arctica	L	DRY	10.5	0.547	LIM	7.0	0.742	LD	9.9	1.000
Xanthoria elegans	L	DRY	67.1	0.001*	LIM	25.3	0.257	LD	57.2	0.001*
Xanthoria polycarpa	L	DRY	5.6	1.000	AND	3.7	1.000	AD	11.1	1.000
Conocephalum conicum	LV	WET	9.9	0.337	LIM	6.6	0.451	AW	19.8	0.157
Reboulia hemispherica?	LV	WET	13.7	0.398	LIM	18.5	0.061	AW	27.5	0.108
Bryum caespiticium	M	WET	4.4	1.000	AND	3.0	1.000	AW	8.9	1.000
Bryum pallens	M	WET	11.1	0.339	AND	1.9	1.000	AW	5.8	1.000
Bryum sp.	M	INT	5.6	0.862	LIM	18.5	0.052	LI	11.1	0.509
Bryum turbinatum	M	INT	6.7	0.746	LIM	14.8	0.101	LI	13.3	0.419
Calliergon cf.	M	WET	15.4	0.233	AND	10.7	0.236	AW	19.7	0.268
Cratoneuron filicinum	M	WET	22.2	0.030*	LIM	4.3	1.000	LW	13	0.419
Distichium capillaceum	M	WET	3.5	0.932	LIM	6.7	0.507	LW	7.1	0.789
Dicranoweisia cirrata	M	INT	5.6	1.000	AND	3.7	1.000	AI	11.1	1.000
Dicranella sp.	M	WET	5.6	1.000	LIM	3.7	1.000	LW	11.1	1.000
Didymodon vinealis	M	WET	16.7	0.089	AND	7.2	0.496	AW	21.7	0.148
Encalypta affinis	M	INT	5.6	1.000	LIM	3.7	1.000	LI	11.1	1.000
Eurhynchium praelongum	M	INT	5.6	1.000	LIM	3.7	1.000	LI	11.1	1.000
Hygrohypnum luridum	M	WET	5.6	1.000	LIM	3.7	1.000	LW	11.1	1.000
Hygrohypnum molle	M	WET	5.6	1.000	AND	3.7	1.000	AW	11.1	1.000
Hymenostylium recurvirostre	M	INT	10.0	0.300	AND	5.9	0.745	AI	7.8	1.000
Hypnum sp.	M	INT	5.6	1.000	AND	3.7	1.000	AI	11.1	1.000
Leptobryum pyriforme	M	WET	11.1	0.339	AND	2.6	1.000	AW	7.8	1.000
Philonotis fontana	M	WET	85.0	0.001*	AND	26.1	0.580	AW	55	0.001*
Pohlia wahlenbergii	M	WET	11.1	0.335	LIM	2.1	1.000	LW	6.4	1.000
Plagiomnium ellipticum	M	WET	11.1	0.351	LIM	2.4	1.000	LW	7.3	1.000
Psuedoleskella tectorum	M	INT	5.6	1.000	AND	3.7	1.000	AI	11.1	1.000
Schistidium spp.	M	DRY	46.9	0.008*	LIM	51.6	0.002*	LD	65.1	0.002*
Weissia controversa	M	WET	17.4	0.166	AND	9.7	0.603	AW	15.5	0.592
Achillea millefolium	P	INT	5.6	1.000	LIM	3.7	1.000	LI	11.1	1.000
Agoseris laciniata	P	WET	5.6	1.000	LIM	3.7	1.000	LW	11.1	1.000
Agrostis stolonifera	P	WET	11.1	0.346	LIM	2.2	1.000	LW	6.7	1.000
Agrostis variabilis	P	WET	5.6	1.000	LIM	3.7	1.000	LW	11.1	1.000
Androsace septentrionalis	P	WET	5.6	1.000	LIM	3.7	1.000	LW	11.1	1.000
Arenaria congesta	P	WET	5.6	1.000	AND	3.7	1.000	AW	11.1	1.000

Table E.1.1. cont.

		Water			Substrate			Combination		
	LF[1]	Trt[2]	IV[3]	*p*-val[4]	Trt[2]	IV[3]	*p*-val[4]	Trt[2]	IV[3]	*p*-val[4]
Artemisia michauxiana	P	WET	5.6	1.000	LIM	3.7	1.000	LW	11.1	1.000
Aster borealis	P	WET	5.6	1.000	LIM	3.7	1.000	LW	11.1	1.000
Aster glaucodes	P	DRY	5.6	1.000	LIM	3.7	1.000	LD	11.1	1.000
Carex atrata	P	WET	5.6	1.000	AND	3.7	1.000	AW	11.1	1.000
Calamagrostis canadensis	P	WET	5.6	1.000	LIM	3.7	1.000	LW	11.1	1.000
Dodecatheon pulchella	P	WET	5.6	1.000	LIM	3.7	1.000	LW	11.1	1.000
Elymus trachycaulus	P	WET	6.7	0.777	AND	4.4	1.000	AW	4.4	1.000
Epilobium clavatum	P	WET	77.8	0.001*	LIM	19.5	0.424	LW	58.4	0.001*
Erigeron compositus	P	DRY	4.4	0.766	LIM	11.1	0.252	LD	8.9	0.407
Erigeron peregrinus	P	WET	5.6	1.000	LIM	3.7	1.000	LW	11.1	1.000
Heracleum lanatum	P	WET	5.6	1.000	LIM	3.7	1.000	LW	11.1	1.000
Luzula spicata	P	INT	7.4	0.765	LIM	14.8	0.131	LI	14.8	0.403
Mimulus glabratus	P	WET	5.6	1.000	AND	3.7	1.000	AW	11.1	1.000
Mimulus guttatus	P	WET	66.3	0.001*	LIM	11.6	0.981	LW	34.8	0.044*
Phleum alpinum	P	WET	5.6	1.000	LIM	3.7	1.000	LW	11.1	1.000
Phlox multiflora	P	DRY	5.6	1.000	LIM	3.7	1.000	LD	11.1	1.000
Picea glauca	P	WET	5.6	1.000	LIM	3.7	1.000	LW	11.1	1.000
Poa reflexa	P	WET	4.4	1.000	LIM	7.4	0.526	LW	8.9	1.000
Poa secunda	P	WET	5.6	1.000	LIM	3.7	1.000	LW	11.1	1.000
Saxifraga cespitosa	P	WET	22.2	0.028*	LIM	5.2	0.750	LW	15.6	0.207
Saxifraga odontoloma	P	WET	50.0	0.001*	LIM	12.3	0.536	LW	37	0.005*
Saxifraga rhomboidea	P	WET	16.7	0.121	LIM	5.9	0.483	LW	17.8	0.159
Saxifraga rivularis	P	WET	16.7	0.108	AND	11.1	0.215	AW	33.3	0.022*
Sagina saginoides	P	WET	5.6	1.000	AND	3.7	1.000	AW	11.1	1.000
Salix sp.	P	WET	5.6	1.000	AND	3.7	1.000	AW	11.1	1.000
Senecio canus	P	INT	7.4	0.759	LIM	11.1	0.244	LI	14.8	0.417
Sedum lanceolatum	P	DRY	4.8	1.000	LIM	18.5	0.046*	LD	9.5	0.755
Sedum rhodanthum	P	WET	9.3	0.323	AND	4.9	0.748	AW	5.6	1.000
Taraxacum sp.	P	INT	5.6	1.000	LIM	3.7	1.000	LI	11.1	1.000
Trisetum wolfii	P	WET	11.1	0.328	LIM	2.2	1.000	LW	6.7	1.000

[1] LF = Life form: F = fern, L = lichen, LV = liverwort, M = Moss, P = vascular plant.

[2] Trt = Treatment. For water: DRY = dry, INT = intermediate, WET = wet. For substrate: AND = andesite, LIM = limestone. For combination treatment: AD = andesite dry, AI = andesite intermediate, AW = andesite wet, LD = lime dry, LI = lime intermediate, LW = lime wet.

[3] IV = ISA indicator values calculated from fidelity and abundance within treatments.

[4] *P*-values are from tests of the H_0: the maximum IV value is no greater than expected by chance. Calculated using Monte Carlo procedures with 1000 permutations.

Appendix E.2: Species List for Cliff Sites

This list contains vascular plants, mosses, and lichens occurring in or near (<10m) from cliff transects. Asterisks indicate previously unreported species for Yellowstone National Park. New moss reports are uncertain due to a current re-annotation and cataloguing process for bryophyte specimens at the YNP herbarium (YELLO).

PLANTAE

Anthophyta

Achillea millefolium L. var. *lanulosa* (Nutt.) Piper
Agoseris aurantiaca (Hook.) Greene
Agoseris glauca (Pursh) Raf. var. *laciniata* (Eaton) Smiley
Agrostis exarata Trin.
Agrostis stolonifera L.
Agrostis variabilis Rydb.
Alnus viridis (Vill.) Lam. & DC. var. *sinuata* Regel
Androsace septentrionalis L. var. *subulifera* Gray
Arenaria congesta Nutt.
Arabis lyallii Wats.
Artemisia michauxiana Bess.
Aster borealis Prov.
Aster glaucodes Blake
Bromus carinatus H. & A.
Castilleja sp. Mutis ex L. f.
Carex atrata L. var. *erecta* Boott
Carex hoodii Boott
Calamagrostis canadensis (Michx.) Beauv.
Cirsium eatonii (Gray) Robins.
Collinsia parviflorum Lindl.
Collema linearis Nutt.
Dodecatheon pulchellum (Raf.) Merr.
Elymus trachycaulus (Link) Gould ex Shinners var. *trachycaulus*
Epilobium angustifolium L.
Epilobium clavatum Trel.
Epilobium lactiflorum Hausskn.
Erigeron compositus Pursh var. *discoideus* Gray
Erigeron peregrinus (Banks ex Pursh) Greene
Fragaria vesca L.
Geranium viscossisimum Fisch. & Meyer ex Meyer var. *viscossisimum*
Heracleum sphondylium L. var. *lanatum* (Michx.) Dorn
Lithophragma parviflorum (Hook.) Nutt. ex T. & G.
Luzula spicata (L.) DC.

Mimulus guttatus DC.
Mimulus lewisii Pursh
Myosotis arvensis (L.) Hill
Osmorhiza depauperata Phil.
Parnassia fimbriata Konig
Phacelia hastata Dougl. ex Lehm.
Phleum alpinum L.
Phlox multiflora A. Nels.
Picea glauca (Moench) Voss
Poa pattersonii Vasey
Poa reflexa Vasey & Scribn. ex Vasey
Poa secunda Presl
Ribes sp.
Rorippa tenerrima Greene
Rubus parviflorus Nutt.
Rubus sp.
Sagina saginoides (L.) Karsten
Saxifraga cespitosa L. var. *minima* Blank.
Saxifraga flagellaris Willd. ex Sternb. var. *crandallii* (Gand.) Dorn
Saxifraga odontoloma Piper
Saxifraga rhomboidea Greene
Saxifraga rivularis L. var. *debilis* (Engelm. ex Gray) Dorn
Saxifraga subapetela E. Nels.
Salix sp.
Senecio canus Hook.
Sedum lanceolatum Torrey
Sedum rhodanthum Gray
Taraxacum sp. Hall
Trisetum spicatum (L.) Richt.
Trisetum wolfii Vasey
Veronica sp.

Pterophyta
Cryptogramma arctostichoides R. Br.
Cystopteris fragilis (L.) Bernh.

Bryophyta (New reports within list unknown)
Bryum caespiticium Hedw.
Bryum pallens Sw.
Bryum spp.
Bryum turbinatum (Hedw.) Turn.
Calliergon cf.
Conocephalum conicum (L.) Lindb.
Cratoneuron filicinum (Hedw.) Spruce
Dicranella spp.

Dicranoweisia cirrata (Hedw.) Lindb.
Didymodon vinealis (Brid.) Zand
Distichium capillaceum (Hedw.) B.S.G.
Encalypta affinis Hedw.
Encalypta vulgaris Hedw.
Eurhynchium praelongum (Hedw.) B.S.G.
Hygrohypnum luridum (Hedw.)
Hygrohypnum molle (Hedw.) Loeske
Hymenostylium recurvirostre (Hedw.) Dix *cf*
Hypnum spp.
Leptobryum pyriforme (Hedw.) Wils.
Orthotrichum anomalum Hedw.
Orthotrichum cupulatum Hoff. ex Brid.
Philonotis fontana (Hewd.) Brid.
Plagiomnium ellipticum (Brid.) Kop.
Pohlia wahlenbergii (Web. & Mohr) Andr.
Psuedoleskella tectorum (Funck ex Brid.) Kindb. ex Broth.
Psuedoleskella nervosa (Brid.) Nih.
Schistidium spp.
Weissia controversa Hedw.

Hepatophyta

Conocephalum conicum *(L.) Underw.*
Reboulia hemispherica (L.) Raddi?

LICHENS

Acarospora glaucocarpa (Ach.) Körber
Allantoparmelia alpicola (Th. Fr.) Essl.*
Aspicilia aliena (Zahlbr.) Oksner *
Aspicilia caesiocinerea (Nyl. ex Marlbr.) Arnold
Aspicilia calcarea (L.) Mudd*
Aspicilia cinerea (L.) Körner
Aspicilia contorta (Hoffm.) Kremp.
Bellemerea cinereorufescens (Ach.) Clauzade & Roux
Buellia alboatra (Hoffm.) Th. Fr.*
Caloplaca citrina (Hoffm.) Th. Fr.
Caloplaca epithallina Lynge
*Caloplaca invadens Lynge**
Caloplaca saxicola (Hoffm.) Nordin
Candelariella aurella (Hoffm.) Zahlbr
Candelariella vitellina (Hoffm.) Müll.
Candelariella xanthostigma (Ach.) Lettau

Catapyrenium cinereum (Pers.) Koerber
Catillaria chalybeia (Borrer) A. Massal.*
Collema coccophorum Tuck.
Collema polycarpon Hoffm.
Collema tenax (Sw.) Ach.
Collema undulatum Laurer *ex* Flotow
Collema undulatum Laurer *ex* Flotow var. *granulosum* Degel*
Dermatocarpon intestiniforme (Körber) Hasse*
Dermatocarpon miniatum (L.) W. Mann
Endocarpon pulvinatum Th. Fr.
Gyalidea hyalinescens (Nyl.) Vezda*
Lecanora cenisia Ach.
Lecanora crenulata Hook.
Lecanora dispersa (Pers.) Sommerf.
Lecidea atrobrunnea (Raymond *ex* Lam. & DC.) Schaerer
Lecidea tessellata Flörke
Lecidella stigmatea (Ach.) Hertel & Leuckert
Lobothallia alphoplaca (Wahlenb.) Hafellner
Lempholemma cladodes (Tuck.) Zahlbr. *
Leptogium subaridum P.M. Jörg & Goward*
Phaeophyscia constipata (Norrlin & Nyl.) Moberg*
Phaeophyscia decolor (Kashiw.) Essl.
Physcia caesia (Hoffm.) Fürnr.
Physcia dubia (Hoffm.) Lettau
*Placidium (Catapyrenium) norvegicum (Breuss) Breuss**
Placynthium nigrum (Hudson) Gray
Protoblastenia calva (Dickson) Zahlbr.*
Psora tuckermanii R. Anderson *ex* Timdal
Psora himalayana (L. Bab.) Timdal
Rhizocarpon geographicum (L.) DC.
Rhizocarpon geminatum Körber
Rhizoplaca melanopthalma (DC.) Leucher & Poelt
Rinodina cf calcigena (Th. Fr.) Lynge*
Rinodina cf *oleaca**
Staurothele areolata (Ach.) Lettau
Staurothele drummondii (Tuck.) Tuck.
Staurothele fissa (Taylor) Zwackh
Thelidium sp. A. Massal*
Toninia alutacea (Anzi) Jatta*
Toninia candida (Weber) Th. Fr.
Verrucaria arctica Lynge*
Xanthoria elegans (Link) Th. Fr.
Xanthoria polycarpa (Hoffm.) Rieber
Xanthoria sorediata (Vainio) Poelt
Xanthoparmelia cumberlandia (Gyelnik) Hale

Appendix E.3: Complete sorted relevé for cliff species. LF = life-form: P = flowering plants, F = fern, M = moss, L = lichen. LI = lichen information: c = crustose, sq = squamous, f = foliose. Cells contain cover data: 0% = ".", 0.01-1% = A, 1-2% = B, 2-5% = C, 5-25% = D, >25% = E. The first letter in the row listing sites describes substrate: C = andesite-conglomerate, L = lime. The second letter describes water: W = wet, I = intermediate, D = dry; i.e. CW1= Conglomerate Wet treatment at site 1.

	LF	LI	CW7	CW8	CW9	CW2	CW5	CW6	CW3	CW4	CW1	LW7	LW8	LW9	LW6	LW4	LW2	LW3	LW5	LW1	CI6	CI8	CI2	CI3	CI1	LI9	LI7	LI8	LI2	LI3	LI1	LI5	LI6	LD8	LD9	LD6	LD4	LD7	LD3	LD2	LD1	LD5	LI4	CD9	CD7	CD8	CD6	CD5	CD4	CD2	CD3	CD1	CI7	CI9	CI5	CI4
Cryptogramma arctostichoides	F		D	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sagina saginoides	P		.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Mimulus glabratus	P		.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Arenerea congesta	P		.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex atrata	P		.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix spp.	P		.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Agoseris lanciniata	P		.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Picea glauca	P		.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Heracleum lanatum	P		.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Aster borealis	P		.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Calamagrostis canadensis	P		.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
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Erigeron peregrinus	P		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Artemesia michauxiana	P		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Phleum alpinum	P		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Androsace septentrionalis	P		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Agrostis variabilis	P		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dodecatheon pulchellum	P		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Achillea millifolium	P		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Taraxacum spp.	P		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Phlox multiflora	P		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Aster glaucodes	P		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga rivalis	P		A	A	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga rhomboidea	P		A	.	.	.	.	.	.	.	.	C	B	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga cespitosa	P		C	A	.	.	.	.	.	.	.	C	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Agrostis stolonifera	P		.	.	.	.	.	.	.	A	.	.	.	.	.	.	B	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga odontoloma	P		.	C	D	.	A	A	.	.	.	C	D	D	A	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Epilobium clavatum	P		.	C	D	.	B	A	A	A	.	C	A	B	C	.	D	A	C	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Mimulus guttatus	P		.	.	C	D	C	B	C	C	C	.	.	.	.	E	C	D	C	B	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cystopteris fragilis	F		B	A	.	A	.	.	.	.	.	.	B	.	.	.	A	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trisetum wolfii	P		.	.	.	A	.	.	.	.	.	.	.	.	.	.	B	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sedum rhodanthum	P		.	.	.	.	.	.	B	.	.	.	.	.	.	.	.	.	.	A	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Elymus trachycaulus	P		.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	A	.	.	.	.	A	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Luzula spicata	P		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	A	.	.	.	.	.	.	.	.	.	A	B	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa reflexa	P		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sedum lanceolatum	P		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	A	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	A	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Senecio canus	P		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	A	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.
Erigeron compositus	P		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	A	.	.	.	B	.	.	.	.	.	.	.	.	.	.	.	.	.
Hygrohypnum molle	M		.	D	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dicranella species	M		.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
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Hygrohypnum luridum	M		.	.	.	.	.	.	.	.	.	.	.	.	D	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Eurhynchium praelongum	M		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Encalypta affinis	M		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lempholemma cladodes	M		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
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Dicranoweisia cirrata	M		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.
Bryum pallens	M		C	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Leptobryum pyriforme	M		E	.	.	.	.	.	.	.	.	D	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Didymodon vinealis	M		.	B	.	.	.	E	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pohlia wahlenbergii	M		.	.	E	.	.	.	.	.	.	.	.	E	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plagiomnium ellipticum	M		.	.	.	.	.	D	.	.	.	.	D	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Appendix E.3 cont.

	LF	LI	CW7	CW8	CW9	CW2	CW5	CW6	CW3	CW4	CW1	LW7	LW8	LW9	LW6	LW4	LW2	LW3	LW5	LW1	CI6	CI8	CI2	CI3	CI1	LI9	LI7	LI8	LI2	LI3	LI1	LI5	LI6	LD8	LD9	LD6	LD4	LD7	LD3	LD2	LD1	LD5	LI4	CD9	CD7	CD8	CD6	CD5	CD4	CD2	CD3	CD1	CI7	CI9	CI5	CI4
Cratoneuron filicinum	M		C	.	.	.	D	.	.	.	.	E	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Calliergon cf.	M		.	E	C	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hymenostylium recurvirostre	M		.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Weissia controversa	M		.	.	.	A	.	.	.	.	D	A	.	.	.	.	.	A	.	.	.	.	.	.	B	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Conocephalum conicum	LV		C	.	B	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Philonotis fontana	M		D	D	.	D	D	D	E	D	D	A	D	.	C	D	D	D	D	D	C	.	A	.	.	.	.	A	A	.	C	B	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.
Cyanobacteria	A		.	C	.	.	D	.	.	E	.	.	C	.	E	A	.	.	E	.	D	.	A	.	A	D	.	C	.	.	.	.	D	.	.	.	.	.	.	.	C	.	D	.	.	.	.	A	.	.	.	.	.	.	.	.
Reboulia hemispherica?	LV		.	.	A	.	.	D	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A
Bryum caespiticium	M		.	.	.	.	.	.	.	.	B	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Distichium capillaceum	M		.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	B	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.
Bryum turbinatum	M		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	A	.	.	.	.	.	.	.	A	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Bryum spp.	M		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	A	B	.	.	.	.	.	.	A	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Schistidium spp.	M		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	A	.	.	A	A	C	.	B	.	C	A	.	C	C	B	D	B	.	C	D	D	D	A	.	.	A	.	.	B	A	.	.	.	.	.	.
Psuedoleskella tectorum	M		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B
Dermatocarpon intestiniforme	L	f	.	.	.	.	.	.	A	.	.	.	.	.	.	.	A	D	A	.	.	.	A	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dermatocarpon miniatum	L	f	.	.	.	.	.	.	.	.	.	D	B	.	.	A	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	A	B	A	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	A	.	.	.	.
Collema spp.	L	f	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	B	.	.	.	.	.	.	.	.	.	.	.	E	.	.	E	E	.	.	.	.	.	D	.	.	.	.	A	C	.	.	.	.	.	.	.
Collema undulatum v. *granulosum*	L	f	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	D	.	.	.	.	.	E	D	.	.	.	.	.	.	.	D	D	C	D	.	.	.	.	.	.	.	.	D	D	.	.	.	.
Gyalidea hyalinescens	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	D	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Acarospora glaucocarpa	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	B	.	B	.	.	.	.	.	D	C	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.
Placynthium nigrum	L	Sq	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	E	.	.	.	E	E	E	.	.	.	.	.	C	A	.	.	E	.	.	.	.	.	C	A	A	.	.	.	.	.	.	.	.	.	.
Staurothele drummondii	L	c	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	A	.	.	A	.	A	.	.	A	.	.	D	E	.	.	E	E	.	D	.	A	D	B	A	C	D	.	D	B	C	.	C	D	C
Collema spp. (all)	L	f	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	C	.	.	D	.	.	.	.	.	E	D	.	E	.	.	E	E	.	D	D	D	D	D	.	.	.	.	A	C	.	D	D	.	.	.	B
Candelariella spp. (all)	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	B	.	.	.	B	.	.	B	.	.	B	B	A	C	.	C	C	C	D	B	A	C	D	D	C	D	A	D	.	.	C	C	.
Collema tenax	L	f	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	D	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A
Aspicilia caesiocineria	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	D	.	.	.	.	.	.	.	.	.	.	.	.	B	B	.	.	.	.	C	.	.	.	D	E	D	E	E	E	D	B	.	D	C	A	D
Candelariella spp.	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	A	.	.	.	.	.	.	.	.	.	B	A	A	B	.	B	C	.	D	A	A	C	D	C	C	D	A	D	.	.	C	B	.
Lecidella stigmatea	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B	.	.	.	A	.	.	.	D	.	.	.	C	.	D	.	.	D	D	D	.	.	.	.	B	.	.	C	.	.
Caloplaca epithallina	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	B	.	.	.	.	.	.	.	.	.	.	D	C	.	.	.	.	.	.	C	.	.	.
Psora himalalayana	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	C	D	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.
Xanthoria elegans	L	f	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	D	A	.	D	.	C	C	D	D	A	A	.	.	B	D	.	A	B	C	.	.	A	C
Phaeophyscia decolor	L	f	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	C	.	D	.	.	.	.	.	.	.	A	.	.
Caloplaca species	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	D	.	.	.	.	.	.	.	.	.	D	.	.
Staurothele areolata	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	D	.	.	.
Aspicilia aliena	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.
Leptogium subaridum	L	f	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	A	C	.	.	.	.	.	.	.	.	B	.	.	.	.	.	.	.	.	.	.	.	.
Candelariella aurella	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.
Lecanora dispersa	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.
Verrucaria arctica	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	D	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.
Lecanora crenulata	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	B	E	.	A	.	.	.	.	.	.	.	.	D	.	.	.	.	.
Aspicilia cinerea	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B	.	.	.	.	.	B	.	.	.	.	.	.	.	.	.
Physcia dubia	L	f	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	A	C	C	.	.	.	.	.	.	.	.	.	.
Rhizocarpon geographicum	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	B	C	A	.	.	.	.	.	.	.	.	.	.
Endocarpon pulvinatum	L	Sq	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	C	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.
Lobothallia alphoplaca	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	A	A	A	.	.	.	.	.	.	.
Toninia alutacea	L	Sq	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	B	.	.	.	.	.	A	.	.	.	.	.	A	.	.	.	.	.	.	.
Rinodina spp.	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	C	A	.	.	.	.	.
Staurothele fissa	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B	.	A	.	.	.	.	.	.	.	.	.	D	.	.	D	D	.	.	D	.	.	.	D	.	D	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Toninia candida	L	Sq	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	A	.	C	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lichen UNKN4LD7	L		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	D	.	.	.	.	.	.	A	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lichen unknown	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Candelariella vitellina	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Collema polycarpon	L	f	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Appendix E.3 cont.

	LF	LI	CW7	CW8	CW9	CW2	CW5	CW6	CW3	CW4	CW1	LW7	LW8	LW9	LW6	LW4	LW2	LW3	LW5	LW1	CI6	CI8	CI2	CI3	CI1	LI9	LI7	LI8	LI2	LI3	LI1	LI5	LI6	LD8	LD9	LD6	LD4	LD7	LD3	LD2	LD1	LD5	LI4	CD9	CD7	CD8	CD6	CD5	CD4	CD2	CD3	CD1	CI7	CI9	CI5	CI4
Thelidium spp.	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Aspicilia spp.	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Catapyrenium norvegicum	L	Sq	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Catillaria chalybeia	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Catapyrenium sp.	L	Sq	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Catapyrenium cereneum	L	Sq	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lichen UNKN2LD3	L		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Psora tuckermanii	L	Sq	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lecanora species	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lecidea atrobrunnea	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	D	C	.	C	A	.	.	.	.	.	.	.
Rhizoplaca melanopthalma	L	f	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	A	B	.	.	.	.	.	.	.
Lichen UNKN3CD3	L		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	D	.	C	.	.	.	.	.
Lichen UNKN1CD5	L		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	D	.	.	.	.	.	.	.	.
Lecidea spp.	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B	.	.	.	.	.	.	.
Xanthoria polycarpa	L	f	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	D	.	.	.	.	.	.	.
Physcia spp.	L	f	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.
Caloplaca saxicola	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	D	.	.	.	A	C	.	.	.	.
Aspicilia calcarea	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.
Rhizocarpon geminatum	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	D	D	.	.	.	.	.	.	C	.	.	.
Aspicilia contorta	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	D	.	.	.	.	.	.	.	.	.	A	.	.
Rhizocarpon spp.	L	c	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	B	A	.	.	.	.	.	D	D

APPENDIX F

APPENDICES PERTAINING TO CHAPTER 7--

USING GEOMETRIC AND NON-GEOMETRIC INTERNAL EVALUATORS TO COMPARE EIGHT VEGETATION CLASSIFICATION METHODS

APPENDIX F.1: Algorithms and Equations Used in Chapter 7

Average Silhouette Width (ASW, Rousseeuw 1987)[*]

1. Consider i, an element from cluster A,
   $a(i)$ = average dissimilarity of i to all other objects of A,
2. Now consider all other clusters $C \neq A$,
   $d(i, C)$ = average dissimilarity of i to all objects in $C \neq A$
   $b(i) = \min d(i, C)$

$$sw(i) = b(i) - a(i) / \max\{a(i), b(i)\}$$

$sw(i)$ = silhouette width for object (sample) i in cluster A

$$ASW = \frac{\sum_{i=1}^{n} sw(i)}{N} \tag{7.1}$$

ASW = Average Silhouette Width
N = number of objects (samples) in classification

C-index (Hubert and Levin 1975)

$$C = \frac{d_w - d_{\min}}{d_{\max} - d_{\min}} \tag{7.2}$$

C = C-index
d_w = the sum of within cluster similarity for all clusters

To calculate d_{min} and d_{max} assume that p is the number of pairs of samples for which both samples are located in the same cluster. The sum of p-pairs of samples with smallest distance = d_{min}. The sum of p-pairs of samples with largest distance = d_{max}.
Note: minimum responses = optimal solutions

Gamma (Goodman and Kruskal 1954)

A quadruple is concordant if distances within the quadruple agree with one of the following two conditions: $d(a,b) < d(c,d)$ when a and b are in the same cluster and c and d are in different clusters, or $d(a,b) > d(c,d)$ when a and b are in different clusters and c and d are in the same cluster.

A quadruple is disconcordant if distances within the quadruple agree with one of the following two conditions: $d(a,b) < d(c,d)$ when a and b are in different clusters and c and d are in the same

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[*] For bibliographic information on Appendix F see the Chapter 7 literature cited section.

cluster, or *d(a,b) > d(c,d)* when *a* and *b* are in the same cluster and *c* and *d* are in different clusters.

$$\gamma = \frac{N_c - N_d}{N_c + N_d} \tag{7.3}$$

γ = Goodman-Kruskal index (Gamma)
N_c = number of concordant quadruples
N_d = number of disconcordant quadruples

Note: This explanation of the Goodman-Kruskal index borrows heavily from a description by Bolshakova and Azuaje (In press)

ISA average p-value, and number of ISA significant indicators at α =0.05 (Dufrêne and Legendre 1997, McCune and Grace 2002)

1. To calculate IV scores, first calculate mean abundance (MA) of species *j* in group *k,*

$$\forall j,k \qquad MA_{jk} = \frac{\sum_{i=1}^{n_k} a_{ijk}}{n_k}$$

a_{ijk} = abundance of species *j* in sample unit *i* of cluster *k.*
n_k = number of sample units in group *k*

and relative abundance (RA) of species *j* in group *k*

$$\forall j,k \qquad RA_{jk} = \frac{MA_{jk}}{\sum_{k=1}^{g} MA_{jk}}$$

g = total number of groups

2. Then transform data to presence/absence,

$$b_{ij} = \begin{cases} 1 \text{ when } a_{ij} > 0 \\ 0 \text{ when } a_{ij} = 0 \end{cases}$$

and calculate relative frequency (RF)

$$\forall j,k \qquad RF_{jk} = \frac{\sum_{i=1}^{nk} b_{ijk}}{n_k}$$

3. Finally calculate Indicator Values (IV)

$$\forall j,k \qquad IV_{jk} = 100(RA_{jk} \times RF_{jk}) \tag{7.4}$$

Note: IV scores were tested for significance with Monte Carlo procedures, resulting in *p*-values. Average *p*-value, and significant number of indicators at $\alpha = 0.05$, were derived from these tests. Minimum average *p*-value responses indicate optimal clustering solutions.

ISAMIC (Roberts 2005)

$$I = \frac{\sum_{i=1}^{n} \left(2\sum_{k=1}^{g} \left| C_{ik} - 0.5 \right| \right) \Big/ g}{n} \tag{7.5}$$

I = average ISAMIC score
C_{ik} = constancy of species *i* in group *k*
g = number of groups ($k = 1, 2, ..., g$)
n = number of species
*Constancy of spp. *i* in cluster *k* = # of samples in cluster *k* with spp *i* / # of samples in cluster *k*

Morisita's Index of niche overlap (adapted from Horn 1966)

$$C_H = \frac{2\sum_{i=1}^{n} p_{ij} p_{ik}}{\sum_{i=1}^{n} p_{ij}^2 + \sum_{i=1}^{n} p_{ik}^2} \tag{7.6}$$

C_H = adapted Morisita index of niche overlap
p_{ij} = proportional occurrence of species *i* with respect to all species in cluster *j*
p_{ik} = proportional occurrence of species *i* with respect to all species in cluster *k*
n = total number of species

Note: C_H scores were calculated for all pairwise niche overlap measures between groups. For *g* groups: [(*g*2-*g*)/2 = no. of comparisons]. The mean of these pairwise relationships was calculated to represent a measure of overlap for a particular classification solution. Minimum niche overlap indicates optimal solutions

PARTANA ratio (Roberts 2005)

$$P = \frac{\displaystyle \sum_{z=1}^{C} \sum_{\substack{i=1 \\ i \in z}}^{N-1} \sum_{\substack{j=i+1 \\ j \in z}}^{N} S_{ij} \Bigg/ \sum_{z=1}^{C} (n_z^2 - n_z)/2}{\displaystyle \sum_{i=1}^{N-1} \sum_{\substack{j=i+1 \\ \omega_i \neq \omega_j}}^{N} S_{ij} \Bigg/ \sum_{z=1}^{C-1} \sum_{k=z+1}^{C} n_z \cdot n_k} \tag{7.7}$$

P = PARTANA ratio
N = total number of objects (samples) in dataset numbered i thru N
C = number of clusters
n_z = number of objects (samples) in the z th cluster (z = 1, 2, ..., C)
ω = membership; thus $\omega i \neq \omega j$ indicates that i and j are objects from different clusters
S_{ij} = the similarity of objects i and j.

Note: $S_{ij} = 1 - d_{ij}$, when d = a dissimilarity measure, and $S_{ij} = 1 - d_{ij}/$ [max (all possible pairwise distances)], when d is a metric distance measure.

Point Biserial Correlation (PBC, Brogden 1949)

$$PBC = corr(D, B) \tag{7.8}$$

PBC = Point Biserial Correlation
D = dissimilarity data matrix
B = a symmetric matrix of ones and zeroes with the same dimensions as D; 0 = samples in the same cluster, 1 = samples in different clusters.