Ecological Process and the Blister Rust Epidemic:
Cone Production, Cone Predation, and Seed Dispersal in
Whitebark Pine (*Pinus albicaulis*)

By:

Shawn Thomas McKinney

B.A. University of Colorado-Boulder, Boulder, CO, 1996

M.S. University of Colorado-Denver and Health Sciences Center, Denver, CO, 2004

Dissertation
presented in partial fulfillment of the requirements for
the degree of
Doctor of Philosophy

Department of Forest Management
College of Forestry and Conservation
The University of Montana
Missoula, MT

Summer 2007

Approved by:

Dr. David A. Strobel, Dean
Graduate School

Dr. Carl Fiedler, Chairperson
Forest Management, College of Forestry and Conservation

Dr. Elizabeth Crone
Wildlife Biology, College of Forestry and Conservation

Dr. Anna Sala
Division of Biological Sciences

Dr. Diana Tomback
Biology, CU-Denver and Health Sciences Center

Dr. Hans Zuuring
Forest Management, College of Forestry and Conservation

McKinney, Shawn T., Ph.D., July 2007   College of Forestry and Conservation

Ecological Process and the Blister Rust Epidemic: Cone Production, Cone Predation, and Seed Dispersal in Whitebark Pine (*Pinus albicaulis*)

Chairperson: Carl E. Fiedler

  Whitebark pine (*Pinus albicaulis*), a high elevation foundation species, is experiencing population declines throughout the northern part of its range. The introduced fungal pathogen, *Cronartium ribicola* (white pine blister rust), infects whitebark pine and kills cone-bearing branches and trees. Blister rust has spread nearly rangewide and damage and mortality are highest in the northwest US and southwest Canada. Mortality caused by mountain pine beetle (*Dendroctonus ponderosae*) population upsurges, and successional replacement and loss of regeneration opportunities from fire suppression, are also impacting some whitebark pine populations. Within this dissertation, I present three manuscripts that address the impact of whitebark pine's decline on species interactions and ecological processes within subalpine forests. Research was conducted in three ecosystems in the Rocky Mountains USA that are distinct in whitebark pine health conditions (rust infection and mortality) and abundance. In the first manuscript, I explore how the relationship between whitebark pine and Clark's Nutcracker (*Nucifraga columbiana*), its primary seed disperser, is being affected by whitebark's decline. Nutcrackers were less likely to use and disperse seeds from forests where cone production is below a threshold. In the second manuscript, I describe habitat use of whitebark pine forests by red squirrels (*Tamiasciurus hudsonicus*). Squirrel residency and impact of cone predation increased with decreasing whitebark pine abundance. The third manuscript focuses on the tree-level ecological process, predispersal cone survival, as a function of coarse scale whitebark pine abundance. Surviving trees in high mortality forests were found to have a lower rate and higher variability of cone survival, suggesting that the putative levels of rust-resistance in surviving trees of high mortality forests may not be passed on to future generations. At the ecosystem level, the Northern Divide had the highest levels of rust infection and tree mortality and lowest nutcracker interaction and regeneration levels; the Greater Yellowstone had the lowest infection and mortality levels and nutcrackers were present and dispersing seeds at all research sites in all years, while the Bitterroot Mountains were intermediate in these comparisons. These findings provide important components for developing a long-term strategy to conserve and restore whitebark pine ecosystems in the Rocky Mountains.

DEDICATION

I dedicate this dissertation to my family, without whom I would never have achieved this goal. My wife, Lisa, in particular for always believing in me and challenging me to do my best; my son, Finnegan for being my inspiration; my father, Thomas for looking after my family while I was in the field and for always being there when we needed him. To my mom, Emily, and sister, Laura who have always been a big part of who I am.

Finally, I dedicate this dissertation to the loving memory of Morgan McKinney (May 28, 1991–August 21, 2006); field companion, camp guardian, and best friend. Morgan, you are always in my heart and forever in my soul.

ACKNOWLEDGMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1

Whitebark Pine Community Ecology and Decline: An Overview

Whitebark Pine

Whitebark pine (*Pinus albicaulis*), a subalpine and treeline forest species, ranges throughout the western United States and Canada. In general, whitebark pine occurs as a climax species on the coldest and driest sites – areas too harsh for its competitors to thrive – and occurs as a seral species on protected, lower elevation sites that favor its shade-tolerant competitors (Arno and Weaver 1990). It comprises long chains on mountain ridges and forms isolated high-elevation patches between continuous forest, providing both corridor and stepping stone connectivity that allows for movement of numerous wildlife species.

Many important ecological functions in high-elevation ecosystems are provided by whitebark pine, such as regulating runoff, stabilizing soil, reducing erosion, colonizing sites after wildfire, and facilitating the forest successional process (see Tomback et. al. 2001 for overview). Runoff from spring snowmelt is tempered by whitebark pine growing at high elevations, resulting in later melt-off and higher stream flows in the summer (Farnes 1990). Regulated runoff and the physical presence of tree roots act to stabilize soils and thereby reduce soil erosion (Farnes 1990). As an early seral species, whitebark pine often is the first species to become established following large subalpine forest fires (Tomback 1986; Tomback et al. 1993; Tomback 1994). The early establishment of whitebark pine on these burned, harsh sites can ameliorate conditions

and create microsites for seedling establishment of other conifer species, thus facilitating forest succession (Callaway 1998).

Whitebark pine is the only North American 'stone pine' species (subsection *Cembrae*, section *Strobus*, subgenus *Strobus*, genus *Pinus*, family Pinaceae) (Price et al., 1998). *Cembrae* pines have five needles per fascicle; terminal umbos on ovulate cones; and large, wingless seeds retained in indehiscent cones (i.e., cone scales remain closed even after seeds ripen) (Price et al. 1998). Wingless seeds and indehiscent cones are traits considered to be derived and are explained by the coevolved seed dispersal mutualism between *Cembrae* pines and members of the genus *Nucifraga* (the nutcrackers, family Corvidae) (Lanner 1980; Tomback 1983; Tomback and Linhart 1990). The cone morphology of *Cembrae* pines precludes seed dispersal by wind and increases the likelihood that seeds will remain in cones until they are removed and dispersed by *Nucifraga* birds (Tomback 2005).

The large, wingless seeds of whitebark pine are the heaviest (mean mass = 175 mg seed^{-1}) of all subalpine conifers found throughout its range (Tomback et al. 2001). Large seed mass coupled with a relatively high fat content (Lanner and Gilbert 1994) make whitebark pine seeds an important high-energy food for many granivorous birds and mammals (Tomback 1978; Hutchins and Lanner 1982). Its seeds are particularly important for Clark's Nutcracker (*Nucifraga columbiana*), the primary seed disperser of whitebark pine; red squirrels (*Tamiasciurus hudsonicus*), which cut down whitebark pine cones and store them in middens; and grizzly bears (*Ursus arctos*), which raid squirrel middens and consume whitebark pine seeds. Specifically, whitebark pine seeds are a critical food source for grizzlies in the Greater Yellowstone Ecosystem (Kendall 1983;

Mattson et al. 1991). During periods when the pine's seeds are plentiful and used

intensively, the bear population increases – in periods when they are not, the population

decreases (Pease and Mattson 1999). Lacking this dietary staple, grizzlies often descend

into inhabited areas searching for food, resulting in dramatic increases in human/bear

confrontations and sometimes in death to the bear. Indeed, grizzly bear death rates are

nearly double in years when few seeds are consumed (Mattson et al. 1992).

Whitebark pine increases the biodiversity of its community through the

characteristics that allow it to colonize burned sites; modify conditions in the harsh

upper-subalpine environment; and provide high-energy seeds, shelter, and nesting sites

for wildlife (Tomback and Kendall 2001). Because of these important ecological

functions that act to enhance biodiversity, whitebark pine is considered a keystone

species of upper subalpine ecosystems (Tomback et al. 2001).

Clark's Nutcracker

The Clark's Nutcracker and whitebark pine are coevolved mutualists (Tomback

1982; Tomback and Linhart 1990), whereby the pine is obligately dependent upon the

bird for dispersal of its large, wingless seeds. In late summer and early fall, nutcrackers

extract ripe whitebark pine seeds from the closed cones, transport seeds in a specialized

sublingual pouch that is unique to the genus *Nucifraga* (Bock et al. 1973), and store from

one to 15 seeds in small caches at an average depth of 2.5 cm below the ground

(Tomback 1978; Tomback 1982; Hutchins and Lanner 1982). Nutcrackers often use

recently disturbed areas such as burns and clearcuts for seed caching, which results in

early successional establishment of whitebark pine (Tomback 1986; Tomback et al.

2001). Clark's Nutcracker seed dispersal and caching behavior provide the only

ecologically significant vector for whitebark pine seedling establishment (Tomback 1982;

Hutchins & Lanner 1982).

Whereas whitebark pine depends nearly exclusively on nutcrackers, the bird

harvests and caches seeds of other large-seeded pines (e.g., Tomback 1978; 1998).

Indeed, the biology of the Clark's Nutcracker is closely tied to seed production of various

Pinus species (Tomback 1978; 1998). Nutcrackers forage on pine seeds throughout the

summer and early fall, derive much of their winter and spring food from seeds collected

the previous fall, and in early spring, feed nestlings with pine seeds gathered from the

previous fall's caches (Mewaldt 1956; Vander Wall 1988). Detailed studies from several

forest types in western North America estimate that an individual nutcracker's stored

seeds represent from 1.8 to 5 times the energy required to survive the winter (Vander

Wall & Balda 1977; Tomback 1982; Vander Wall 1988). In addition, the birds are

sensitive to rates of energy gain and increase their foraging efficiency by adjusting for

changes in seed ripeness within forests, and by selecting trees with higher cone densities

and cones with higher proportions of edible seeds (Vander Wall & Balda 1977; Tomback

1978; Tomback & Kramer 1980; Vander Wall 1988).

In early summer, nutcrackers forage in subalpine forests and assess the

developing cone crop at a time when the energetic payoff is less than the energetic

expenditure (Vander Wall 1988). This adaptation presumably buffers populations from

the impacts of cone crop failure by alerting them to future seed shortages before they

occur (Vander Wall et al. 1981). Nutcrackers either emigrate or irrupt from the subalpine

environment in search of alternative food in years of poor seed production, depending on

whether the scarcity is geographically localized or widespread, respectively (Davis &

Williams 1957, 1964; Bock & Lepthien 1976). During these years, nutcrackers exhibit

tremendous plasticity in foraging behavior, consuming a diversity of food sources from

ground squirrels and chipmunks to dung beetles and yellowjackets (Davis & Williams

1957). However, mortality is likely higher and reproduction lower during cone failure

years (Vander Wall et al. 1981). Nutcrackers apparently return to subalpine forests the

spring following years of mass migration and again assess the current year's cone crop

(Vander Wall et al. 1981). Thus the size, mortality, and reproductive rates of nutcracker

populations are likely closely associated with cone production of their preferred *Pinus*

species.

Red Squirrel

The red squirrel is a highly territorial, arboreal granivore and fungivore.

Territories are maintained by a single adult that cuts conifer cones and stores them in

middens (Smith 1981). Middens are accumulations of cone debris, sometimes as large as

7 m across and 0.5 m deep, that cover the ground to the exclusion of all living plants

(Finley 1969). Red squirrels are efficient central-place foragers (Elliott 1988) that can

harvest up to 100% of *Pinus* cone crops (Flyger and Gates 1982). The squirrels

preferentially select cones from the tree species with the highest cone energy content (i.e.,

the energy available to squirrels in the seed endosperm and embryos of cones = no. of

seeds cone^{-1} * calories seed^{-1}) (Smith 1970).

The geographical ranges of the red squirrel and whitebark pine are sympatric in

the Rocky Mountains where both species maintain a boreal affinity. Red squirrels prefer

whitebark pine cones over those of other conifers in mixed species subalpine forests (Hutchins and Lanner 1982). In these habitat conditions, red squirrels are the most efficient predator on whitebark pine seeds because they remove cones from trees at a rapid rate, taking as much as 80% of the cone crop and depleting the numbers available for nutcrackers (Hutchins and Lanner 1982; McKinney and Tomback 2007).

Previous research on red squirrels has documented a preference for habitat conditions that ensure a dependable supply of conifer cones and fungi (dense forests of mixed conifer species), allow for adequate cone storage (cool and moist forest floor), and provide escape from predators (closed canopies) (see Steele 1998 for overview). However, suboptimal habitats that do not possess all of these characteristics can be temporarily used during periods of population growth (Rusch and Reeder 1978). Individuals will disperse into suboptimal habitat, cut cones to eat *in situ* or carry back to a territory, or attempt to form a territory there. However, strong philopatry, increased predation risk with increasing dispersal distance, and lower survival, indicate that squirrel occurrence in suboptimal habitat is most often transient (Larsen and Boutin 1994).

Previous studies in the Greater Yellowstone Ecosystem have shown that red squirrel densities increase as the basal area of lodgepole pine (*Pinus contorta*) increases in whitebark pine habitat, suggesting the importance of alternative food sources for squirrels (Mattson and Reinhart 1997). Although the large seeds of whitebark pine are preferred by red squirrels, lodgepole pine and other conifers produce cones in years when whitebark pine does not, ensuring a dependable food supply. Reinhart and Mattson (1990) found fewer resident squirrels in stands of nearly-pure whitebark pine compared to mixed species stands containing whitebark pine. They speculated that pure whitebark

pine forests were not hospitable habitat for squirrels because of lower basal area and tree diversity, greater cone crop variability, and harsher environmental conditions compared to mixed conifer species forests (Reinhart and Mattson 1990).

Whitebark Pine Decline

Whitebark pine's future is uncertain throughout the Rocky Mountains – with local to regional extinction a real possibility. Populations are declining primarily because of the disease white pine blister rust, caused by *Cronartium ribicola* (division Basidiomycota, order Uredinales), a fungal pathogen native to Eurasia (McDonald and Hoff 2001). Since its introduction near Vancouver, Canada in 1910, *C. ribicola* has been spreading across western North American forests. Previous attempts to control it, including elimination of *Ribes*, one of its alternate hosts, were in vain (McDonald and Hoff 2001). Whitebark pine shows high susceptibility to blister rust (Hoff et al. 1980), and blister rust now occurs throughout the Canadian range of whitebark pine (Campbell and Antos 2000; Zeglen 2002) and most of its US range (Kendall and Keane 2001; Schwandt 2006).

Blister rust disrupts whitebark pine's regeneration process by first infecting and killing cone-bearing branches and then entire trees, and thus reduces cone production within trees and forest stands (McDonald and Hoff 2001; McKinney and Tomback 2007). Mean blister rust infection levels were 66% (range on average from 17% to 89%) and mean mortality was 35% (range on average of 8% to 58%) in stands sampled throughout the northwestern US and southwestern Canada (Kendall and Keane 2001).

Cronartium ribicola is acting as a selective force by causing differential survival among whitebark pine trees in rust-infected forests. Studies have shown that surviving whitebark pine trees from high-mortality stands possess higher levels of heritable resistance than trees from low-mortality stands (Hoff et al. 1994), and that more than 40 percent of the progeny of high-mortality survivors display resistance to blister rust (Hoff et al. 2001). The long-term persistence of whitebark pine in the presence of blister rust will require a dramatic increase in the frequency of rust-resistant alleles, which was estimated to be only 1-5% within populations first exposed to the rust (Hoff et al. 1994). Recent investigations demonstrate that whitebark pine does have genetic variation in rust resistance, increasing in frequency from southeast to northwest in the US Rocky Mountains (Mahalovich et al., 2006).

Whitebark pine has additional challenges to its survival. Nearly a century of fire suppression has resulted in successional replacement of some seral whitebark pine communities in the Northern Rocky Mountains and elsewhere by more shade-tolerant conifers, including subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*), which were more limited historically (Murray et al. 2000; Brown et al. 1994; Keane and Arno 1993; Arno 1986). Natural fire also plays a key role in whitebark pine's reproductive ecology because nutcrackers tend to cache in recently burned and open-canopied sites (Tomback 1986; Morgan and Bunting 1990; Tomback et al. 1990). Furthermore, recent upsurges of mountain pine beetles (*Dendroctonus ponderosae*), which may be related to warming trends, are now rapidly killing whitebark pine (Logan and Powell 2001). In areas where fire occurs, and where the whitebark pine seed source

is nearly destroyed from earlier pine beetle infestations and blister rust, regeneration is slow and seedlings die from blister rust (Tomback et al. 1995).

Alarming declines in whitebark pine populations threaten the key ecological roles and considerable biodiversity these forests provide. In response, federal land managers are applying restoration treatments to counter the threats of blister rust, advancing succession, and mountain pine beetle. The overall recovery strategy for whitebark pine includes both restoration planting of nursery-grown, rust-resistant seedlings and facilitated natural regeneration (focused silvicultural cutting and prescribed burning to provide hospitable sites for nutcracker seed dispersal and caching) (Schwandt 2006; Mahalovich et al. 2006; Schoettle 2004; Keane and Arno 2001). Increasing the frequency of genetic resistance to the blister rust pathogen within populations is the most promising management strategy for conserving whitebark pine. And the most effective way to increase rust-resistance is by planting seedlings grown from stock with known genetic resistance (Bingham 1983). However, because restoration planting is costly, spatially restricted, and uncertain in outcome, the natural regeneration approach should be implemented wherever feasible.

Dissertation Summary

Research that lead to this dissertation took place in three ecosystems in the Rocky Mountains U.S.A. that are distinct in whitebark pine health conditions (rust infection and mortality) and abundance. I present three chapters of original research that collectively address the impact of whitebark pine's decline on species interactions and ecological processes within Rocky Mountain subalpine ecosystems. By understanding how basic

ecological relationships have changed within communities suffering reduced abundance of whitebark pine, we will be able to forecast the potential for whitebark pine to recover, anticipate the reaction of other species, and provide key information to help guide whitebark pine restoration decisions.

In the first manuscript I address the impact of whitebark pine decline on habitat use by Clark's Nutcracker. Identifying nutcrackers' response to reduced whitebark pine abundance is paramount to forecasting the potential for natural regeneration and for natural increases in rust-resistant alleles. However, given the nutcracker's tendency to emigrate when cone crops are small, and because of increasing losses of cone production capacity within whitebark pine stands, the risk of local and even regional disruption to the nutcracker-whitebark pine mutualism exists. In this manuscript, I address the question of whether there is a threshold of whitebark pine cone production below which the likelihood of nutcracker seed dispersal precipitously drops. The objectives of this study are to quantify the relationship between cone production and whitebark pine stand structure and health attributes, and to model the probability of nutcracker seed dispersal as a function of cone production.

I describe red squirrel habitat use and subsequent cone predation in whitebark pine forests under varying conditions of health and composition in the second manuscript. Red squirrels thrive in mixed conifer forests but appear to prefer whitebark pine cones compared to other associated conifer species. Furthermore, squirrels can harvest cones at such a rapid rate that few seeds are available for nutcracker dispersal. Since blister rust acts to reduce whitebark pine cone production, it is important to quantify the impact of squirrels on reduced cone production. My fundamental question,

then, is how do changes in whitebark pine relative abundance influence habitat use and relative rates of cone predation by red squirrels.

The third chapter investigates how changes in whitebark pine forest conditions at a coarse scale are related to conditions and processes at the tree level. In many high mortality forests, phenotypically rust-resistant trees survive that have the potential to benefit from the selective advantage created by the blister rust epidemic. However, this potential selective advantage of the few rust resistant individuals will not be realized if their seeds do not survive to be dispersed by nutcrackers. My fundamental question in this third manuscript is whether coarse scale differences in whitebark pine forest attributes equate to differences in rate, variation, and scale dependence of predispersal cone survival, a key tree-level ecological process.

The integrated objective of these three investigations is to provide important components for developing a long-term strategy to conserve and restore whitebark pine ecosystems in the Rocky Mountains.

Literature Cited

Arno, S. F. 1986. Whitebark pine cone crops – A diminishing source of wildlife food? Western Journal of Applied Forestry 1:92-94.

Arno, S. F., and T. Weaver. 1990. Whitebark pine community types and their patterns on the landscape. Pages 97-105 *in* W. C. Schmidt and K. J. McDonald, editors. Proceedings—Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource. USDA Forest Service General Technical Report INT-270, Ogden, Utah.

Bingham, R. T. 1983. Blister rust resistant western white pine for the Inland Empire: the story of the first 25 years of the research and development program. USDA Forest Service General Technical Report INT-146, Ogden, Utah, USA.

Bock, C. E., and L. W. Lepthien. 1976. Synchronous eruptions of boreal seed-eating birds. The American Naturalist 110:559-571.

Bock, W. J., R. P. Balda, and S. B. Vander Wall. 1973. Morphology of the sublingual pouch and tongue musculature in Clark's nutcracker. Auk 90:491-519.

Brown, J. K., S. F. Arno, S. W. Barrett, and J. P. Menakis. 1994. Comparing the prescribed fire program with presettlement fires in the Selway-Bitterroot Wilderness. International Journal of Wildland Fire 4:157-168.

Callaway, R. M. 1998. Competition and facilitation on elevation gradients in subalpine forests of the northern Rocky Mountains, USA. Oikos 82:561-573.

Campbell, E. A., and J. A. Antos. 2000. Distribution and severity of white pine blister rust and mountain pine beetle on whitebark pine in British Columbia. Canadian Journal of Forest Research 30:1051-1059.

Davis, J., and L. Williams. 1957. Irruption of the Clark Nutcracker in California. The Condor 59:297-307.

Davis, J., and L. Williams. 1964. The 1961 Irruption of the Clark's Nutcracker in California. The Wilson Bulletin 76:10-18.

Elliott, P. F. 1988. Foraging behavior of a central-place forager: field tests of theoretical predictions. The American Naturalist 331:159-174.

Farnes, P. E. 1990. SNOTEL and snow course data describing the hydrology of whitebark pine ecosystems. Pages 302-304 *in* W. C. Schmidt and K. J. McDonald, editors. Proceedings—Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource. USDA Forest Service General Technical Report INT-270, Ogden, Utah, USA.

Finley, R. B., Jr. 1969. Cone caches and middens of *Tamiasciurus* in the Rocky Mountain region. Miscellaneous Publications of the University of Kansas Museum of Natural History 51:233-273.

Flyger, V., and J. E. Gates. 1982. Pine squirrels: *Tamiasciurus hudsonicus, T. douglasii*. Pages 230-237 *in* J. A. Chapman and G. A. Feldhamer, editors. Wild mammals of North America. John Hopkins University Press, Baltimore, Maryland, USA.

Hoff, R. J., R. T. Bingham, and G. I. McDonald. 1980. Relative blister rust resistance of white pines. European Journal of Forest Pathology 10:307-316.

Hoff, R. J., S. K. Hagle, and R. G. Krebill. 1994. Genetic consequences and research challenges of blister rust in whitebark pine forests. Pages 118-126 *in* W. C. Schmidt and F. K. Holtmeier, editors. Proceedings—International Workshop on

Subalpine Stone Pines and Their Environment: the Status of Our Knowledge. USDA Forest Service General Technical Report INT-309, Ogden, Utah, USA.

Hoff, R. J., D. E. Ferguson, G. I. McDonald, and R. E. Keane. 2001. Strategies for managing whitebark pine in the presence of white pine blister rust. Pages 346-366 *in* D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, D.C., USA.

Hutchins, H. E., and R. M. Lanner. 1982. The central role of Clark's Nutcracker in the dispersal and establishment of whitebark pine. Oecologia 55:192-201.

Keane, R. E., and S. F. Arno. 1993. Rapid decline of whitebark pine in Western Montana: Evidence from 20-year remeasurements. Western Journal of Applied Forestry 8:44-47.

Keane, R. E., and S. F. Arno. 2001. Restoration concepts and techniques. Pages 367-400 *in* D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, D.C., USA.

Kendall, K. C. 1983. Use of pine nuts by grizzly and black bears in the Yellowstone area. International Conference on Bear Research and Management 5:166-173.

Kendall, K. C., and R. E. Keane. 2001. Whitebark pine decline: infection, mortality, and population trends. Pages 221-242 *in* D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, D.C., USA.

Lanner, R. M. 1980. Avian seed dispersal as a factor in the ecology and evolution of limber and whitebark pine. Pages 15-48 *in* B. P. Dancik and K. O. Higginbotham,

editors. Proceedings of the sixth North American forest biology workshop. University of Alberta, Edmonton, Alberta, Canada.

Lanner, R. M., and B. K. Gilbert. 1994. Nutritive value of whitebark pine seeds and the question of their variable dormancy. Pages 206-211 *in* W. C. Schmidt and F. K. Holtmeier, editors. Proceedings—International Workshop on Subalpine Stone Pines and Their Environment: the Status of Our Knowledge. USDA Forest Service General Technical Report INT-309, Ogden, Utah, USA.

Larsen, K. W., and S. Boutin. 1994. Movements, survival, and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. Ecology 75:241-223.

Little, E. L. Jr., 1971: Atlas of United States Trees. Volume 1. Conifers and important hardwoods. USDA Forest Service Miscellaneous Publication No. 1146. Washington, D.C.

Logan, J. A., and J. A. Powell. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). American Entomologist 47:160-172.

Mahalovich, M. F., K. E. Burr., and D. L. Foushee. 2006. Whitebark pine germination, rust resistance, and cold hardiness among seed sources in the Inland Northwest: Planting strategies for restoration. USDA Forest Service Proceedings RMRS-P-43.

Mattson, D. J., and D. P. Reinhart. 1997. Excavation of red squirrel middens by grizzly bears in the whitebark pine zone. Journal of Applied Ecology 34:926-940.

Mattson, D. J., B. M. Blanchard, and R. R. Knight. 1991. Food habits of Yellowstone grizzly bears, 1977-1987. Canadian Journal of Zoology 69:1619-1629.

Mattson, D. J., B. M. Blanchard, and R. R. Knight. 1992. Yellowstone grizzly bear

   mortality, human habituation, and whitebark pine seed crops. Journal of Wildlife

   Management 56:432-442.

McDonald G. I., and R. J. Hoff. 2001. Blister rust: An introduced plague. Pages 193-220

   in D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine

   communities: ecology and restoration. Island Press, Washington, D.C., USA.

McKinney, S. T., and D. F. Tomback. 2007. The influence of white pine blister rust on

   seed dispersal in whitebark pine. Canadian Journal of Forest Research 37:1044-

   1057.

Mewaldt, L. R. 1956. Nesting behavior of the Clark Nutcracker. The Condor 58:3-23.

Morgan, P., and S. C. Bunting. 1990. Fire effects in whitebark pine forests. Pages 166-

   170 *in* W. C. Schmidt and K. J. McDonald, editors. Proceedings-Symposium on

   whitebark pine ecosystems: Ecology and management of a high-mountain

   resource. General Technical Report INT-270. U.S. Department of Agriculture,

   Rocky Mountain Research Station, Ogden, Utah, USA.

Murray M. P., S. C. Bunting, and P. Morgan. 2000. Landscape trends (1753-1993) of

   whitebark pine (*Pinus albicaulis*) forests in the West Big Hole Range of

   Idaho/Montana, U.S.A. Arctic, Antarctic, and Alpine Research 32:412-418.

Pease, C. M., and D. J. Mattson. 1999. Demography of the Yellowstone grizzly bears.

   Ecology 80:957-975.

Price, R. A., A. Liston, and S. H. Strauss. 1998. Phylogeny and systematics of *Pinus*.

   Pages 49-68 *in* D. M. Richardson, editor. Ecology and Biogeography of *Pinus*.

   Cambridge University Press, Cambridge, United Kingdom.

Reinhart, D. P., and D. J. Mattson. 1990. Red squirrels in the whitebark zone. Pages 256-263 *in* W. C. Schmidt and K. J. McDonald, editors. Proceedings-Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource. General Technical Report INT-270. U.S. Department of Agriculture, Rocky Mountain Research Station, Ogden, Utah, USA.

Rusch, D. A., and W. G. Reeder. 1978. Population ecology of Alberta red squirrels. Ecology 59:400-420.

Schoettle, A. W. 2004. Developing proactive management options to sustain bristlecone and limber pine ecosystems in the presence of a non-native pathogen. Pages 146-155 *in* W. D. Shepperd and L. G. Eskew, compilers. Silviculture in special places: Proceeding of the National Silviculture Workshop. Proceedings RMRS-P-34. U.S. Department of Agriculture, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Schwandt, J. W. 2006. Whitebark pine in peril: A case for restoration. USDA Forest Service Report R1-06-28.

Smith, C. C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecological Monographs 40:349-371.

Smith, C. C. 1981. The indivisible niche of *Tamiasciurus*: an example of nonpartitioning of resources. Ecological Monographs 51:343-363.

Steele, M. A. 1998. Tamiasciurus hudsonicus. Mammalian Species 586:1-9.

Tomback, D. F. 1978. Foraging strategies of Clark's nutcracker. Living Bird 16:123-161.

Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: A mutualism hypothesis. Journal of Animal Ecology 51:451-467.

Tomback, D. F. 1983. Nutcrackers and pines: coevolution or coadaptation? Pages 179-

   223 *in* M. H. Nitecki, editor. Coevolution. University of Chicago Press, Chicago,

   Illinois, USA.

Tomback, D. F. 1986. Post-fire regeneration of krummholz whitebark pine: a

   consequence of nutcracker seed caching. Madrono 33:100-110.

Tomback, D. F. 1994. Effects of seed dispersal by Clark's nutcracker on early postfire

   regeneration of whitebark pine. Pages 193-198 *in* W. C. Schmidt and F. K.

   Holtmeier, editors. Proceedings—International Workshop on Subalpine Stone

   Pines and Their Environment: the Status of Our Knowledge. USDA Forest

   Service General Technical Report INT-309, Ogden, Utah, USA.

Tomback, D. F. 1998. Clark's nutcracker (*Nucifraga columbiana*). Number 331 *in* A.

   Poole and F. Gill, editors. The birds of North America. The Birds of North

   America Incorporated, Philadelphia, Pennsylvania, USA.

Tomback, D. F. 2005. The impact of seed dispersal by Clark's Nutcracker on whitebark

   pine: Multi-scale perspective on a high mountain mutualism. Pages 181-201 *in* G.

   Broll and B. Keplin, editors. Mountain Ecosystems: Studies in treeline ecology.

   Springer-Verlag, New York, New York, USA.

Tomback, D. F., and K. A. Kramer. 1980. Limber pine seed harvest by Clark's

   Nutcracker in the Sierra Nevada: Timing and foraging behavior. The Condor

   82:467-468.

Tomback, D. F., and Y. B. Linhart. 1990. The evolution of bird-dispersed pines.

   Evolutionary Ecology 4:185-219.

Tomback, D. F., and K. C. Kendall. 2001. Biodiversity losses: the downward spiral. Pages 243-262 *in* D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, D.C.

Tomback, D. F., L. A. Hoffmann, and S. K. Sund. 1990. Coevolution of whitebark pine and nutcrackers: implications for forest regeneration. Pages 118-129 *in* W. C. Schmidt and K. J. McDonald, editors. Proceedings-Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource. General Technical Report INT-270. U.S. Department of Agriculture, Rocky Mountain Research Station, Ogden, Utah, USA.

Tomback, D. F., S. K. Sund, and L. A. Hoffman. 1993. Post-fire regeneration of *Pinus albicaulis*: Height-age relationships, age structure, and microsite characteristics. Canadian Journal of Forest Research 23:113-119.

Tomback, D. F., J. K. Clary, J. Koehler, R. J. Hoff, and S. F. Arno. 1995. The effects of blister rust on post-fire regeneration of whitebark pine: the Sundance Burn of northern Idaho (U.S.A.). Conservation Biology 9:654-664.

Tomback, D. F., S. F. Arno, and R. E. Keane. 2001. The compelling case for management intervention. Pages 3-25 *in* D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, D.C.

Vander Wall, S. B. 1988. Foraging of Clark's Nutcrackers on rapidly changing pine seed resources. The Condor 90:621-631.

Vander Wall, S. B., and R. P. Balda. 1977. Coadaptations of the Clark's Nutcracker and

    the pinon pine for efficient seed harvest and dispersal. Ecological Monographs

    74:89-111.

Vander Wall, S. B., S. W. Hoffman, and W. K. Potts. 1981. Emigration behavior of

    Clark's Nutcracker. The Condor 83:162-170.

Zeglen, S. 2002. Whitebark pine and white pine blister rust in British Columbia, Canada.

    Canadian Journal of Forest Research 32:1265-1274.
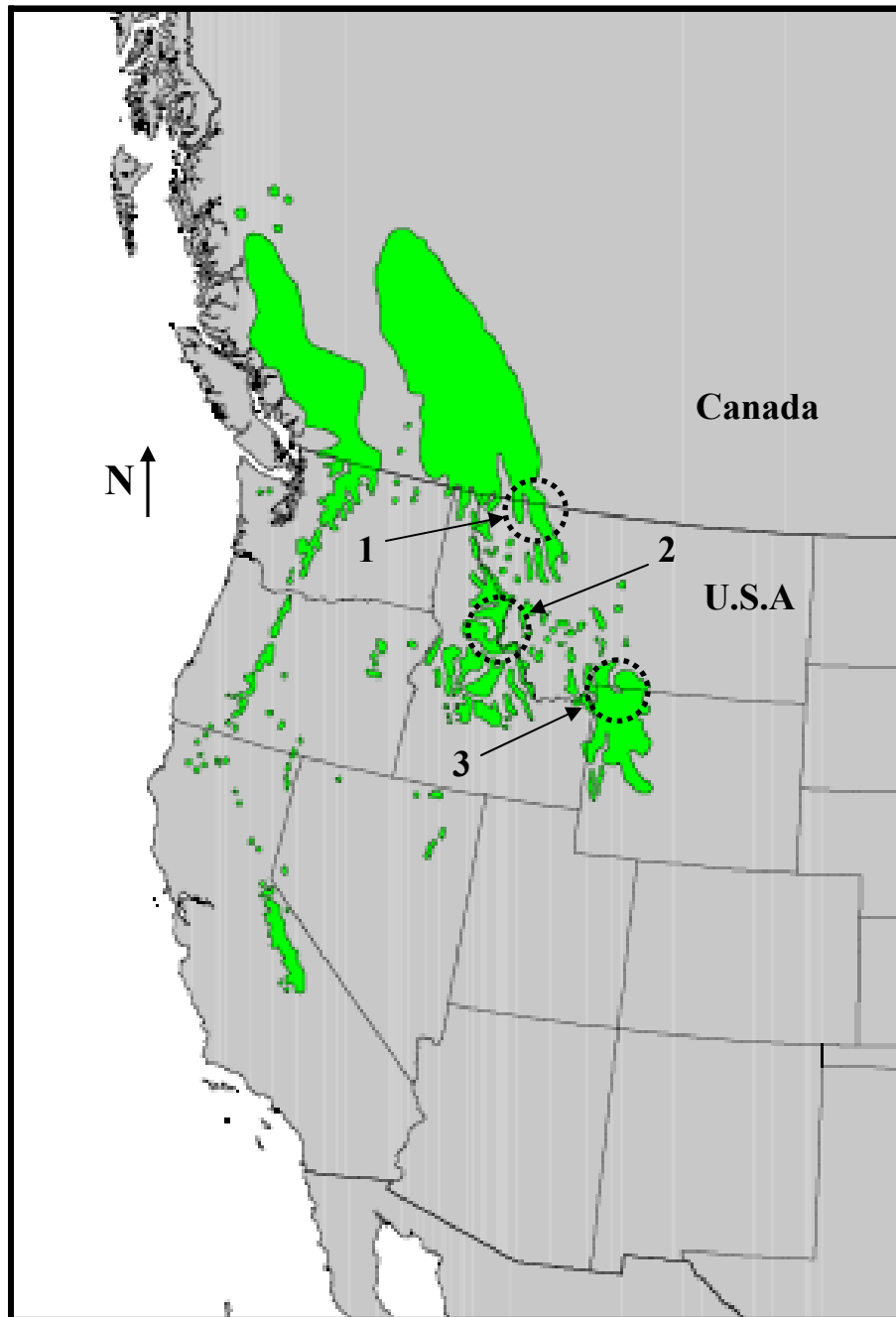
Figure 1. Geographic distribution of whitebark pine (from Little 1971), including locations of the three study ecosystems described in this dissertation – shown in dashed circles: (1) the Northern Divide, (2) the Bitterroot Mountains, and (3) the Greater Yellowstone.

Chapter 2

White Pine Blister Rust Threatens the Clark's Nutcracker-Whitebark Pine Mutualism: Implications for Restoration in the Northern Rocky Mountains, USA

Shawn T. McKinney[1], Carl E. Fiedler[1], Diana F. Tomback[2]

[1]College of Forestry and Conservation, University of Montana, Missoula, MT 59812
[2]Department of Biology, University of Colorado at Denver and Health Sciences Center, Denver, CO 80217

Abstract

Human-induced disruptions to seed dispersal mutualisms are a significant conservation concern because they increase the extinction risk of both plant and animal species. Large-seeded plants are particularly vulnerable because they often have highly specialized dispersal systems and lack compensatory regeneration mechanisms. Whitebark pine (*Pinus albicaulis* [Engelmann]) is a keystone subalpine species, obligately dependent upon the Clark's Nutcracker (*Nucifraga columbiana*) for dispersal of its large, wingless seeds. Nutcrackers are sensitive to rates of energy gain and emigrate from subalpine forests during periods of cone shortages. The exotic fungal pathogen, *Cronartium ribicola*, which causes white pine blister rust, reduces whitebark pine cone production by killing cone-bearing branches and trees. Blister rust mortality is as high as 90% in some whitebark pine forests and it now occurs nearly everywhere within the pine's range. To evaluate the risk of mutualism disruption, we quantified forest health conditions and ecological interactions between nutcrackers and whitebark pine in three Rocky Mountain, U.S.A. ecosystems that differed in levels of rust infection. Nutcracker occurrence and probability of seed dispersal were strongly related to whitebark pine cone production, which was positively correlated with live whitebark pine basal area, and

negatively correlated with tree mortality and rust infection. We estimated that a threshold level of ≈ 1,000 cones ha^{-1} is needed to ensure seed dispersal by nutcrackers, and that this level of cone production can be met by forests with average whitebark pine basal area > 5.0 m^2 ha^{-1}. The risk of mutualism disruption is greatest in the Northern Rocky Mountains, where three-year mean cone production and basal area are below these threshold levels, and nutcracker occurrence, seed dispersal, and whitebark pine regeneration were the lowest of the three ecosystems. Managers can use these threshold values to differentiate between restoration sites requiring planting of rust-resistant seedlings and sites where nutcracker seed dispersal can be expected.

Introduction

Plant-animal mutualisms often involve ecological services performed by animal species, e.g., pollination and seed dispersal, in exchange for desirable food resources, e.g., nectar and seeds. Recent perturbations to such interactions from various anthropogenic disturbances pose a significant conservation concern (Christian 2001). In theory, the risk of mutualism disruption increases with decreasing redundancy in animal species performing the critical role (Bond 1994). In particular, the local extirpation of animal species performing seed dispersal services has immediate consequences for large-seeded plants (McConkey & Drake 2002; Meehan et al. 2002; Travest & Riera 2005). Without seed dispersal vectors, plant populations suffer reduced recruitment, greater attrition, and thus increased risk of local extinction (Cordeiro & Howe 2001, 2003; Loiselle & Blake 2002). Less well known is the population response of vertebrate seed dispersers to declines in mutualist plant species, and in turn the feedback effects on the plants.

The regulation and persistence of animal populations in a given locale are largely determined by food availability and rates of energy assimilation (Lack 1954). When food is locally scarce, many animal species respond by changing their foraging behavior (e.g., seasonal migration). Granivorous birds in particular respond to cyclic productivity of conifer cone crops, whereby crop failure is followed by mass emigration of bird populations (Bock & Lepthien 1976). Cone crops of many conifer species fluctuate temporally – perhaps as a selective response to reduce predation and increase reproduction (Janzen 1971) – but since these fluctuations are ephemeral, animal populations ultimately return. However, contemporary cone production in some forest ecosystems may be more variable over space and time due to a myriad of health effects (e.g., atmospheric warming, air pollution, insect population upsurges, and exotic species). If birds have evolved an emigration response to food scarcity, a prolonged decrease in food production may result in mutualism disruption with potentially drastic implications for both the animal and plant species involved.

The Clark's Nutcracker (*Nucifraga columbiana*, family Corvidae) and whitebark pine (*Pinus albicaulis* [Engelmann], family Pinaceae, subgenus *strobus*) are coevolved mutualists (Tomback 1982; Tomback and Linhart 1990), whereby the pine is obligately dependent upon the bird for dispersal of its large, wingless seeds. In late summer and early fall, nutcrackers extract ripe whitebark pine seeds from cones which remain closed, transport seeds in a specialized sublingual pouch, and cache them in the ground at an average depth of 2.5 cm (Tomback 1982). Nutcracker seed dispersal is the only ecologically significant vector for whitebark pine seedling establishment (Tomback 1982; Hutchins & Lanner 1982). Whereas whitebark pine depends nearly exclusively on

nutcrackers, nutcrackers harvest and cache seeds of other large-seeded pines (e.g., Tomback 1978; 1998).

The biology of the Clark's Nutcracker is closely tied to seed production of various *Pinus* species (Tomback 1978; 1998). Nutcrackers forage on pine seeds throughout the summer and early fall, derive much of their winter and spring food from seeds collected the previous fall, and in early spring, feed nestlings with pine seeds gathered from the previous fall's caches (Mewaldt 1956; Vander Wall 1988). Detailed studies from several forest types in western North America have shown that individual nutcracker seed caches yield from 1.8 to 5 times the energy required to survive the winter (Vander Wall & Balda 1977; Tomback 1982; Vander Wall 1988). In addition, the birds are sensitive to rates of energy gain. Nutcrackers increase their foraging efficiency by adjusting for changes in seed ripeness within forests and by selecting trees with higher cone densities and cones with higher proportions of edible seeds (Vander Wall & Balda 1977; Tomback 1978; Tomback & Kramer 1980; Vander Wall 1988).

In early summer, nutcrackers forage in subalpine forests and assess the developing cone crop at a time when the energetic payoff is less than the energetic expenditure (Vander Wall 1988). This adaptation presumably buffers the birds from the impacts of cone crop failure by alerting them to future seed shortages before they occur (Vander Wall et al. 1981). Nutcrackers either emigrate or irrupt from the subalpine environment in search of alternative food in years of poor seed production, depending on whether the meager crop is geographically localized or widespread, respectively (Davis & Williams 1957, 1964; Bock & Lepthien 1976). During these years, nutcrackers exhibit tremendous plasticity in foraging behavior, consuming a diversity of food sources from

ground squirrels and chipmunks to dung beetles and yellowjackets (Davis & Williams 1957). However, mortality is likely higher and reproduction lower during emigration and irruption years (Vander Wall et al. 1981). Nutcrackers apparently return to subalpine forests the spring following years of mass migration and again assess the current year's cone crop (Vander Wall et al. 1981). Thus the size, mortality, and reproductive rates of nutcracker populations are likely closely associated with cone production of their preferred *Pinus* species.

Cronartium ribicola is the fungal pathogen that causes white pine blister rust. Since its introduction to western North America in 1910 (see McDonald & Hoff 2001 for review), blister rust has spread throughout much of the range of whitebark pine, with mortality as high as 90% in some Rocky Mountain forests (Keane et al. 1994; Kendall & Keane 2001; Schwandt 2006). Blister rust reduces cone production by girdling and killing cone-bearing branches and trees of five-needled white pines (genus *Pinus*, subgenus s*trobus*) (McDonald & Hoff 2001). In western Montana and eastern Idaho, whitebark pine cone production was significantly lower in rust-damaged stands compared to stands with little damage but otherwise similar in forest structure and composition (McKinney & Tomback 2007). Furthermore, lower cone production in rust-damaged stands was associated with significantly higher rates of predispersal seed predation and fewer observations of nutcracker seed dispersal (McKinney & Tomback 2007).

The long-term persistence of whitebark pine in the presence of blister rust will require a dramatic increase in the frequency of rust-resistant alleles, which was estimated to be only 1-5% within populations first exposed to the rust (Hoff et al. 1994). However, recent investigations demonstrate that whitebark pine does have genetic variation in rust

resistance, increasing in frequency from southeast to northwest in the US Rocky Mountains (Mahalovich et al., 2006). The overall recovery strategy for whitebark pine includes both restoration planting of nursery-grown, rust-resistant seedlings and facilitated natural regeneration (focused silvicultural cutting and prescribed burning to provide hospitable sites for nutcracker seed dispersal and caching) (Schwandt 2006; Mahalovich et al. 2006; Schoettle 2004). Because restoration planting is costly, spatially restricted, and uncertain in outcome, the natural regeneration approach should be implemented wherever feasible.

Given the nutcracker's tendency to emigrate when cone crops are small, and because of increasing losses of cone production capacity within forest stands, the risk of local and even regional disruption to the nutcracker-whitebark pine mutualism exists. Therefore, we want to know whether there is a threshold of whitebark pine cone production below which the likelihood of nutcracker seed dispersal declines precipitously. The objectives of this study are to quantify the relationship between cone production and whitebark pine stand structure and health attributes, and to model the probability of nutcracker seed dispersal as a function of cone production. This information can be used by the U.S. Department of Agriculture, Forest Service, and Department of Interior, Park Service to implement conservation and restoration strategies for whitebark pine in the Rocky Mountains.

Methods

Sampling Design

We established multiple research sites within three distinct ecosystems in the Central and Northern Rocky Mountains (U.S.A): (1) The Northern Divide in

northwestern Montana consisted of 10 sites located in Glacier National Park and the Flathead National Forest (48.8°N to 48.3°N, 113.3°W to 114.4°W, 1 928 m to 2 209 m asl), (2) The Bitterroot Mountains in west-central Montana and east-central Idaho comprised six sites in the Bitterroot and Salmon National Forests (46.5°N to 45.5°N, 113.9°W to 114.4°W, 2 364 m to 2 648 m asl), and (3) The Greater Yellowstone in southwestern Montana and northwestern Wyoming was represented by eight sites located in Yellowstone National Park and the Gallatin and Shoshone National Forests (45.1°N to 44.8°N, 109.5°W to 110.6°W, 2 529 m to 2 970 m asl). The Northern Divide ecosystem is located ca. 300 km north of the Bitterroot Mountain ecosystem while the Greater Yellowstone ecosystem is situated ca. 300 km southeast. The number of sites chosen within each ecosystem resulted from a trade-off among the following factors: the specific requirements of funding agencies, accessibility of whitebark pine stands, and maximization of geographic extent and sample size.

Field sampling took place each year from June-September. Northern Divide sites were sampled from 2004 to 2006; Bitterroot Mountain sites in 2001, 2002 and 2006; and Greater Yellowstone sites in 2005 and 2006. Research sites within each ecosystem were established by delineating rectangular boundaries that were 100 m wide by ≥ 200 m long within contiguous forest stands. Sites were subdivided into 1-ha squares (100 m $\times$ 100 m) to provide better control over nutcracker and vegetation sampling.

Clark's Nutcracker observations

Research sites were visited at least three times during a field season: 29 June to 17 July, 20 July to 16 August, and 19 August to 6 September. Nutcracker observations were conducted between 0700 and 1900 hours and followed the protocol established by

McKinney and Tomback (2007): one researcher moved throughout a 1-ha square and recorded the number of nutcrackers observed within a 1-hr period, avoiding a double count of birds. Nutcracker foraging behavior was differentiated with respect to seed predation and seed dispersal. Nutcrackers consume unripe whitebark pine seeds in early- to mid-summer, acting as seed predators, but become seed dispersers when seed caching begins in late-summer and early-fall (see Tomback 1998 for overview). We counted a seed dispersal event when a nutcracker was observed placing seeds in its sublingual pouch, or was seen with a bulging sublingual pouch (Vander Wall & Balda 1977; Tomback 1978).

Cone production and vegetation sampling

From a corner of each 1-ha square, random numbers for azimuth degree and distance were generated and followed until an ovulate cone-bearing whitebark pine tree was encountered. Selected cone trees were a minimum of 25 m apart, with one to four sampled trees ha^{-1}. We conducted cone counts between 29 June and 15 July of each year using tripod-mounted Leica spotting scopes with 10x to 60x zoom eyepieces and handheld tally devices. Two to three observation points that allowed for unobstructed views of the canopy were used to census cones on each tree. We established two 10 m x 50 m (500 m^2)belt transects along random azimuths within each 1-ha square at each research site to collect tree and site-level data. We recorded species and diameter ($\pm$ 0.1 cm) at breast height (dbh, 1.4 m) for all trees $\geq$ 7 cm dbh. We calculated basal area (BA, m^2 ha^{-1}) from the dbh for each tree and summed BA by transect, species, and research site. We inspected all living whitebark pine trees $\geq$ 7 cm dbh for the presence of ovulate cones and blister rust infection symptoms. A tree was identified as infected if it exhibited

active or inactive branch or stem cankers (Hoff 1992), which are swellings caused by the rust's mycelia growing into branch or stem phloem tissue (McDonald & Hoff 2001). On each transect, we also measured dbh of standing dead whitebark pine trees and tallied all whitebark pine seedlings ≤ 50 cm in height.

Data Analyses

We used S-Plus 7.0, SPSS 10.0, and Microsoft Excel for all computations and analyses. Statistical tests were evaluated at an *a priori* significance level of $p = 0.05$. Analyses of nutcracker occurrence and habitat use were conducted at multiple spatial (site and ecosystem) and temporal levels (individual year and all years), and data were converted accordingly. We converted nutcracker data to the proportion of total observation hours (all years combined) with ≥ 1 bird detected for each research site ($n = 24$). We then calculated the mean number of nutcrackers (no. hr^1) occurring in each ecosystem by summing the number of birds detected in each ecosystem and dividing by the corresponding total number of observation hours. Each research site on a given year (site-year, $n = 42$) was coded as one (1) if we observed at least one nutcracker seed dispersal event and zero (0) if not. Whitebark pine cone production estimates were calculated as the product of the mean number of cones $tree^{-1}$ and the number of cone-bearing trees ha^{-1} for each research site-year ($n = 42$), and for overall site means ($n = 24$).

To investigate the influence of food-energy availability on nutcracker occurrence, we performed simple linear regression analysis of the proportion of total observation hours with ≥ 1 nutcracker on mean whitebark pine cone production across all research sites ($n = 24$). Cone values (i.e., cone production estimates) were transformed as $[(\ln$ cones $ha^{-1})^2]$ to meet assumptions of normality, and residual analysis was performed to

30

confirm assumptions of homoscedasticty of error variance. We used correlation analysis

(Pearson's simple correlation coefficient) to quantify the strength of the linear

relationships among site-level values of nutcracker occurrence, cone production, live

whitebark pine basal area, and mortality to investigate how bird occurrence and food

production were related to measurable forest variables affected by blister rust. Cone

production was transformed as above and basal area was also natural log-transformed to

satisfy normality assumptions.

To determine whether and how ecosystems differed in whitebark pine forest

health parameters, we performed a Multivariate Analysis of Variance (MANOVA) and

used Scheffe's *post hoc* multiple comparisons tests of ecosystem values for blister rust

infection (%), tree mortality (%) and live basal area (m^2 ha^{-1}). The F statistic for Box's

Test and Levene's Test were evaluated to determine whether equality of covariance

matrices and error variances among groups were violated, respectively.

We used a logistic regression model with binomial error and a logit link to

estimate intercept and slope (b_0 and b_1) coefficients for the probability of nutcracker seed

dispersal as a function of transformed whitebark pine cone production. We performed a

χ^2 test to determine whether the frequency of nutcracker seed dispersal differed among

ecosystems.

Results

The three measures of whitebark pine forest health conditions – blister rust

infection (%), tree mortality (%), and live basal area (m^2 ha^{-1}) – varied among the three

ecosystems (Table 1). There was a significant difference in the population mean vectors

for the three variables among ecosystems (MANOVA, Wilk's Lambda $F_{6,38} = 11.43$, $p <$

0.001) with univariate analysis of variance tests showing significant differences in population mean values for infection ($F_{2,21} = 4.47$, $p = 0.024$), mortality ($F_{2,21} = 54.73$, $p < 0.001$), and live basal area ($F_{2,21} = 10.11$, $p = 0.001$). However, research sites in the Bitterroot Mountains were not significantly different than those in the Greater Yellowstone relative to the three forest health variables ($p > 0.05$ all pairwise comparisons: Table 1). Northern Divide sites did have significantly greater infection and mortality levels and lower live whitebark pine basal area than Greater Yellowstone sites, and significantly greater mortality and lower live whitebark pine basal area than Bitterroot Mountain sites ($p < 0.05$ all pairwise comparisons: Table 1).

The proportion of total observation hours (all years combined) with at least one Clark's Nutcracker sighting increased linearly with increasing values of transformed whitebark pine cone production [(ln cones ha^{-1})^2] across all research sites ($R^2 = 0.765$: Fig. 1). This regression model was significant (Model $F_{1,22} = 71.68$, $p < 0.001$), indicating that the frequency of nutcracker occurrence at a site was strongly associated with the number of available seeds, and thus potential food-energy for the bird. Further, the model's estimated intercept and slope coefficients indicate that the chance of nutcracker occurrence in a whitebark pine forest becomes negligible (proportion ≈ 0) when cone production averages < 130 cones ha^{-1} ((ln cones ha^{-1})^2 < 23.64: Fig. 1).

Both nutcracker occurrence (proportion of all years' observation hours) and cone production (mean of all years) were negatively correlated with whitebark pine tree mortality (%), and positively correlated with live whitebark pine basal area (ln BA, m^2 ha^{-1}) at the site level ($n = 24$, $p < 0.01$ in all cases, Pearson's simple correlation

coefficient: Table 2), suggesting that these measurable site variables can be important indicators of cone production and thus, bird occurrence.

Annual nutcracker occurrence fluctuated with annual whitebark pine cone production within and among ecosystems (Fig. 2). Within ecosystems, when a given year's cone production was greater relative to other years, the frequency of nutcracker occurrence was also greater. This trend was true for each ecosystem-year (i.e., a given ecosystem on a given year; $n = 8$) except the Northern Divide in 2006; in that ecosystem-year, cone production was slightly lower than 2005, while nutcracker occurrence was slightly higher (Fig. 2). Among ecosystems, cone production and nutcracker occurrence were lowest each sample year in the Northern Divide and highest in the Greater Yellowstone (Fig. 2). Annual variation was greatest in the Bitterroot sites, perhaps reflecting the greater heterogeneity in blister rust infection and live whitebark pine basal area among research sites within that ecosystem (Fig. 2, Table 1).

We used seed dispersal results (i.e., whether or not a seed dispersal event was recorded) from 34 site-years in a binary logistic regression model to estimate the probability of seed dispersal as a function of transformed whitebark pine cone production $[(\ln \text{cones ha}^{-1})^2]$ (Fig. 3). Using a cutoff probability value of 0.50, the model correctly classified 92.3% (12/13) and 90.5% (19/21) of the original non-dispersed and dispersed sites, respectively, with 91.2% (31/34) of all original site-years correctly classified. Thus, the model predicted non-dispersed and dispersed sites equally well. We also randomly selected, and held out from the logistic regression, cone production and seed dispersal data from eight site-years to use with the model's estimated coefficients (b_0 and b_1) to further assess its predictive ability. Five of the eight (60%) site-years were correctly

33

classified (cutoff probability = 0.50). The three misclassified site-years were non-dispersed, had intermediate cone production values, and were predicted to have dispersal probabilities > 0.50, but < 0.70 (Table 3). This test demonstrated that the model performed better at low and high cone production values. However, when the cutoff probability of seed dispersal was set equal to 0.70, only 5.3% (1/19) of all non-dispersed sites were misclassified and predicted to have seed dispersal (Fig. 3, Table 3). Based on the logistic regression model equation, a whitebark pine forest has a predicted seed dispersal probability ≥ 0.70 when average cone production ≥ 700 cones ha^{-1} ((ln cones ha^{-1})$^2 \geq 42.9$: Fig. 3).

There was a significant ecosystem effect on the likelihood of whitebark pine seed dispersal by Clark's Nutcracker across all sites and years ($\chi^2 = 17.18$, df $= 2$, $n = 42$, $p < 0.001$). We failed to observe at least a single nutcracker–and thus a seed dispersal event– during the period of seed dispersal in 80% of the Northern Divide site-years ($n = 20$), while 40% of site-years ($n = 10$) in the Bitterroot Mountains failed to have any birds during this critical time. In contrast, nutcrackers were present and dispersing seeds in all sites in all years in the Greater Yellowstone ecosystem ($n = 12$).

An ecosystem-level comparison (all sites and years aggregated) showed that mean whitebark pine cone production (no. ha^{-1}) and bird abundance (no. hr^{-1}) were lowest in the Northern Divide, which corresponded to the lowest density of whitebark pine regeneration (seedlings ≤ 50 cm ha^{-1}: Table 4). The Northern Divide had 80% and 75% fewer seedlings than the Bitterroot Mountains and Greater Yellowstone, respectively. Mean whitebark pine cone production and bird abundance were highest in the Greater Yellowstone among the three ecosystems. The Bitterroot Mountains had slightly higher

mean regeneration, but with much greater heterogeneity (%SE) compared to the Greater

Yellowstone (Table 4).

Discussion

Our results indicate that there is a threshold of whitebark pine cone production

below which there is a rapid decline in the frequency of Clark's Nutcracker occurrence

and seed dispersal. When cone production declines from 700 to 300 cones ha^{-1} [(42.9 to

32.5 ln cones ha^{-1})^2] the estimated frequency of nutcracker occurrence declines from 0.4

to 0.12 and probability of seed dispersal from 0.7 to 0.3 (Fig.1 & Fig.3). If the trends

identified here continue to manifest themselves, the likelihood exists that ecologically

significant Clark's Nutcracker seed dispersal services in the Northern Divide ecosystem

will be lost, effectively disconnecting the dispersal mutualism between nutcracker and

whitebark pine. If tree and seedling mortality from white pine blister rust continue,

coupled with tree loss from the native mountain pine beetle (*Dendroctonus ponderosae*),

Northern Divide populations will become smaller and more isolated with increased risk

of extinction due to stochastic perturbations (Shaffer 1981).

Clark's Nutcrackers showed sensitivity to available food energy at the site level,

increasing in frequency of occurrence with increasing whitebark pine cone production

across all research sites. At the ecosystem level, the Greater Yellowstone can be

interpreted heuristically as a natural control and used to compare the effects of whitebark

pine forest health conditions on cone production, nutcracker occurrence, probability of

seed dispersal, and environmental carrying capacity for the bird. Although blister rust

infection in the Greater Yellowstone is high enough to lead to significant future mortality,

it was the lowest of the three ecosystems and apparently not enough to impact live basal

35

area and cone production, as they related to nutcracker activity, in any substantial way. Live whitebark pine basal area and cone production were highest in the Greater Yellowstone; nutcrackers were present in 96% of the sampled hours; 100% of the research sites had seed dispersal; and the overall mean number of birds was 6.1 hr^{-1} – 20 times greater than the Northern Divide. Infection and mortality increased and basal area and cone production decreased in the Bitterroot Mountains compared to the Greater Yellowstone; nutcracker values were also lower (42% presence in hours sampled, 60% of sites with dispersal, 2.0 birds hr^{-1}). Whitebark decline is most severe in the Northern Divide, where infection and mortality levels are the highest and live basal area and cone production the lowest among the three ecosystems. Nutcrackers rarely visited Northern Divide sites during the three years of investigation, and then only in low numbers (14% presence in hours sampled, 20% of sites with dispersal, 0.3 birds hr^{-1}). As blister rust infection and tree mortality increase, live whitebark pine basal area and cone production decrease, thereby diminishing nutcracker occurrence and seed dispersal at the ecosystem level.

Clark's Nutcracker biology and white pine blister rust

The ultimate factor relative to survival that influences an emigration response in nutcrackers is lack of food to cache, which translates to diminished survival through the subalpine winter and decreased reproduction (e.g., Lack 1954). The proximate stimulus is less certain. Vander Wall and colleagues (1981) proposed that nutcrackers cue in on the absence of the green cones of limber (*P. flexilis*) and piñon pines (*P. edulis* & *P. monophylla*), thereby triggering irruptions prior to actual food shortage. However, unripe whitebark pine cones are dark purple rather than green, suggesting that the birds either

can recognize the absence of both colors, or respond to some more general cue. Blister rust infection reduces cone production in whitebark pine forests, directly constraining the factor determining whether nutcrackers settle and remain in a forest to disperse seeds. Whether this evolved survival response to food shortage will result in a prolonged absence of nutcrackers from high mortality/low cone producing areas is unknown. But if it does, a positive feedback scenario is likely: decreasing regeneration with increasing mortality, and accelerated population decline.

Vander Wall and Balda (1977) estimated that a single adult nutcracker requires 4.95×10^4 KJ of edible energy to survive a subalpine winter. Tomback (1982) calculated whitebark pine seed edible dry mass energy to be 32.3 KJ g^{-1} and mean seed mass 8.0×10^{-2} g. Given an average of 45 seeds cone^{-1} (Tomback 1978), we estimated that a single adult bird would require a minimum of 426 cones to cache the necessary 19,150 seeds. Adult nutcrackers appear to cache from 1.8 to 5 times the minimum amount needed (Vander Wall & Balda 1977; Tomback 1982; Vander Wall 1988). Some of these caches may be consumed by rodents (e.g., Tomback 1980) and others fed to nestling and juvenile nutcrackers (Mewaldt 1956; Tomback 1978). Given this energy range (1.8x to 5x minimum energy requirements), one adult would need to cache the seeds from 767 to 2,130 cones. Our results provide an interesting comparison to these values. Cone production in the Northern Divide ecosystem was below the minimum level of this energy range (641.2 ± 214.2 cones ha^{-1}: mean ± SE; $n = 20$ sites) and nutcrackers were rare and in low numbers (Fig. 2 & Table 4). Twenty percent of Northern Divide sites did, however, have at least one observation of whitebark pine seed dispersal by a nutcracker. Cone production in these dispersed sites was within the energy range (1,420.9 ± 719.2

cones ha^{-1}; $n = 5$). Moreover, mean cone production of all dispersed sites – regardless of ecosystem – was above the maximum of the required energy range (2,618.7 ± 433.3 cones ha^{-1}; $n = 23$); conversely, mean production was below the minimum in all nondispersed sites (356.3 ± 94.8 cones ha^{-1}; $n = 19$). Thus, our results fit well within the context of several independently derived estimates of nutcracker energy requirements, and further support the interpretation that the birds are able to assess cone crops and will be absent from forests with cone production below minimum levels.

Management recommendations

Based on previous estimates and the results from our study, we propose that a threshold of 1,000 cones ha^{-1} averaged over a given site is needed to ensure that nutcrackers will be present at the time of seed dispersal. For example, our models predict nutcracker occurrence frequency of 0.46 (Fig. 1) and seed dispersal probability of 0.83 (Fig. 2) for a site with mean production of 1,000 cones ha^{-1}. These estimates are not without error, and the spatial extent over which cone production must occur needs more detailed investigation. They do, however, form a reasonably sound basis to begin to formulate whitebark pine management and restoration decisions.

If estimates of cone production are not readily obtainable for a given management jurisdiction, live whitebark pine basal area can be used instead as a predictor of cone production. Mean cone production was significantly correlated with mean basal area over the 24 sites sampled (r = 0.81: Table 2). Graphical analysis of mean cone production plotted against basal area suggests that 5.0 m^2 ha^{-1} defines the lower level of mean live whitebark pine basal area needed to produce an average of 1,000 cones ha^{-1}. Furthermore, research sites where nutcracker seed dispersal was never observed had a mean live

whitebark pine basal area of 1.58 ($\pm$SE 0.78) m^2 ha^{-1} ($n = 7$); sites with nutcracker seed

dispersal observed in some years (and not in others) had a mean basal area of 5.03 ($\pm$

1.01) m^2 ha^{-1} ($n = 7$); while sites with observations of nutcracker seed dispersal in all

years had a mean basal area of 15.27 ($\pm$ 2.51) m^2 ha^{-1} ($n = 10$). Therefore, we estimate

that whitebark pine forests with mean basal area $\approx$ 5.0 m^2 ha^{-1} will be able to produce $\approx$

1,000 cones ha^{-1}, at least in some high production years, and consequently attract and

maintain nutcracker presence through the critical period of seed dispersal. However,

because blister rust was present in all three of our study ecosystems, and because there is

substantial variability in cone production from site to site due to site quality, the proposed

cutoff value should be taken cautiously and managers should evaluate site-specific

conditions.

Although the mutualism between Clark's Nutcracker and whitebark pine is not

currently threatened throughout their ranges of sympatry, our results clearly show a

trajectory of decreasing interaction between the bird and pine in the Northern Divide

Ecosystem. Our results point to decreased nutcracker seed dispersal services as the

principal mechanism behind reduced regeneration in the Northern Divide (Table 4). It is

apparent that active management will be needed to reverse this downward trend. Sites

with < 5.0 m^2 ha^{-1} of live whitebark pine and producing < 1,000 cones ha^{-1} will require

planting of rust-resistant seedlings to thwart further whitebark pine losses. Given the high

levels of rust infection and tree mortality, and the low levels of live basal area

documented in this study, it is likely that many whitebark forests in the Northern Divide

are no longer sustainable without planting. However, our data show that sites that exceed

the 5.0 m^2 ha^{-1} threshold can still rely on nutcracker seed dispersal at least in some years,

although these forests will lose whitebark pine over time as blister rust infection kills trees and damages canopies. Managers are encouraged to identify such sites and use appropriate silvicultural treatments to increase nutcracker caching habitat at least for the immediate future. As an example, if a whitebark pine forest has > 5.0 m^2 ha^{-1} of live basal area, is at least 10 ha in area, and not isolated from other whitebark forests, it could serve as a natural seed source for a restoration project. Removal (cutting) of competing shade-tolerant trees followed by prescribed burning at a location within 10 km of the whitebark seed source would likely attract nutcracker caching and increase the likelihood of natural regeneration (Keane and Arno 2001). Site-specific knowledge of whitebark pine forest attributes would also allow fire managers to make informed decisions regarding "wildland fire use," which entails deciding when and where to allow lighting-ignited fires to burn. Wildland fires could be allowed to burn in subalpine forests where the probability of nutcracker seed dispersal is high and the potential for damage to humans and property is low. Finally, knowing which forests within a management jurisdiction have whitebark pine basal area below 5.0 m^2 ha^{-1} would allow managers to prioritize areas for planting the limited number of rust-resistant seedlings.

Conclusions

Insular species are at greater risk of extinction than continental species (MacArthur & Wilson 1967), and plant-animal mutualists have proven no exception (Meehan et al. 2002). The same effect of increasing risk of local extinction with increasing isolation has been demonstrated on continents where habitat has become insularized because of anthropogenic habitat change (Cordeiro & Howe 2003). Here we provide evidence of a threat to a North American bird-pine mutualism that is not due to

habitat destruction, overhunting, or isolation, but rather because of an invasive species causing decreased abundance and food production in the pine. Our results demonstrate that easily measured site variables (cone production and live basal area) can be used to predict the degree to which a fundamental ecological interaction (bird-pine seed dispersal) has been altered by human-induced factors. Moreover, by quantifying interactions within three distinct ecosystems that varied in forest health parameters, we were able to identify and estimate thresholds that are needed to maintain the mutualism. Knowledge of these thresholds should prove useful for informing management and focusing restoration activities, and serve as an example to other systems where a mutualism is threatened in parts of two species' sympatric ranges.

Acknowledgments

Literature cited

Bock, C. E., and L. W. Lepthien. 1976. Synchronous eruptions of boreal seed-eating birds. The American Naturalist **110**:559-571

Bond, W. J. 1994. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. Philosophical Transactions of the Royal Society of London B **344**:83-90.

Christian, C. E. 2001. Consequences of a biological invasion reveal the importance of mutualism for plant communities. Nature **413**:635-639.

Cordeiro, N. J., and H. F. Howe. 2001. Low recruitment of trees dispersed by animals in African forest fragments. Conservation Biology **15**:1733-1741.

Cordeiro, N. J., and H. F. Howe. 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. Proceedings of the National Academy of Sciences **100**:14052-14056.

Davis, J., and L. Williams. 1957. Irruption of the Clark Nutcracker in California. The Condor **59**:297-307.

Davis, J., and L. Williams. 1964. The 1961 Irruption of the Clark's Nutcracker in California. The Wilson Bulletin **76**:10-18.

Hoff, R. J. 1992. How to recognize blister rust infection on whitebark pine. Forest Service Research Note INT-RN-406.

Hoff, R. J., S. K. Hagle, and R. G. Krebill. 1994. Genetic consequences and research challenges of blister rust in whitebark pine forests. Pages 118-126 *in* W. C. Schmidt and F. K. Holtmeier, editors. Proceedings—International Workshop on Subalpine Stone Pines and Their Environment: the Status of Our Knowledge.

General Technical Report INT-GTR-309. U.S. Department of Agriculture, Rocky Mountain Research Station, Ogden, Utah, USA.

Hutchins, H. E., and R. M. Lanner. 1982. The central role of Clark's Nutcracker in the dispersal and establishment of whitebark pine. Oecologia **55**:192-201.

Janzen, D. H. 1971. Seed predation by animals. Annual Review of Ecology and Systematics **2**:465-492.

Keane, R. E., and S. F. Arno. 2001. Restoration concepts and techniques. Pages 367-400 *in* D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, D.C., USA.

Keane, R. E., P. Morgan, and J. P. Manakis. 1994. Landscape assessment of the decline of whitebark pine (*Pinus albicaulis*) in the Bob Marshall Wilderness Complex, USA. Northwest Science **68**:213-229.

Kendall, K. C., and S. F. Arno. 1990. Whitebark pine–an important but endangered wildlife resource. Pages 264-273 *in* W. C. Schmidt and K. J. McDonald, editors. Proceedings-Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource. General Technical Report INT-270. U.S. Department of Agriculture, Rocky Mountain Research Station, Ogden, Utah, USA.

Lack, D. 1954. The natural regulation of animal numbers. Oxford University Press, London, UK.

Loiselle, B. A., and J. G. Blake. 2002. Potential consequences of extinction of frugivorous birds for shrubs of a tropical wet forest. Pp. 397-406 *in* D.J. Levey,

W.R. Silva, and M. Galetti, eds. Seed dispersal and frugivory: ecology, evolution, and conservation. CABI Publishing, Wallingford, UK.

MacArthur, R. H., and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, N.J., USA.

Mahalovich, M. F., K. E. Burr., and D. L. Foushee. 2006. Whitebark pine germination, rust resistance, and cold hardiness among seed sources in the Inland Northwest: Planting strategies for restoration. Forest Service Proceedings RMRS-P-43.

McConkey, K. R., and D. R. Drake. 2002. Extinct pigeons and declining bat populations: are large seeds still being dispersed in the tropical pacific? Pp. 381-395 *in* D.J. Levey, W.R. Silva, and M. Galetti, eds. Seed dispersal and frugivory: ecology, evolution, and conservation. CABI Publishing, Wallingford, UK.

McDonald G. I., and R. J. Hoff. 2001. Blister rust: An introduced plague. Pages 193-220 *in* D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, D.C., USA.

McKinney, S. T., and D. F. Tomback. 2007. The influence of white pine blister rust on seed dispersal in whitebark pine. Canadian Journal of Forest Research **37**:1044-1057.

Meehan, H. J., K. R. McConkey, and D. R. Drake. 2002. Potential disruptions to seed dispersal mutualisms in Tonga, Western Polynesia. Journal of Biogeography **29**:695-712.

Mewaldt, L. R. 1956. Nesting behavior of the Clark Nutcracker. The Condor **58**:3-23.

Schoettle, A. W. 2004. Developing proactive management options to sustain bristlecone and limber pine ecosystems in the presence of a non-native pathogen. Pages 146-

15 5*in* W. D. Shepperd and L. G. Eskew, compilers. Silviculture in special places: Proceeding of the National Silviculture Workshop. Proceedings RMRS-P-34. U.S. Department of Agriculture, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Schwandt, J. W. 2006. Whitebark pine in peril: A case for restoration. Forest Service Report R1-06-28.

Shaffer, M. L. 1981. Minimum population sizes for species conservation. BioScience **31**:131-134.

Tomback, D. F. 1978. Foraging strategies of Clark's nutcracker. Living Bird **16**:123-161.

Tomback, D. F. 1980. How nutcrackers find their seed stores. Condor **82**:10-19.

Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: A mutualism hypothesis. Journal of Animal Ecology **51**:451-467.

Tomback, D. F. 1998. Clark's nutcracker (*Nucifraga columbiana*). Number 331 *in* A. Poole and F. Gill, editors. The birds of North America. The Birds of North America Incorporated, Philadelphia, Pennsylvania, USA.

Tomback, D. F., and K. A. Kramer. 1980. Limber pine seed harvest by Clark's Nutcracker in the Sierra Nevada: Timing and foraging behavior. The Condor **82**:467-468.

Tomback, D. F., and Y. B. Linhart. 1990. The evolution of bird-dispersed pines. Evolutionary Ecology **4**:185-219.

Travest, A., and N. Riera. 2005. Disruption of a plant-lizard seed dispersal system and its ecological effects on a threatened endemic plant in the Balearic Islands. Conservation Biology **19**:421-431.

Vander Wall, S. B. 1988. Foraging of Clark's Nutcrackers on rapidly changing pine seed

    resources. The Condor **90**:621-631.

Vander Wall, S. B., and R. P. Balda. 1977. Coadaptations of the Clark's Nutcracker and

    the piñon pine for efficient seed harvest and dispersal. Ecological Monographs

    74:89-111.

Vander Wall, S. B., S. W. Hoffman, and W. K. Potts. 1981. Emigration behavior of

    Clark's Nutcracker. The Condor **83**:162-170.

Table 1.   Mean (±SE) values of whitebark pine forest health parameters from three ecosystems in the Rocky Mountains (U.S.A.).*

Ecosystem (no. of research sites)	Blister rust infection (%)	Tree mortality (%)	Live basal area ($m^2\ ha^{-1}$)
Northern Divide (10)	82.2a (6.7)	68.4a (4.1)	1.9a (0.6)
Bitterroot Mountains (6)	64.9ab (11.4)	17.3b (3.7)	10.5b (3.6)
Greater Yellowstone (8)	49.3b (7.6)	14.5b (4.4)	14.5b (2.4)

*Ecosystems with the same letter are not different at α = 0.05 (Scheffe's multiple comparisons test).

Table 2. Pearson's simple correlation coefficients of Clark's Nutcracker occurrence and whitebark pine site characteristics in the Rocky Mountains (U.S.A).*

Site variable	nutcracker occurrence (proportion of time)	cone production [$(ln\ cones\ ha^{-1})^2$]	basal area ($ln\ m^2\ ha^{-1}$)	tree mortality (%)
nutcracker occurrence	1.000	0.875	0.793	-0.797
cone production[a]		1.000	0.808	-0.711
basal area[a]			1.000	-0.779
tree mortality[a]				1.000

*All correlations are significant at α = 0.01 (n = 24).
[a]Values are for whitebark pine trees only.

Table 3. Results from independent data set used to test logistic regression predictions of

whitebark pine seed dispersal by Clark's Nutcracker.*

Cone production $[(ln\ cones\ ha^{-1})^2]$	Dispersal observed[a]	Dispersal predicted	Correctly classified[b]
63.1	1	0.983	yes
55.8	1	0.948	yes
42.8	0	0.696	no
41.9	0	0.665	no
41.8	0	0.662	no
30.4	0	0.241	yes
29.7	0	0.219	yes
28.1	0	0.179	yes

*Logistic equation y = exp(-6.02 + 0.16*x) / 1 + exp(-6.02 + 0.16*x).
[a]1 = nutcracker observed during seed dispersal period, 0 = not observed.
[b]Classification cutoff value = 0.50.

Table 4.   Ecosystem comparison of whitebark pine cone production, nutcracker abundance, and regeneration.

Ecosystem (no. of sites)	Cones (no ha^{-1})				Clark's nutcracker (no hr^{-1})				Seedlings <50 cm (no ha^{-1})			
	mean	%SE	min	max	mean	%SE	min	max	mean	%SE	min	max
Northern Divide (10)	641.2	33.4	57.2	4068.5	0.3	33.3	0	10	70.2	30.2	0	343.2
Bitterroot Mountains (6)	1055.5	25.2	218.7	2516.8	2.0	15.0	0	33	360.5	65.8	0	2370.0
Greater Yellowstone (8)	3635.2	17.9	911.7	7126.9	6.1	13.1	0	25	281.5	28.6	0	928.7
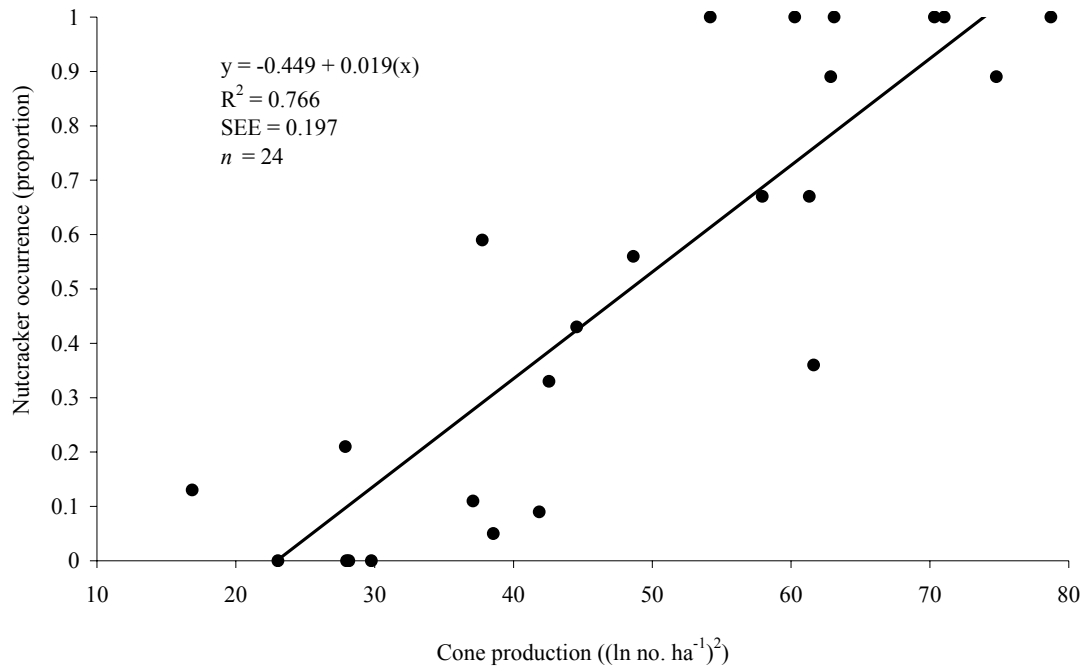
Figure 1. The proportion of total observation hours (all years combined) with ≥ 1 Clark's Nutcracker present as a function of mean whitebark pine cone production in Rocky Mountain forest sites (U.S.A.). Best-fit linear regression line shown.
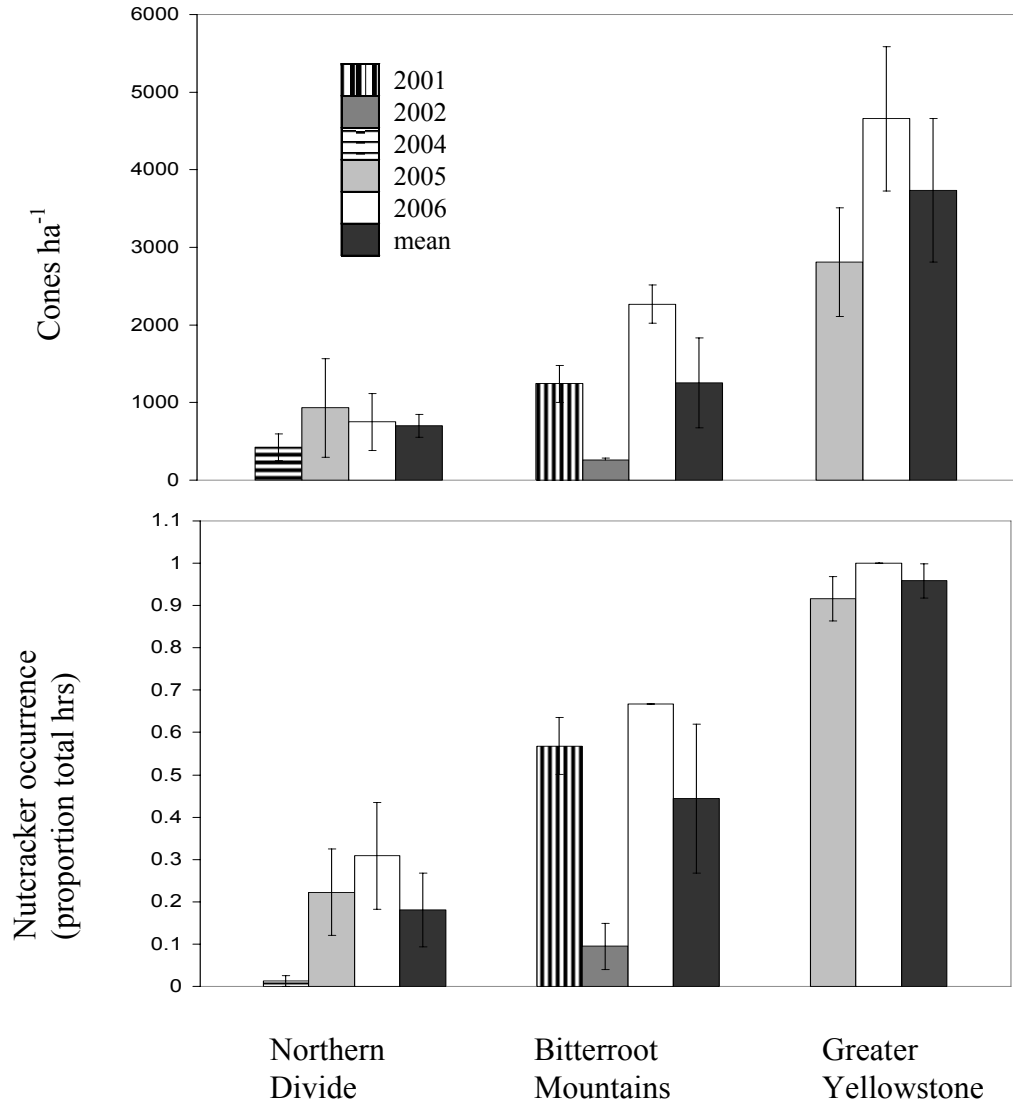
Figure 2. Annual fluctuations (mean ±SE) of whitebark pine cone production and Clark's

Nutcracker occurrence within and among three ecosystems in the Rocky Mountains. (U.S.A.).
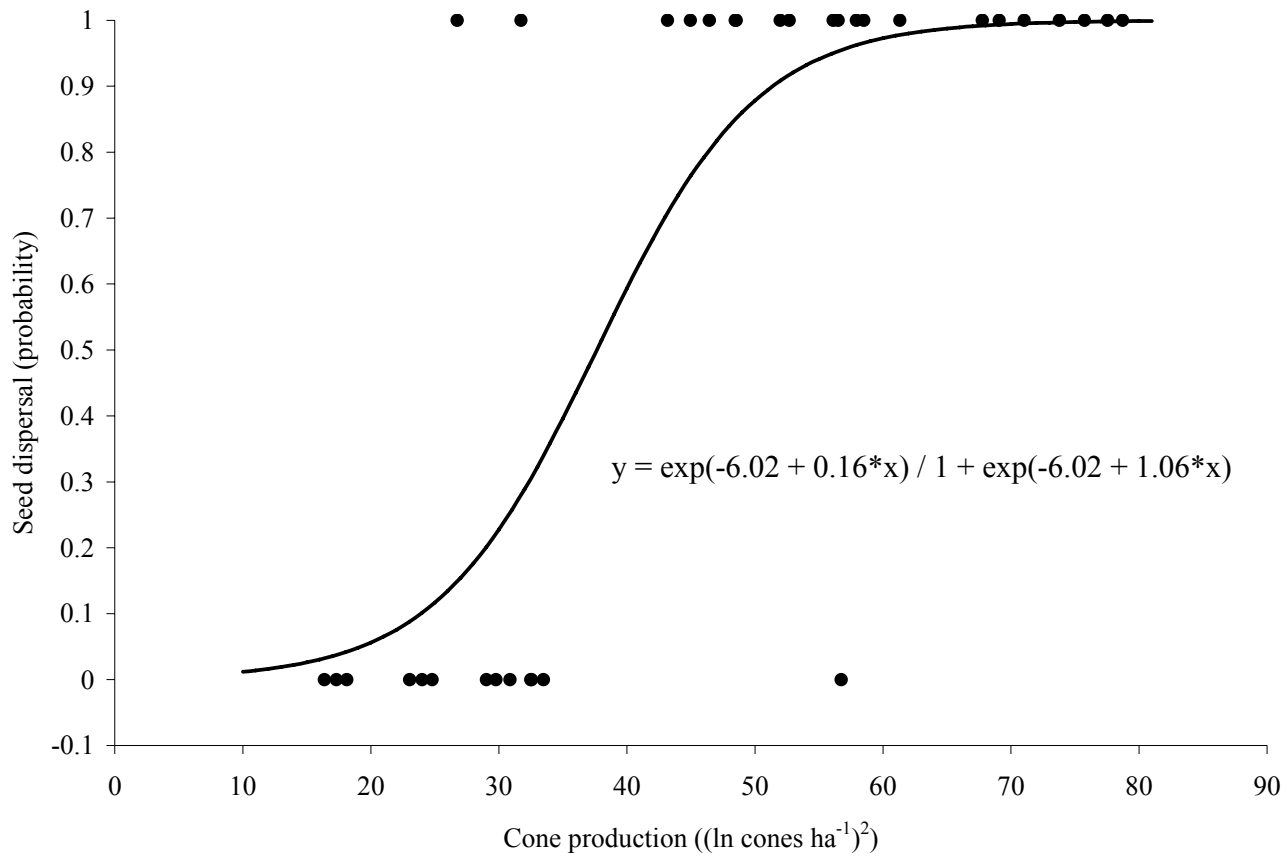
Figure 3. Clark's Nutcracker seed dispersal (1 = dispersed, 0 = not dispersed) as a function of whitebark pine cone production in Rocky Mountain forest sites (U.S.A.). Prediction line and equation from binary logistic regression shown.

The equation shown in the figure is:

$$y = \exp(-6.02 + 0.16*x) / 1 + \exp(-6.02 + 1.06*x)$$

The x-axis is labeled: Cone production $((\ln \text{ cones ha}^{-1})^2)$

The y-axis is labeled: Seed dispersal (probability)

Chapter 3

Red Squirrel habitat use and cone predation increase with declining whitebark pine abundance in Rocky Mountain subalpine forests, USA

Shawn T. McKinney, Carl E. Fiedler

College of Forestry and Conservation, University of Montana, Missoula, MT 59812

Abstract

Long evolved plant-animal interactions can be disrupted by recent changes to forest ecosystems. We examined one such interaction between *Pinus albicaulis* (whitebark pine), a subalpine forest species experiencing population declines in the northern part of its range, and *Tamiasciurus hudsonicus* (North American red squirrel), a voracious and efficient conifer seed predator, at 20 forest sites in the Rocky Mountains, USA. Our objectives were to (1) quantify and model *T. hudsonicus* habitat selection as a function of subalpine forest structure, composition, and site characteristics; (2) evaluate whether *P. albicaulis* forest type represents optimal squirrel habitat; (3) determine whether *P. albicaulis* cone predation by squirrels is sensitive to the pine's relative abundance; and (4) compare forest conditions, structure, composition, and cone predation between two ecosystems, one in the Northern Rocky Mountains where *P. albicaulis* is suffering sharp declines, and one in the Central Rocky Mountains where it is not.

Models with total basal area (m^2 ha^{-1}), mean canopy cover (%), mean canopy height (m), and tree species diversity (Simpson's index) provided the most support for estimating squirrel habitat selection based on Akaike's Information Criterion. Forest types differed in composition (*P. albicaulis* relative abundance) but not structure or associated site characteristics. Mixed species forest type had a greater proportion of

squirrel detections that were residential compared to transient, significantly greater mean cone predation, and lower year-to-year variation in predation than the *P. albicaulis* forest type. Cone predation declined as the relative abundance of *P. albicaulis* increased across all research sites, regardless of location. Absolute and relative abundances of *P. albicaulis* were significantly lower, and tree mortality, blister rust (*Cronartium ribicola*) infection, crown kill, and cone predation were significantly higher in Northern Rocky Mountain sites relative to those of the Central Rockies. Silvicultural cutting treatments that move existing mixed species forest type into *P. albicaulis* forest type, or treatments such as prescribed burning and planting rust-resistant seedlings that create *P. albicaulis* forest type in the future, could lower cone predation in the short- and long-term, respectively, and slow or reverse losses of *P. albicaulis* from subalpine forests.

Key words: Whitebark pine; Pinus albicaulis; *North American red squirrel;* Tamiasciurus hudsonicus; *cone predation*; *forest condition, structure, and composition*; *white pine blister rust*; Cronartium ribicola; *Northern and Central Rocky Mountains, USA.*

Introduction

Human induced changes to forest ecosystems can alter plant-animal interactions, which in turn may lead to disproportionate effects on plant species and thereby change community composition. Both the loss of animal seed dispersers, whether from forest fragmentation (Cordeiro and Howe 2003) or overhunting (Meeham et al. 2002), and the introduction of animal seed predators (Christian 2001) have induced local declines in plant species and shifts in community composition. However, what is not well known is how declines in plant abundance–without corresponding declines in animal abundance– will affect plant-animal interactions. Specifically, if a plant species is declining but a seed predator remains intact, will the effects on the plant be more dramatic? Understanding how modern perturbations that disproportionately affect plant species may influence plant-animal interactions, and thus the trajectory of community change, can help improve management strategies in these systems. The issue becomes especially compelling when the plant in question is a keystone species within its community. Differential vertebrate seed predation in a declining foundational tree species is identified in this paper and management options are provided to reduce associated impacts in two forest types and two geographic regions.

The genus of arboreal squirrels, *Tamiasciurus*, and modern members of the genus *Pinus* have coexisted in North America since at least the late Pliocene (ca. 1.7 Ma) (Hafner 1984, Axelrod 1986). The coevolutionary interactions between the two taxa, with *Tamiasciurus* evolving adaptations for specialized feeding on pine seeds, and *Pinus* evolving cone and seed morphologies to inhibit seed predation, are well documented (e.g., Smith 1970, Elliott 1974, Benkman et al. 1984). The modern distribution of *Pinus*

in North America, unprecedented in extent in the geologic past (Axelrod 1986), underscores the ability of pines to adapt to challenges posed by efficient vertebrate seed predators.

Today, many North American coniferous forests are faced with anthropogenic influences (e.g., invasive species, climatic change, and altered disturbance regimes) that can negatively and disproportionately affect *Pinus* species. In western North America for example, the exotic fungal pathogen, *Cronartium ribicola*, whose only tree hosts are five-needled white pines (genus *Pinus,* subgenus *Strobus*), has spread south to New Mexico and east to South Dakota since its introduction near Vancouver, British Columbia in 1910 (see McDonald and Hoff 2001 for review); mountain pine beetles (*Dendroctonus ponderosae*), whose only hosts are *Pinus* species, are experiencing population explosions that have been linked to drought and climatic warming (Logan and Powell 2001); and fire exclusion has lead to increases in shade-tolerant conifer species and decreases in shade-intolerant *Pinus* in some fire-adapted ecosystems (Arno 1980, Moore et al. 1999). All three of these agents have somewhat predictable effects on *Pinus* species within mixed conifer communities–a shift in community composition toward decreasing *Pinus* abundance. How changes in relative community composition will affect interactions between *Pinus* seed producers and *Tamiasciurus* seed predators, however, is less certain, but will likely depend on the squirrel's food choices and preferences. For example, if declines in pine populations result in changes to squirrel habitat use, then cone predation rates in *Pinus* will not be proportional to declines in abundance. However, if squirrels do not move to alternate habitats and food sources, then cone predation rates should increase with decreasing abundance of the pine.

We addressed this question by studying *Tamiasciurus hudsonicus* (North American red squirrel) habitat use in Rocky Mountain *Pinus albicaulis* (whitebark pine) forests. The species' geographical ranges are sympatric in the Rocky Mountains where both maintain a boreal affinity. Both species are present in late Pleistocene deposits (ca. 0.8–0.5 Ma) (Kurtén and Anderson 1980, Baker 1990), suggesting a prolonged ecological interaction.

Pinus albicaulis is a keystone species of upper subalpine ecosystems (Tomback and Kendall 2001) that occurs in nearly-pure stands on the coldest and driest sites, and in mixed association with other conifers on less severe, lower elevation sites (Arno and Hoff 1990). Its seeds are large and relatively high in energy compared to other conifers, wingless, and retained in indehiscent cones (i.e., cone scales remain closed after seeds ripen) (McCaughey and Schmidt 1990, Lanner and Gilbert 1994). The uniqueness of these traits is explained by the coevolved mutualism with the Clark's nutcracker (*Nucifraga columbiana*), the primary seed disperser of *P. albicaulis* (Tomback 1982). Indeed, Clark's nutcracker seed dispersal and caching behavior provide the only ecologically significant vector for *P. albicaulis* seedling establishment (Tomback 1982; Hutchins & Lanner 1982).

Pinus albicaulis, a five-needled white pine, is faced with multiple challenges to its long-term persistence, including high susceptibility to *C. ribicola* (white pine blister rust) (Hoff et al. 1980), mountain pine beetle upsurges (Logan and Powell 2001), and successional replacement by shade-tolerant conifers and loss of regeneration opportunities due to fire exclusion (Brown et al. 1994, Murray et al. 2000). Declines in *P.*

albicaulis are occurring nearly rangewide, but tree mortality and damage are highest in the northern part of its range (i.e., interior Northwest U.S. and southern Alberta and British Columbia). Mean blister rust infection levels are 66% (range on average from 17% to 89%) and mean mortality is 35% (range on average of 8% to 58%) in stands sampled throughout the northwestern US and southwestern Canada (Kendall and Keane 2001). Furthermore, Keane et al. (1996) estimated that within this region the area of *P. albicaulis* forest cover type has declined 45% over the past 100 years. The high infection and mortality levels in the pine's northern range are contrasted with reported levels in the southern range in southwestern Montana and northwestern Wyoming where mean infection is 10% (range on average of 2% to 13%) and average mortality is 8% (range on average of 7% to 10%) (Kendall and Keane 2001 and references therein).

Tamiasciurus hudsonicus, a highly territorial granivore and fungivore and efficient central-place forager (Elliott 1988), is capable of harvesting up to 100% of *Pinus* cone crops (Flyger and Gates 1982). Territories are maintained by a single adult that cuts conifer cones and stores them in middens (Smith 1981). Middens are accumulations of cone debris, sometimes piles as large as 7 m across and 0.5 m deep, that cover the ground to the exclusion of all living plants (Finley 1969). The squirrels preferentially select cones from the tree species with the highest cone energy content (i.e., the energy available to squirrels in the seed endosperm and embryos of cones = no. of seeds cone^{-1} * calories seed^{-1}) (Smith 1970). *T. hudsonicus* prefers *P. albicaulis* cones over those of other conifers in mixed species subalpine forests (Hutchins and Lanner 1982). In the Rocky Mountains, the squirrel is the major predispersal seed predator of *P. albicaulis* taking as much as 80% of the cone crop and greatly diminishing the number of seeds

available for nutcracker dispersal (Hutchins and Lanner 1982, McKinney and Tomback 2007).

Previous studies have documented the squirrel's preference for habitat conditions that ensure a dependable supply of conifer cones and fungi (dense forests of mixed conifer species), allow for adequate cone storage (cool and moist forest floor), and provide escape from predators (closed canopies) (see Steele 1998 for overview). However, suboptimal habitats that do not possess all of these characteristics can be temporarily used during periods of population growth (Rusch and Reeder 1978). Individuals will disperse into suboptimal habitat, cut cones to eat *in situ* or carry back to a territory, or attempt to form a territory there. However, strong philopatry, increased predation risk with increasing dispersal distance, and lower survival indicate that squirrel occurrence in suboptimal habitat is most often transient (Larsen and Boutin 1994). Reinhart and Mattson (1990) found fewer resident squirrels in stands of *P. albicaulis* forest type (i.e., nearly-pure *P. albicaulis*) compared to mixed species stands containing *P. albicaulis*. They speculated that the *P. albicaulis* forest type is not hospitable habitat for squirrels because of lower basal area and tree diversity, greater cone crop variability, and harsher environmental conditions found in *P. albicaulis* forest type compared to mixed species type (Reinhart and Mattson 1990).

The purpose of this study was to determine if changes in forest conditions influence *T. hudsonicus* habitat use and subsequent rates of *P. albicaulis* cone predation in Northern and Central Rocky Mountain subalpine forests. Our objectives were to (1) quantify and model *T. hudsonicus* habitat selection as a function of subalpine forest structure, composition, and site characteristics; (2) evaluate whether *P. albicaulis* forest

type represents optimal squirrel habitat; (3) determine whether *P. albicaulis* cone predation by squirrels is sensitive to the pine's relative abundance; and (4) compare forest conditions, structure, composition, and cone predation between two ecosystems, one in the Northern Rocky Mountains where *P. albicaulis* is suffering sharp declines, and one in the Central Rocky Mountains where it is not. By comparing two ecosystems with contrasting mortality and infection levels, our research provides insights into the relationship between forest conditions and cone predation and the potential trajectory of change in forest community composition. To our knowledge, no previous study has investigated whether changes in forest composition influence habitat use by squirrels and subsequent effects on cone predation. This information can be used by the U.S. Department of Agriculture, Forest Service, and Department of Interior, Park Service to implement conservation and restoration strategies for *P. albicaulis* in the Rocky Mountains.

Methods

Study Area

We conducted research from June to September, 2004-2006, within two distinct geographic areas in the Rocky Mountains, USA. Research within the Northern Divide Ecosystem (NDE) of northwestern Montana took place in Glacier National Park and the Flathead National Forest (48.8°N to 48.3°N, 113.3°W to 114.4°W). Elevation of research sites ranged from 1 928 m to 2 209 m above sea level. In the Greater Yellowstone Ecosystem (GYE) of southwestern Montana and northwestern Wyoming, research was conducted within Yellowstone National Park and the Gallatin and Shoshone National

Forests (45.1°N to 44.8°N, 109.5°W to 110.6°W). Elevation of sites ranged from 2 529 m to 2 970 m above sea level.

Forest communities at research sites were comprised of *P. albicaulis*, *P. contorta* (lodgepole pine)*, Abies lasiocarpa* (subalpine fir), *Picea engelmannii* (Engelmann spruce)*, and *Pseudotsuga menziesii* (Douglas-fir) in various combinations and relative abundances.

Sampling Design

We chose the two study ecosystems (NDE and GYE) because they represent distant points along a gradient of *P. albicaulis* forest conditions (i.e., tree mortality, blister rust infection, and crown kill). We selected individual research sites based on the presence of cone-bearing *P. albicaulis*. Multiple research sites within ecosystems were selected to capture variation in tree species composition and structure and in the altitudinal range of *P. albicaulis* and *T. hudsonicus* co-occurrence. Thus the research site was the sampling unit of investigation (NDE $n = 10$, GYE $n = 8$). We established research sites by delineating rectangular boundaries that were 100 m wide by $\geq$ 200 m long within contiguous forest stands (site area: min = 2 ha, max = 7 ha, mean = 2.6 ha). The actual size of a site was determined by the density of cone-bearing *P. albicaulis*, so that forests with low densities of cone-bearing trees (e.g., 1 ha^{-1}) required larger sampling areas. Sites were subdivided into 1-ha squares (100 m × 100 m) to provide better control over vegetation and squirrel sampling.

Field Methods

We generated random numbers for azimuth degree and distance and followed them from a corner of each 1-ha square until we encountered a cone-bearing *P. albicaulis*

tree without going off the site. Selected cone trees were ≥ 25 m apart with a minimum of one and maximum of four sampled trees ha^{-1} (cone trees site^{-1}: min = 4, max = 16, mean = 10.6). We marked cone trees with metal identification tags and logged tree coordinates with a handheld Global Positioning System unit (Garmin, ± 10 m) for later relocation. Initial ovulate cone counts were conducted between 29 June and 15 July of each year. We used tripod-mounted Leica spotting scopes with 10x to 60x zoom eyepieces and handheld tally devices to count cones. Two to three observation points that allowed for unobstructed views of a tree's canopy were used to census cones on each tree. We returned to the same observation points between 19 August and 4 September of each year and counted the remaining cones. Because cones are indehiscent at maturity and rarely fall to the ground without vertebrate assistance, we were able to ascribe cone loss to one of two species. Nutcrackers extract seeds while the cone remains attached to the branch, leaving a characteristic dished-out cone after seed harvesting, and rarely dislodge cones from branches (Hutchins and Lanner 1982, Tomback 1998). Squirrels use their sharp teeth and strong temporal muscles to either cut branch tips and drop individual or whorls of cones, or to cut the base of a single cone and eat it *in situ* (Smith 1970, Hutchins and Lanner 1982). Because *T. hudsonicus* was the only mammal in the study area capable of cutting cones from the canopy, we attributed the difference between the initial and final cone numbers to squirrel predation (McKinney and Tomback 2007). Percent cone predation for each site was calculated annually and overall (i.e., within a year and all years combined) as the sum of cones lost to squirrels (by year, all years) divided by the sum of initial cone counts (by year, all years), multiplied by 100.

We established two 10 m x 50 m (500 m^2) belt transects along random azimuths within each hectare of each research site to collect tree- and site-level data. All trees with diameter at breast height (dbh, 1.4 m) $\geq$ 7 cm were recorded by species and dbh ($\pm$ 0.1 cm); canopy cover ($\pm$ 5 %) was estimated at each transect midpoint with a convex forest densitometer in four cardinal directions; and canopy height ($\pm$ 1 m) and site slope ($\pm$ 1 degree) were measured with a clinometer. We calculated basal area (BA, m^2 ha^{-1}) from the dbh for each tree and summed BA by transect, species, and research site. The four canopy cover readings at each transect were averaged, converted into percent canopy cover, and then used to calculate the site mean. We inspected all living *P. albicaulis* trees $\geq$ 7 cm dbh for the presence of ovulate cones and blister rust infection symptoms. A tree was identified as infected if it exhibited active or inactive branch or stem cankers (Hoff 1992), which are fusiform swellings produced by the rust's mycelia growing into phloem tissue of a branch or stem (McDonald & Hoff 2001). We estimated percent crown kill ($\pm$ 5 %) for all infected trees, considering the crown to extend from the top of the tree down to the lowest branches (McKinney and Tomback 2007). Standing dead *P. albicaulis* were also measured for dbh. Uncertainty associated with determining the primary mortality agent prevented us from ascribing cause of death.

At each research site, we used two strip transects (Eberhardt 1978) 50 m wide by the length of the site to survey for two types of *T. hudsonicus* signs–active middens and fresh cones. Active middens (i.e., cone-eating and storage sites) were identified by the presence of recently cut cones, cone scales, or chewed cone cores on or within larger multiple year accumulations of cone debris (Finley 1969). Hence active middens were evidence of current *T. hudsonicus* residence. Fresh cones were defined as *P. albicaulis*

cone debris of the current year that was not on, in, or within 5 m of a midden (Côté and Ferron 2001). Current year status was determined by debris having purple cone scales, white cores, white seed coats, and softness. Since the seeds of the fresh cone category were eaten *in situ* and not connected with an active midden, fresh cones were not indicative of a squirrel's residence. One person ran a transect tape and maintained a consistent azimuth while each of two researchers surveyed for active middens and fresh cones within 25 m on either side of the transect line. Detections were recorded at 50 m interval lengths, summed for each category, and divided by the total area sampled to calculate the mean number of middens and fresh cones m^{-2}. We calculated the relative proportion of each detection category to total detections for each site. Given the large size and conspicuous nature of an active midden (Finley 1969), and our search intensity, we assumed a detection probability of a squirrel's residence $\approx$ 1(Burnham et al. 1980).

In 2006, additional resources allowed us to modestly expand the geographic extent of our study by sampling two additional research sites in the Bitterroot Mountains of west-central Montana (46.5°N, 114.2°W, 2 364 m to 2 575 m). These sites were intermediate in latitude and elevation to the NDE and GYE sites. Data were collected using the same design and sampling protocols employed at the NDE and GYE sites. The Bitterroot Mountain sites, ~300 km south of the NDE and ~300 km northwest of the GYE, provided an opportunity to gather squirrel detection data and model habitat use across a broader geographic area and range of forest conditions. Therefore, data from these sites were included in the analysis of squirrel habitat use, but not in the ecosystem comparisons because of the small number of sites.

Data Analyses

Prior to analysis, data were summarized at the site level, and a significance level of $P = 0.05$ was assumed for subsequent hypothesis testing. We calculated a Simpson's diversity index value for each site based on total tree species BA. We used S-Plus 7.0, SPSS 10.0, and Microsoft Excel for all statistical analyses and computations.

T. hudsonicus habitat use – Active middens were expressed as the number ha^{-1} for each site and served as the response variable for the habitat selection analysis. Exponential and Gamma distributions were fit to the midden data and their log-likelihoods compared to determine which error distribution best fit the data. However, because several sites had zero values for middens, a value of 0.5 was added to each site's midden value and then naturally-log transformed (Sokal and Rohlf 1995) before calculating log-likelihoods. We established *a priori* hypotheses to explain midden occurrence as a function of forest parameters based on forest composition (tree species diversity and cone-bearing *P. albicaulis*), structure (basal area, canopy cover, and canopy height), *P. albicaulis* health condition (tree mortality), and site slope. We used generalized linear models with Gamma error distribution and identity link for all possible combinations of these seven variables. Thus, $2^7 = 128$ possible models, including a null model (intercept only), were compared. We used an information-theoretic approach to identify models that were best supported by the data based on Akaike's Information Criterion (AIC) corrected for small sample sizes (AIC$_c$) and on calculated Akaike weights (Burnham and Anderson 2002). The top model set was determined by calculating evidence ratios so that a model was included in the top set if the best model's weight was ≤ 3 times its weight (w_{best}:$w_i \leq 3$). We then recalculated Akaike weights for all models in

the top set (i.e., the probability of being the best model out of the top set) for use in model averaging. Lastly, we estimated the relative importance of each of the seven variables by summing the Akaike weights of all models within which a given variable occurred (Burnham and Anderson 2002).

We classified sites into one of two forest types based on the relative proportion of total basal area represented by *P. albicaulis*. Research sites were classified as *P. albicaulis* forest type if *P. albicaulis* constituted more than 50% of the total basal area, and mixed forest type if this condition was not met (i.e., proportion *P. albicaulis* $\leq$ 50%). Because we were concerned only with trees of cone-bearing size, basal area (BA, m^2 ha^{-1}) was computed for trees $\geq$ 9.0 cm.

Three comparisons were made to evaluate the hypothesis that *P. albicaulis* forest type represents optimal squirrel habitat. First, the number of active midden and fresh cone detections were summed and their proportions calculated for each forest type. A chi-square analysis was then performed on the relative proportion of detections that were residential (middens) versus transient (fresh cones) by forest type. Second, a one-tailed independent samples t-test was used to determine whether population mean cone predation (%) by squirrels was lower in *P. albicaulis* forest type. Cone predation was square root transformed to meet assumptions of normality, and Levene's Test was evaluated to determine whether equal variances could be assumed. Third, the coefficient of variation (%) for cone predation was calculated based on the annual means of each forest type to see if *P. albicaulis* type had higher annual variation associated with predation.

We used Multivariate Analysis of Variance (MANOVA) to determine if forest types differed in population mean vectors for forest structure, composition, and site slope. Forest structure was represented by the dependent variables total BA (m^2 ha^{-1}), canopy cover (%), and canopy height (m). Forest composition was estimated as the proportion of total BA represented by *P. albicaulis*. Canopy cover and canopy height were natural log-transformed to meet assumptions of normality. We evaluated the multivariate assumption of equality of covariance matrices of forest types with Box's Test and the univariate assumption of equality of error variance with Levene's Test.

We used simple linear regression to model the relationship between cone predation (all years) and the relative abundance of *P. albicaulis* (proportion of total BA) across all sites ($n = 20$).

Forest conditions: an ecosystem comparison – We used MANOVA to determine if the NDE had significantly greater population mean vectors for the forest condition parameters - mortality, blister rust infection, and rust-induced crown kill (mean % by site). Crown kill was natural log-transformed to meet assumptions of normality. We evaluated the multivariate assumption of equality of covariance matrices between ecosystems with Box's Test and the univariate assumption of equality of error variance with Levene's Test.

We tested the hypotheses that the NDE had lower absolute and proportional *P. albicaulis* BA and higher mean cone predation with one-tailed independent samples *t*-tests. For all three *t*-tests, the *F* statistic for Levene's Test was evaluated to determine whether equal variances could be assumed and therefore which *t*-value (equal or unequal variances) to interpret.

Results

T. hudsonicus Habitat Use

The model containing total site BA only had the most support for estimating

active middens (R^2 = 0.419). However, models containing mean canopy cover, tree

species diversity, and mean canopy height could not be excluded based on their AIC_c

values and evidence ratios ≤ 3. The addition of diversity increased R^2 to 0.459, while

diversity alone yielded an R^2 = 0.321, indicating a suitability between total site BA and

diversity. Hence, five models constituted the top model set (Table 1). Variables that did

not occur in the top model set were the number of *P. albicaulis* cone-bearing trees ha^{-1},

tree mortality (%), and site slope (degrees). The model equations and recalculated Akaike

weights for models in the top set (Table 1) were used to obtain a single, model-averaged

equation to estimate midden density (m, no. m^{-2}).

m = [(model 1 * 0.368) + (model 2 * 0.223) + (model 3 * 0.155) + (model 4 * 0.131) +

(model 5 * 0.123)] – 0.5   (1)

The terms model 1, 2, 3, 4, and 5 refer to the model equation output for each of the

models ranked one through five, respectively (Table 1). Midden density (m) is estimated

by multiplying the output from each model's equation times the associated Akaike weight

(Top w_i in Table 1) and then summing the products. A value of 0.5 is subtracted because

we initially added 0.5 to each site's midden count (see Data Analyses).

We were unable to obtain results for 16 of the 128 models because iterations were

terminated prematurely due to singularities. We ascribed weights of zero to these failed

models when ranking all models and variables (Table 5). The ranking of the seven

variables we obtained by summing the Akaike weights across all models in which the

variable occurred resulted in the following order: (1) total basal area (0.481), (2) mean canopy cover (0.346), (3) tree species diversity (0.343), (4) mean canopy height (0.244), (5) *P. albicaulis* cone trees (0.201), (6) site slope (0.191), and (7) *P. albicaulis* tree mortality (0.180).

The proportion of resident (active middens) relative to transient (fresh cones) signs of *T. hudsonicus* differed between forest types ($\chi^2 = 6.717$, df = 1, $n = 126$, $P = 0.01$), with the mixed species type having the highest resident to transient ratio (Table 2). Likewise, mean cone predation by squirrels was significantly higher in the mixed species forest type relative to the *P. albicaulis* type (one-tailed independent samples t-test $t_{18} = 3.248$, $P = 0.002$) (Table 2). The coefficient of variation for cone predation over the three years of the study was 6.5 times higher in *P. albicaulis* forest type than in the mixed species type (Table 2).

There were significant differences in the population mean vectors for forest structure, composition, and site slope between forest types (MANOVA Wilks' Lambda $F_{5,14} = 7.794$, P = 0.001); however, univariate testing results (multiple one-way ANOVAs) showed no significant differences in population mean values for forest structure parameters (total BA, canopy cover, and height) and site slope between forest types, but a significant difference in composition (proportion *P. albicaulis* BA) (Table 3, Table 6). Cone predation decreased in a linear fashion over all research sites as the proportion of *P. albicaulis* BA to total BA increased (Fig. 1).

Forest Conditions: An Ecosystem Comparison

To assess the differences in forest condition parameters between ecosystems, we documented mortality, blister rust infection, and crown kill in 4 496 *P. albicaulis* trees

(NDE = 2 404, GYE = 2 092) in 18 research sites over a three year period (Table 7). There was a significant difference between ecosystems in the population mean vectors for these three parameters (MANOVA Wilks' Lambda $F_{3,14}$ = 9.806, P = 0.001) with pair-wise comparisons showing significantly greater mortality ($F_{1,16}$ = 12.663, P = 0.003), infection, ($F_{1,16}$ = 10.403, P = 0.005), and crown kill ($F_{1,16}$ = 14.633, P = 0.001) in the NDE (Fig. 2). *P. albicaulis* BA was also significantly lower in the NDE, both proportionally and absolutely, and cone predation significantly higher than in the GYE (Table 4).

Discussion

T. hudsonicus Habitat Use

The persistence of *T. hudsonicus* populations within coniferous forests requires conditions that provide cover and escape from predators, enough seeds annually to survive long boreal winters, and suitable microsites for storing cones (Smith 1981, Rush and Reeder 1978). Our results of squirrel habitat selection confirm that these factors are also important for *T. hudsonicus* residence within Rocky Mountain subalpine forests containing *P. albicaulis*. Active middens increased with increasing canopy cover and height (cover and predator escape), total BA (potential cone production), and tree species diversity (dependability of annual cone production). While we did not directly measure conditions for cone storage (i.e, soil moisture, duff depth, and temperature), high values for the four variables (BA, cover, height, and tree diversity) in the top habitat model set suggest adequate cone storage conditions.

Several of our results indicate that the *P. albicaulis* forest type does not represent optimal squirrel habitat. First, the fewest detections of active middens relative to fresh

cones occurred in the *P. albicaulis* type (Table 2), suggesting that squirrels generally were not residents within these forests, but could disperse into them, feed on the high energy seeds, and either return to their territories or be depredated. Second, cone predation was significantly lower in the *P. albicaulis* forest type compared to the mixed species type (Table 2). *Tamiasciurus hudsonicus* exhibits the evolved behavior of preferentially selecting the tree species with the highest cone energy content (Kcal cone^{-1}) within mixed species forests (Smith 1970). Of the five conifer species occurring in our research sites, *P. albicaulis* had the highest cone energy content (e.g., *P. albicaulis* = 27.7 Kcal cone^{-1}, next highest *A. lasiocarpa* = 15.7 kcal cone^{-1}) (Tomback 1982, Smith 1970). Thus, if squirrels were residents within *P. albicaulis* type, one would expect the highest cone predation there, not the lowest. Increasing cone predation with decreasing *P. albicaulis* relative abundance (Fig. 1) lends strong support to the hypothesis that squirrels select the tree species with the highest cone energy content but require the more diverse, and hence more stable, food supply of mixed species forests for residential status (Reinhart and Mattson 1990). Third, the coefficient of variation for cone predation over the three years of the study was much higher in the *P. albicaulis* type (Table 2). Large year-to-year fluctuations in cone predation also suggest that squirrel occurrence in these forests was transient and largely dependent upon a given year's cone production.

Our results indicate that *P. albicaulis* forest type is suboptimal squirrel habitat because of the lack of alternative conifer seed sources, and thus, the high uncertainty associated with annual cone production. Comparisons between the two forest types showed that the *P. albicaulis* type was similar to the mixed species type in providing cover and escape from predators (i.e., canopy cover and height), in potential cone

production (i.e., total site BA), and site slope, but differed in the dependability of an annual cone crop large enough to sustain individuals through the long boreal winter (i.e., proportion *P. albicaulis*) (Table 3).

Our analysis of *T. hudsonicus* habitat selection shows that squirrels selected habitats based on the same factors reported important in other parts of their range (Rusch and Reeder 1978, Smith 1981), and that the disparity in habitat suitability among subalpine forest types appears due to differences in abundance of alternative seed sources. Thus, the greater the relative abundance of *P. albicaulis*, the lower the cone predation and the greater the amount of seed remaining for avian dispersal. Indeed, previous research suggests that, historically (i.e., pre-blister rust), *P. albicaulis* forest type was the primary seed source for most regeneration (Hutchins and Lanner 1982).

Forest conditions: an ecosystem comparison – The general trend of decreasing cone predation with increasing *P. albicaulis* relative abundance predominates when comparing research sites (Fig. 1), forest types (Tables 2 and 3), or ecosystems (Table 4). The NDE, with significantly lower absolute and proportional abundances of *P. albicaulis*, experienced significantly higher cone predation than the GYE (Table 4).

Only 10% of the research sites in the NDE were *P. albicaulis* forest type contrasted with 50% in the GYE (Tables 6 and 7). The higher mortality documented in the NDE explains the relatively lower *P. albicaulis* abundance, while the higher blister rust infection and crown kill levels imply continued forest compositional change in this subalpine environment from *P. albicaulis* into mixed species forest type (Fig. 2, Table 4).

Our finding that cone predation increases with decreasing *P. albicaulis* relative abundance suggests that this pine species is faced with an additional risk factor beyond

blister rust, mountain pine beetle, and successional replacement, which can further accelerate the conversion of subalpine forests away from *P. albicaulis* type. A net loss of *P. albicaulis* resulting from disproportionate mortality and reduced regeneration opportunities will lead to lower relative abundances of *P. albicaulis* within stands, fewer stands of *P. albicaulis* forest type, and increased cone predation of the remaining trees. When taken across a broad landscape such as the NDE, the number of seeds available for avian dispersal, and thus natural regeneration, will also decrease.

Management Implications

Both modeling and field studies provide evidence that without fire, *A. lasiocarpa* will eventually replace *P. albicaulis*, and that replacement will be accelerated by mortality from blister rust and pine beetle (Keane 2001). Our results show that *T. hudsonicus* can greatly diminish cone crops where there is severe *P. albicaulis* tree damage and mortality, thus leaving few seeds available for nutcracker seed dispersal. In the Northern Rocky Mountains–NDE, where mortality is high and *P. albicaulis* abundance low, management must move beyond returning historical fire regimes and waiting for natural regeneration. The tools employed, however, would be dependent upon the forest type. For example, in the mixed species type, mortality, rust infection, and successional replacement are the most dramatic. Thus allowing wildland fires to burn, applying silvicultural cutting and prescribed burning treatments that remove shade-tolerant species and leave *P. albicaulis*, and planting rust-resistant seedlings may be the only way to maintain *P. albicaulis* on the landscape (Schwandt 2006; Mahalovich et al. 2006; Schoettle 2004).

Conversely, we found lower levels of mortality, rust infection, and crown kill in the *P. albicaulis* type across all sites sampled (Table 7). Reports from other researchers corroborate our findings that blister rust has not yet caused extensive damage in the *P. albicaulis* forest type (e.g., Keane 2001 and references therein). Given that squirrel predation was also the lowest in the *P. albicaulis* type (Table 2), these forests could serve as seed sources for natural regeneration by nutcrackers and thus require less intensive management (e.g., allowing for wildland fire).

Different complications arise in the management of *P. albicaulis* in the Central Rocky Mountains–GYE. The seeds of *P. albicaulis* are an important source of nutrition for grizzly bears (*Ursus arctos*) in this region, where the bear has just been delisted as a threatened and endangered species. Bears obtain seeds by raiding squirrel middens (Mattson and Reinhart 1997), and our study documents that middens are significantly more likely to occur in the mixed species forest type (see also Reinhart and Mattson 1990). Our surveys in the GYE show that *P. albicaulis* mortality is low (15%), but that current rust infection levels of nearly 50% portend future increases in mortality. Bears would be affected by *P. albicaulis* losses whether from blister rust, successional replacement, or climatic warming (Mattson and Reinhart 1997), and declines in *P. albicaulis* to current levels in the NDE would have serious ramifications for the bear's status in the future. Because grizzly bears rely on squirrels to access *P. albicaulis* seeds, converting stands to *P. albicaulis* type, as outlined above for the NDE, would not be a prudent option. However, planting rust-resistant seedlings prior to severe *P. albicaulis* decline, and allowing high-elevation wildland fires to burn when possible, are the most feasible options in the Greater Yellowstone Ecosystem.

In this paper we demonstrate that human-induced factors that cause disproportionate declines in a conifer species without corresponding effects on a primary seed predator can further accelerate the decline of that species. However, the specific relationships between seed producer and seed predator are dependent on processes occurring at both site and ecosystem levels. Therefore, management treatments proposed to comprehensively address these relationships must account for specific conditions at both levels.

Acknowledgments

Literature Cited

Arno, S. F. 1980. Forest fire history in the northern Rockies. Journal of Forestry **78**:460-465.

Arno, S. F., and R. J. Hoff. 1990. *Pinus albicaulis* Engelm. Whitebark Pine. Pages 268-279 *in* R. M. Burns and B. H. Honkala, technical coordinators. Silvics of North America. Vol. I. Conifers. Agriculture Handbook 654. U.S. Department of Agriculture, Washington, D.C.

Axelrod, D. I. 1986. Cenozoic history of some western American pines. Annals of the Missouri Botanical Garden **73**:565-641.

Baker, R. G. 1990. Late Quaternary history of whitebark pine in the Rocky Mountains. Pages 40-48 *in* W. C. Schmidt and K. J. McDonald, editors. Proceedings-Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource. General Technical Report INT-270. U.S. Department of Agriculture, Rocky Mountain Research Station, Ogden, Utah, USA.

Benkman, C. W., R. P. Balda, and C. C. Smith. 1984. Adaptations for seed dispersal and the compromises due to seed predation in limber pine. Ecology **65**:632-642.

Brown, J. K., S. F. Arno, S. W. Barrett, and J. P. Menakis. 1994. Comparing the prescribed fire program with presettlement fires in the Selway-Bitterroot Wilderness. International Journal of Wildland Fire **4**:157-168.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Burnham, K. P., D. R. Anderson, and J. L. Laake. 1980. Estimation of density from line
transect sampling of biological populations. Wildlife Monographs **72**:1-202.

Christian, C. E. 2001. Consequences of a biological invasion reveal the importance of
mutualism for plant communities. Nature **413**:635-639.

Cordeiro, N. J., and H. F. Howe. 2003. Forest fragmentation severs mutualism between
seed dispersers and an endemic African tree. Proceedings of the National
Academy of Sciences **100**:14052-14056.

Côté, M.,and J. Ferron. 2001. Short-term use of different residual structures by three
sciurid species in a clear-cut boreal landscape. Canadian Journal of Forest
Research **31**:1805-1815.

Eberhardt, L. L. 1978. Transect methods for population studies. Journal of Wildlife
Management **42**:1-31.

Elliott, P. F. 1974. Evolutionary responses of plants to seed-eaters: pine squirrels
predation on lodgepole pine. Evolution **28**:221-231.

Elliott, P. F. 1988. Foraging behavior of a central-place forager: field tests of theoretical
predictions. The American Naturalist **331**:159-174.

Finley, R. B., Jr. 1969. Cone caches and middens of *Tamiasciurus* in the Rocky Mountain
region. Miscellaneous Publications of the University of Kansas Museum of
Natural History **51**:233-273.

Flyger, V., and J. E. Gates. 1982. Pine squirrels: *Tamiasciurus hudsonicus, T. douglasii.*
Pages 230-237 *in* J. A. Chapman and G. A. Feldhamer, editors. Wild mammals of
North America. John Hopkins University Press, Baltimore, Maryland, USA.

Hafner, D. J. 1984. Evolutionary relationships of the nearctic Sciuridae. Pages 3-23 *in* J. O. Murie and G. R. Michener, editors. The biology of ground dwelling squirrels. University of Nebraska Press, Lincoln, Nebraska, USA.

Hoff, R. J. 1992. How to recognize blister rust infection on whitebark pine. Forest Service Research Note INT-RN-406.

Hoff, R. J., R. T. Bingham, and G. I. McDonald. 1980. Relative blister rust resistance of white pines. European Journal of Forest Pathology **10**:307-316.

Hutchins, H. E., and R. M. Lanner. 1982. The central role of Clark's Nutcracker in the dispersal and establishment of whitebark pine. Oecologia **55**:192-201.

Keane, R. E. 2001. Successional dynamics: modeling an anthropogenic threat. Pages 159-192 *in* D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, D.C., USA.

Keane, R. E., J. P. Menakis, and W. J. Hann. 1996. Coarse-scale restoration planning and design in Interior Columbia River Basin Ecosystems: An example for restoring declining whitebark pine forests. Pages 14-19 *in* C. C. hardy and S. F. Arno, editors. The use of fire in forest restoration. General Technical Report INT-GTR-341. U.S. Department of Agriculture, Rocky Mountain Research Station, Ogden, Utah, USA.

Kendall, K. C., and R. E. Keane. 2001. Whitebark pine decline: infection, mortality, and population trends. Pages 221-242 *in* D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, D.C., USA.

Kurtén, B., and E. Anderson. 1980. Pleistocene mammals of North America. Columbia University Press, New York, New York, USA.

Lanner, R. M., and B. K. Gilbert. 1994. Nutritive value of whitebark pine seeds and the question of their variable dormancy. Pages 206-211 *in* W. C. Schmidt and F. K. Holtmeier, editors. Proceedings—International Workshop on Subalpine Stone Pines and Their Environment: the Status of Our Knowledge. General Technical Report INT-GTR-309. U.S. Department of Agriculture, Rocky Mountain Research Station, Ogden, Utah, USA.

Larsen, K. W., and S. Boutin. 1994. Movements, survival, and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. Ecology **75**:241-223.

Logan, J. A., and J. A. Powell. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). American Entomologist **47**:160-172.

Mahalovich, M. F., K. E. Burr., and D. L. Foushee. 2006. Whitebark pine germination, rust resistance, and cold hardiness among seed sources in the Inland Northwest: Planting strategies for restoration. Forest Service Proceedings RMRS-P-43.

Mattson, D. J., and D. P. Reinhart. 1997. Excavation of red squirrel middens by grizzly bears in the whitebark pine zone. Journal of Applied Ecology **34**:926-940.

McCaughey, W. W., and W. C. Schmidt. 1990. Autecology of whitebark pine. Pages 85-96 *in* W. C. Schmidt and K. J. McDonald, editors. Proceedings-Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource. General Technical Report INT-270. U.S. Department of Agriculture, Rocky Mountain Research Station, Ogden, Utah, USA.

McDonald G. I., and R. J. Hoff. 2001. Blister rust: An introduced plague. Pages 193-220 *in* D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, D.C., USA.

McKinney, S. T., and D. F. Tomback. 2007. The influence of white pine blister rust on seed dispersal in whitebark pine. Canadian Journal of Forest Research **37**:1044-1057.

Meehan, H. J., K. R. McConkey, and D. R. Drake. 2002. Potential disruptions to seed dispersal mutualisms in Tonga, Western Polynesia. Journal of Biogeography **29**:695-712.

Moore, M. M., W. W. Covington, and P. Z. Fule. 1999. Reference conditions and ecological restoration: A southwestern ponderosa pine perspective. Ecological Applications **9**:1266-1277.

Murray M. P., S. C. Bunting, and P. Morgan. 2000. Landscape trends (1753-1993) of whitebark pine (*Pinus albicaulis*) forests in the West Big Hole Range of Idaho/Montana, U.S.A. Arctic, Antarctic, and Alpine Research **32**:412-418.

Reinhart, D. P., and D. J. Mattson. 1990. Red squirrels in the whitebark zone. Pages 256-263 *in* W. C. Schmidt and K. J. McDonald, editors. Proceedings-Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource. General Technical Report INT-270. U.S. Department of Agriculture, Rocky Mountain Research Station, Ogden, Utah, USA.

Rusch, D. A., and W. G. Reeder. 1978. Population ecology of Alberta red squirrels. Ecology **59**:400-420.

Schoettle, A. W. 2004. Developing proactive management options to sustain bristlecone and limber pine ecosystems in the presence of a non-native pathogen. Pages 146-15 5*in* W. D. Shepperd and L. G. Eskew, compilers. Silviculture in special places: Proceeding of the National Silviculture Workshop. Proceedings RMRS-P-34. U.S. Department of Agriculture, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Schwandt, J. W. 2006. Whitebark pine in peril: A case for restoration. Forest Service Report R1-06-28.

Smith, C. C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecological Monographs **40**:349-371.

Smith, C. C. 1981. The indivisible niche of *Tamiasciurus*: an example of nonpartitioning of resources. Ecological Monographs **51**:343-363.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. Third edition. W. H. Freeman and Company, New York, New York, USA.

Steele, M. A. 1998. Tamiasciurus hudsonicus. Mammalian Species **586**:1-9.

Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: A mutualism hypothesis. Journal of Animal Ecology **51**:451-467.

Tomback, D. F. 1998. Clark's nutcracker (*Nucifraga columbiana*). Number 331 *in* A. Poole and F. Gill, editors. The birds of North America. The Birds of North America Incorporated, Philadelphia, Pennsylvania, USA.

Tomback, D. F., and K. C. Kendall. 2001. Biodiversity losses: The downward spiral. Pages 243-262 *in* D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, D.C., USA.

Table 1. Selection statistics from maximum likelihood analysis for the top models (evidence ratio ≤ 3) estimating active squirrel middens as a function of habitat characteristics in *Pinus albicaulis* forests - Rocky Mountains, USA, 2004-2006.

Rank	Model	K	Log likelihood	AIC_c	Δ_i	w_i	Evidence ratio	Top w_i	R^2	Model equation
1	total basal area	2	-5.172	15.050	0.000	0.118	1.000	0.368	0.419	y = 0.175+0.060(BA)
2	canopy cover	2	-5.676	16.058	1.007	0.071	1.655	0.223	0.362	y =-0.134+0.030(Cover)
3	tree diversity	2	-6.039	16.784	1.734	0.050	2.379	0.155	0.321	y =0.591+0.010(Div)
4	diversity + basal area	3	-4.808	17.117	2.066	0.042	2.810	0.131	0.459	y = 0.105+0.004(Div)+0.043(BA)
5	canopy cover + canopy height	3	-4.868	17.236	2.185	0.039	2.982	0.123	0.453	y = 0.307+0.047(Cover)+-0.098(Ht)

Notes: K is the number of parameters estimated from the data; AIC_c is the Akaike information criterion corrected for small samples; Δ_i is the difference in AIC_c for model i and the best model; w_i is the AIC_c weight interpreted as the probability of being the best model in the total combined model set; evidence ratio is the best model's weight divided by w_i; Top w_i is the AIC_c weight given the top five models only.

Table 2. *Tamiasciurus hudsonicus* habitat use at 20 *Pinus albicaulis* research sites classified by forest type - Rocky Mountains, USA, 2004-2006.

| | *Tamiasciurus hudsonicus* | | | |
| | Detection type (proportion of total)† | | Cone predation (%) | |
Forest type	Middens	Fresh cones	Mean (SE)‡	Coefficient of variation§
Pinus albicaulis ($n = 7$)	0.19	0.81	13.2 (4.4)	85.5
Mixed species ($n = 13$)	0.41	0.59	47.3 (7.2)	13.0

Notes: Forest type defined by whether *P. albicaulis* comprised > 50% of total site BA, sites were classified as mixed species if condition was not met.

† Detection type relative proportions differed by forest type (χ^2 test, $P < 0.05$).

‡ Predation was significantly higher in mixed species type (one-tailed *t*-test, $P < 0.05$).

§ Calculated based on annual means of forest types.

Table 3. Forest parameter means (± SE) and ANOVA results for subalpine forest research sites classified by forest type - Rocky Mountains, USA, 2004-2006.

Forest parameter	Forest type		ANOVA results		
	Pinus albicaulis	Mixed species	df	*F*	*P*
Total basal area (m^2 ha^{-1})	21.94 (3.43)	23.13 (4.18)	1, 18	0.036	0.851
Canopy cover (%)	49.6 (5.9)	59.1 (7.2)	1, 18	0.234	0.635
Canopy height (m)	11.7 (0.9)	14.6 (1.7)	1, 18	0.901	0.355
Site slope (degrees)	17.9 (2.02)	17.5 (2.11)	1, 18	0.023	0.882
P. albicaulis relative abundance (% BA)	74.96 (7.15)	18.98 (4.88)	1, 18	43.667	<0.001

Note: Forest type defined by whether *P. albicaulis* comprised > 50% of total site BA, sites were classified as mixed species if condition was not met. Canopy cover and height were natural-log transformed for ANOVA, with untransformed means reported.

Table 4.   Ecosystem comparison of *Pinus albicaulis* variable means (± SE) and one-tailed independent samples *t*-test results for research sites - Rocky Mountains, USA, 2004-2006.

| Variable | Ecosystem | | 2-sample t-test results | | |
	Northern Divide	Greater Yellowstone	df	*t*	*P*
Basal area (m^2 ha^{-1})	1.95 (2.04)	14.53 (2.44)	16	2.747	0.007
Relative abundance (% BA)	19.36 (7.32)	53.55 (10.51)	16	5.020	<0.001
Cone predation (%)	56.43 (5.63)	13.07 (6.61)	16	5.483	<0.001

Note: Values are for *P. albicaulis* trees only. Northern Divide sites (*n* = 10) were in northwestern Montana, Greater Yellowstone sites (*n* = 8) were in southwestern Montana and northwestern Wyoming.

Table 5. Selection statistics from maximum likelihood analysis for the entire model set estimating active squirrel middens as a function of habitat characteristics in *Pinus albicaulis* forests - Rocky Mountains, USA, 2004-2006.

Rank	Model variables	K	Log likelihood	AIC_c	Δ_i	w_i	Evidence ratio
1	2	2	-5.172	15.050	0.000	0.118	1.000
2	4	2	-5.676	16.058	1.007	0.071	1.655
3	1	2	-6.039	16.784	1.734	0.049	2.379
4	1+2	3	-4.808	17.117	2.066	0.042	2.810
5	4+5	3	-4.868	17.236	2.185	0.039	2.982
6	2+6	3	-4.918	17.336	2.286	0.038	3.135
7	2+5	3	-4.958	17.416	2.366	0.036	3.264
8	2+7	3	-4.979	17.459	2.409	0.035	3.334
9	1+4	3	-5.010	17.521	2.470	0.034	3.439
10	2+3	3	-5.142	17.785	2.734	0.030	3.924
11	2+4	3	-5.169	17.838	2.788	0.029	4.031
12	1+6	3	-5.314	18.128	3.078	0.025	4.659
13	1+7	3	-5.410	18.321	3.271	0.023	5.131
14	6	2	-6.948	18.601	3.551	0.020	5.901
15	3+4	3	-5.586	18.671	3.621	0.019	6.112
16	1+3	3	-5.663	18.826	3.776	0.018	6.605
17	4+7	3	-5.676	18.851	3.801	0.018	6.689
18	1+5	3	-5.931	19.361	4.311	0.014	8.630
19	5	2	-7.358	19.421	4.371	0.013	8.893
20	3	2	-7.360	19.426	4.376	0.013	8.916
21	1+4+5	4	-4.463	19.592	4.542	0.012	9.687
22	1+2+6	4	-4.654	19.975	4.924	0.010	11.729
23	intercept	1	-8.895	20.012	4.961	0.010	11.949
24	1+2+5	4	-4.674	20.015	4.964	0.010	11.966
25	1+2+3	4	-4.736	20.139	5.089	0.009	12.734
26	2+4+5	4	-4.781	20.229	5.179	0.009	13.320
27	1+2+7	4	-4.790	20.247	5.196	0.009	13.439
28	1+2+4	4	-4.808	20.283	5.233	0.009	13.684
29	2+5+6	4	-4.850	20.366	5.316	0.008	14.266
30	3+4+5	4	-4.864	20.394	5.344	0.008	14.467

31	4+5+6	4	-4.867	20.400	5.350	0.008	14.510
32	4+5+7	4	-4.867	20.401	5.351	0.008	14.517
33	1+3+7	4	-4.868	20.403	5.352	0.008	14.527
34	2+6+7	4	-4.885	20.438	5.387	0.008	14.784
35	2+4+6	4	-4.899	20.464	5.414	0.008	14.984
36	2+5+7	4	-4.905	20.476	5.426	0.008	15.072
37	6+7	3	-6.493	20.487	5.436	0.008	15.152
38	2+3+6	4	-4.912	20.492	5.441	0.008	15.188
39	1+4+6	4	-4.948	20.563	5.513	0.007	15.743
40	1+3+4	4	-4.952	20.571	5.521	0.007	15.803
41	2+3+5	4	-4.955	20.576	5.526	0.007	15.844
42	1+4+7	4	-4.963	20.593	5.543	0.007	15.979
43	2+4+7	4	-4.976	20.618	5.568	0.007	16.179
44	2+3+7	4	-4.976	20.619	5.568	0.007	16.186
45	1+6+7	4	-5.137	20.940	5.890	0.006	19.006
46	5+6	3	-6.749	20.998	5.947	0.006	19.564
47	1+5+7	4	-5.188	21.042	5.992	0.006	20.005
48	3+7	3	-6.797	21.094	6.044	0.006	20.530
49	3+6	3	-6.889	21.277	6.227	0.005	22.495
50	1+5+6	4	-5.314	21.295	6.244	0.005	22.695
51	1+3+6	4	-5.314	21.295	6.244	0.005	22.695
52	5+7	3	-7.016	21.532	6.482	0.005	25.558
53	3+5	3	-7.032	21.564	6.513	0.005	25.958
54	7	2	-8.498	21.702	6.652	0.004	27.821
55	3+4+7	4	-5.585	21.836	6.786	0.004	29.755
56	1+3+5	4	-5.612	21.891	6.841	0.004	30.576
57	1+4+5+7	5	-4.392	23.070	8.019	0.002	55.124
58	1+4+5+6	5	-4.451	23.188	8.138	0.002	58.495
59	1+2+4+5	5	-4.462	23.209	8.159	0.002	59.115
60	1+3+4+5	5	-4.462	23.210	8.159	0.002	59.122
61	1+5+6+7	5	-4.502	23.289	8.238	0.002	61.507
62	1+3+5+7	5	-4.542	23.371	8.320	0.002	64.072
63	3+6+7	4	-6.360	23.388	8.337	0.002	64.623
64	1+2+5+6	5	-4.608	23.502	8.452	0.002	68.434
65	1+2+3+5	5	-4.636	23.558	8.507	0.002	70.352
66	1+2+4+6	5	-4.650	23.585	8.535	0.002	71.338
67	1+2+3+6	5	-4.651	23.588	8.538	0.002	71.438

68	1+2+5+7	5	-4.665	23.615	8.564	0.002	72.398
69	1+2+3+4	5	-4.735	23.756	8.705	0.002	77.678
70	1+2+3+7	5	-4.736	23.757	8.707	0.002	77.749
71	2+4+5+7	5	-4.772	23.829	8.779	0.001	80.598
72	2+4+5+6	5	-4.773	23.832	8.781	0.001	80.692
73	2+3+4+5	5	-4.780	23.846	8.795	0.001	81.263
74	1+2+4+7	5	-4.790	23.866	8.816	0.001	82.085
75	1+3+4+7	5	-4.823	23.933	8.882	0.001	84.863
76	2+3+5+6	5	-4.841	23.969	8.918	0.001	86.403
77	3+4+5+6	5	-4.861	24.007	8.956	0.001	88.070
78	3+4+5+7	5	-4.862	24.011	8.960	0.001	88.236
79	4+5+6+7	5	-4.867	24.019	8.969	0.001	88.616
80	2+3+6+7	5	-4.879	24.043	8.993	0.001	89.682
81	2+4+6+7	5	-4.879	24.044	8.994	0.001	89.741
82	2+3+4+6	5	-4.892	24.070	9.019	0.001	90.894
83	2+3+5+7	5	-4.905	24.095	9.045	0.001	92.047
84	1+3+4+6	5	-4.932	24.150	9.099	0.001	94.602
85	3+5+6	4	-6.744	24.154	9.104	0.001	94.821
86	3+5+7	4	-6.761	24.188	9.138	0.001	96.442
87	2+3+4+7	5	-4.972	24.230	9.180	0.001	98.485
88	1+3+5+6	5	-5.314	24.913	9.863	0.001	138.560
89	1+2+4+5+7	6	-4.357	27.176	12.125	0.000	429.474
90	1+3+4+5+7	6	-4.358	27.178	12.128	0.000	430.048
91	1+4+5+6+7	6	-4.385	27.231	12.180	0.000	441.504
92	1+3+5+6+7	6	-4.409	27.279	12.229	0.000	452.278
93	1+3+4+5+6	6	-4.445	27.351	12.300	0.000	468.742
94	1+2+4+5+6	6	-4.449	27.360	12.310	0.000	471.035
95	1+2+3+4+5	6	-4.461	27.384	12.334	0.000	476.616
96	1+2+5+6+7	6	-4.490	27.441	12.391	0.000	490.444
97	1+2+3+5+7	6	-4.535	27.531	12.480	0.000	512.949
98	1+2+3+5+6	6	-4.604	27.670	12.620	0.000	550.027
99	1+2+4+6+7	6	-4.612	27.687	12.636	0.000	554.467
100	1+2+3+4+6	6	-4.647	27.755	12.705	0.000	573.881

101	1+2+3+4+7	6	-4.734	27.930	12.880	0.000	626.367
102	2+3+4+5+6	6	-4.767	27.995	12.944	0.000	646.874
103	2+3+4+5+7	6	-4.768	27.998	12.948	0.000	648.030
104	3+4+5+6+7	6	-4.861	28.183	13.132	0.000	710.548
105	2+3+4+6+7	6	-4.872	28.205	13.155	0.000	718.702
106	1+2+3+5+7	7	-4.186	31.705	16.655	0.000	4134.924
107	1+3+4+5+6+7	7	-4.353	32.039	16.989	0.000	4886.660
108	1+2+4+5+6+7	7	-4.356	32.045	16.995	0.000	4902.102
109	1+2+3+5+6+7	7	-4.405	32.143	17.093	0.000	5148.339
110	1+2+3+4+5+6	7	-4.438	32.210	17.160	0.000	5322.798
111	1+2+3+4+6+7	7	-4.581	32.495	17.445	0.000	6138.031
112	1+2+3+4+5+6+7	8	-4.132	37.354	22.304	0.000	69682.342
113	4+6	3	failed				
113	1+6+7	4	failed				
113	3+4+6	4	failed				
113	4+6+7	4	failed				
113	5+6+7	4	failed				
113	1+2+6+7	5	failed				
113	1+3+6+7	5	failed				
113	1+4+6+7	5	failed				
113	2+5+6+7	5	failed				
113	3+4+6+7	5	failed				
113	3+5+6+7	5	failed				
113	1+2+3+6+7	6	failed				
113	1+3+4+6+7	6	failed				
113	2+3+5+6+7	6	failed				
113	2+4+5+6+7	6	failed				
113	2+3+4+5+6+7	7	failed				

Notes: Model variable numbers are: 1 - tree diversity (Simpson's index of basal area^2),

2 - total basal area (m^2 ha^{-1}), 3 - cone-producing *P. albicaulis* (number ha^{-1}), 4 - canopy

cover (%), 5 - canopy height (m), 6 - *P. albicaulis* tree mortality (%), 7 - site slope

(degrees). K is the number of parameters estimated from the data; AIC_c is the Akaike

information criterion corrected for small samples; Δ_i is the difference in AIC_c for model *i*

and the best model; w_i is the AIC_c weight interpreted as the probability of being the best

model in the total combined model set; evidence ratio is the best model's weight divided

by w_i.

Table 6. Forest parameter values for 20 *Pinus albicaulis* research sites - Rocky

Mountains, USA, 2004-2006.

Location	Forest type	Total basal area (m² ha⁻¹)	*Pinus albicaulis* relative abundance† (% basal area)	Tree diversity Simpson's index	Mean (± SE)				
					Elevation (m)	Aspect (○)	Slope (○)	Canopy height (m)	Canopy cover (%)
NDE	*Pinus albicaulis*	7.96	62.2	2.26	2181 (2)	177 (4)	15 (0)	6.6 (0.4)	19 (3)
	Mixed	5.52	49.6	2.07	2116 (3)	257 (3)	25 (0)	8.2 (0.5)	21 (4)
	Mixed	34.16	2.5	1.05	2136 (4)	213 (10)	8 (1)	12.4 (0.6)	85 (4)
	Mixed	21.27	1.7	1.37	2169 (2)	201 (8)	5 (1)	10.7 (0.8)	45 (6)
	Mixed	18.90	0	1.97	1887 (15)	130 (51)	15 (4)	25.1 (1.7)	67 (4)
	Mixed	9.48	0	1.65	1806 (11)	91 (17)	13 (1)	21.4 (3.5)	47 (11)
	Mixed	44.13	10.1	1.71	2103 (35)	229 (16)	23 (3)	12.9 (1.6)	84 (8)
	Mixed	3.21	41.3	3.42	2060 (8)	166 (9)	26 (2)	7.4 (0.4)	18 (2)
	Mixed	3.99	6.6	3.29	2080 (20)	227 (11)	30 (1)	9.2 (0.6)	26 (4)
	Mixed	23.80	19.4	3.16	1837 (22)	163 (62)	15 (6)	23.8 (4.7)	77 (13)
	Pinus albicaulis	14.98	100.0	1.00	2814 (6)	197 (9)	24 (2)	11.7 (0.8)	46 (6)
	Pinus albicaulis	25.50	57.3	2.21	2864 (3)	266 (33)	24 (2)	12.8 (0.8)	47 (7)
	Pinus albicaulis	30.22	73.9	1.68	2911 (2)	200 (17)	13 (2)	14.3 (0.9)	54 (7)
GYE	*Pinus albicaulis*	30.36	81.7	1.47	2899 (5)	140 (21)	10 (2)	11.8 (1.5)	71 (5)
	Mixed	40.28	25.0	3.80	2546 (4)	158 (31)	20 (1)	18.4 (0.8)	92 (4)
	Mixed	41.82	19.7	2.24	2744 (4)	205 (4)	20 (1)	15.5 (1.1)	84 (3)
	Mixed	37.48	45.1	2.27	2755 (3)	311 (7)	17 (1)	16.3 (0.9)	68 (5)
	Mixed	16.75	25.7	2.30	2978 (4)	113 (42)	9 (2)	8.5 (0.8)	52 (6)
BM	*Pinus albicaulis*	29.29	97.2	1.06	2561 (5)	271 (28)	20 (1)	11.7 (0.5)	56 (4)
	Pinus albicaulis	15.26	52.4	2.22	2389 (3)	218 (52)	20 (2)	12.9 (0.3)	54 (5)

Notes: Location abbreviations - NDE, Northern Divide Ecosystem, northwestern Montana; GYE, Greater Yellowstone Ecosystem, southwestern Montana and northwestern Wyoming; BM, Bitterroot Mountains, west-central Montana. Forest type defined by whether *P. albicaulis* comprised > 50% of total site BA; sites were classified as mixed species if condition was not met.

†Sites with zero values failed to have live *P. albicaulis* recorded by transect sampling though cone trees were present and selected using alternative methodology (see text).

Table 7. Condition (mortality, rust infection, and crown kill) and cone predation due to *Tamiasciurus hudsonicus* in 20 subalpine forest research sites - Rocky Mountains, USA, 2004-2006.

| Location | Forest type‡ | Forest condition† | | | Cone predation* |
		Tree mortality§	Blister rust infection‖	Crown kill#	
NDE	*Pinus albicaulis*	64.6	88.4	35 (4)	31.6
	Mixed	84.0	83.3	39 (11)	55.2
	Mixed	66.7	92.3	3 (2)	75.0
	Mixed	72.9	87.5	63 (22)	41.0
	Mixed	88.5	28.6	7 (3)	83.2
	Mixed	70.0	100.0	24 (9)	80.3
	Mixed	70.6	88.0	38 (13)	57.8
	Mixed	54.7	90.7	41 (7)	41.1
	Mixed	69.7	100.0	21 (11)	45.3
	Mixed	42.1	63.6	24 (13)	53.8
GYE	*Pinus albicaulis*	10.6	61.5	6 (1)	0.8
	Pinus albicaulis	15.5	37.4	6 (1)	8.7
	Pinus albicaulis	16.4	22.8	2 (1)	8.2
	Pinus albicaulis	4.0	82.7	7 (1)	4.2
	Mixed	4.5	36.8	8 (2)	5.2
	Mixed	34.4	27.6	3 (1)	16.6
	Mixed	30.9	53.9	12 (2)	57.8
	Mixed	0.0	72.0	7 (2)	3.2

Notes: Location abbreviations - NDE, Northern Divide Ecosystem, northwestern Montana; GYE, Greater Yellowstone Ecosystem, southwestern Montana and northwestern Wyoming.

† Values are for *P. albicaulis* trees with ≥ 7 cm diameter at 1.4 m height.

‡ Defined by whether *P. albicaulis* comprised > 50% of total site BA, sites were classified as mixed species if condition was not met.

§ Percentage of dead *P. albicaulis* trees at a site.

‖ Percentage of rust-infected trees at a site.

Mean percent (± SE) estimated from rust infected trees at a site.

* Percentage of cones taken by squirrels relative to the total number produced over all years.
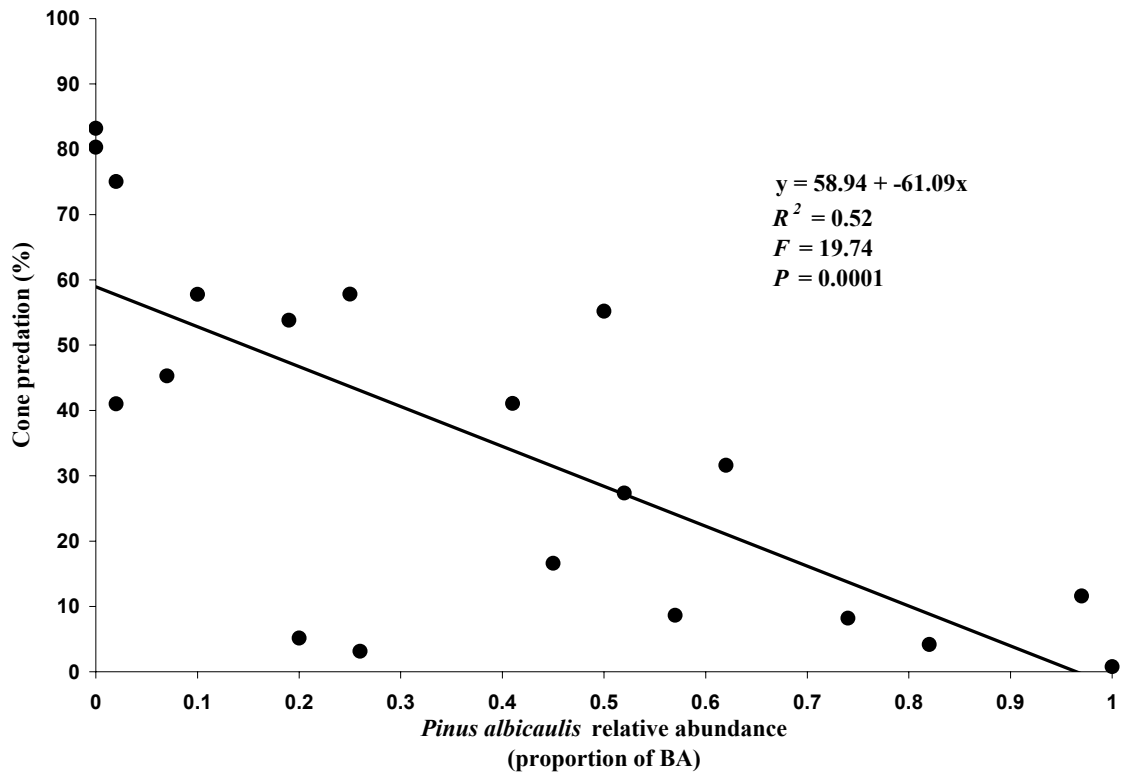
Figure 1. Relationship between *Tamiasciurus hudsonicus* cone predation and the relative abundance of *Pinus albicaulis* at 20 subalpine forest sites in the Rocky Mountains, USA, 2004-2006.
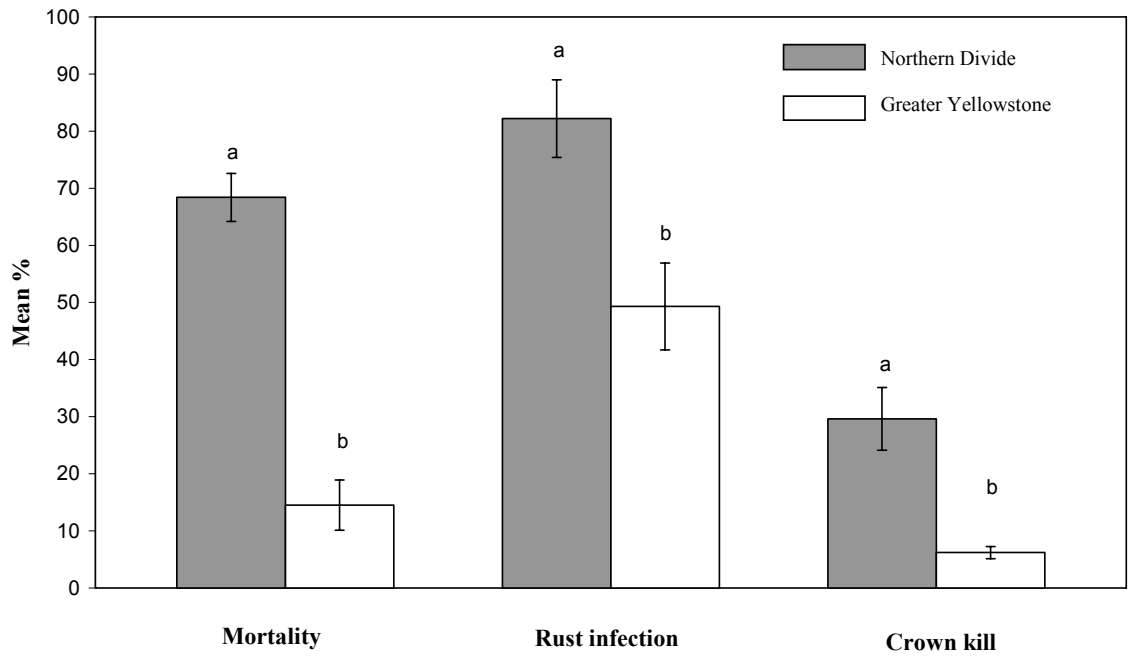
Figure 2. *Pinus albicaulis* forest condition parameters by ecosystem (mean ± SE).

Lowercase letters indicate significant differences (ANOVA, *P* < 0.05) in parameters

between ecosystems.

Chapter 4

Coarse scale declines are manifest in a fine scale ecological process: the paradox of *Pinus albicaulis* tree survival in the Rocky Mountains, USA

Shawn T. McKinney, Carl E. Fiedler

College of Forestry and Conservation, University of Montana, Missoula, MT 59812

Abstract

Coarse scale declines in *Pinus albicaulis* (whitebark pine) have been documented throughout the northwestern U.S. and southwestern Canada. Our fundamental question was whether differences in *P. albicaulis* forest attributes between the Northern Divide (NDE) and Greater Yellowstone (GYE) ecosystems correspond to differences in the tree-level process of predispersal cone survival. We measured structure, composition, health, and environmental parameters at the stand level and habitat variables and cone survival (proportion of cones surviving 45 days of predation pressure) at the tree level at multiple sites within each ecosystem from 2004-2006. Forests in the GYE had significantly greater absolute and relative *P. albicaulis* abundances, higher cone production, lower blister rust (*Cronartium ribicola*) infection, and lower mortality than the NDE. Profound differences in conditions surrounding cone trees corresponded to marked differences between ecosystems. GYE cone tree sites were more similar to the surrounding forest, had greater cone survival rates, lower within site variation, and survival explained by broader scale (topographic) factors than NDE cone tree sites. The potential selective advantage of the putative 1-5% rust resistant trees may not be realized if their cones do not survive to provide seeds for dispersal by Clark's Nutcracker (*Nucifraga columbiana*), necessitating wide-scale planting of rust-resistant seedlings.

Introduction

High elevation ecosystems are known to be especially sensitive to anthropogenic effects. Subalpine forests, for example, have undergone substantial changes over the past century in distribution and species composition due to a myriad of reasons, including atmospheric warming, altered disturbance regimes, exotic species, and grazing pressure (Baker and Moseley, 2007; Camarero and Gutiérrez, 2007; Murray et al., 2000; Keane et al., 1994). Studies addressing the relationship between environmental change and ecological processes, however, have usually occurred at either a coarse scale or a fine scale. Understanding how coarse scale changes relate to fine scale processes furthers our knowledge of forest dynamics and is necessary to anticipate the effects of modern perturbations on these vulnerable mountain ecosystems.

Pinus albicaulis (whitebark pine), an upper subalpine and treeline forest species, is notable for regulating hydrologic processes, stabilizing soil, colonizing burned sites, and providing habitat and high energy seeds for many vertebrate species, including its primary seed dispersal agent–the Clark's Nutcracker (*Nucifraga columbiana*) (see Tomback et al., 2001 for overview). Clark's Nutcracker seed dispersal and caching behavior provide the only ecologically significant vector for whitebark pine seedling establishment (Tomback 1982; Hutchins & Lanner 1982).

Sharp declines in *P. albicaulis* over the past century are primarily due to mortality from the exotic fungal pathogen *Cronartium ribicola* (white pine blister rust) (McDonald and Hoff, 2001). However, population upsurges of native mountain pine beetle (*Dendroctonus ponderosae*), which are linked to drought and climate warming (Logan and Powell, 2001), are also currently killing vast stands of *P. albicaulis*, and a century of

suppressing natural fires has lead to successional replacement by shade tolerant competitors and loss of regeneration opportunities in some Northern Rocky Mountain subalpine forests (Brown et al., 1994; Murray et al. 2000).

Cronartium ribicola was introduced to western North America in 1910 (see McDonald & Hoff 2001 for review), and has since spread throughout much of the range of *P. albicaulis*, with mortality as high as 90% in some Rocky Mountain forests (Keane et al. 1994; Kendall & Keane 2001; Schwandt 2006). *C. ribicola* is especially pernicious because it infects *P. albicaulis* of all age classes, and because it disrupts the pine's regeneration process by girdling and killing cone-bearing branches and trees, and thus reducing cone production (McDonald & Hoff 2001). In the Bitterroot Mountains of western Montana and eastern Idaho, *P. albicaulis* cone production was significantly lower in rust-damaged stands compared to stands similar in forest structure and composition but with little damage (McKinney & Tomback 2007). Furthermore, lower cone production in rust-damaged stands was associated with significantly higher rates of predispersal seed predation and fewer observations of nutcracker seed dispersal (McKinney & Tomback 2007).

Cronartium ribicola is acting as a selective force by causing differential survival among *P. albicaulis* trees in rust-infected forests. Studies have shown that surviving trees from high-mortality stands possess higher levels of heritable resistance than trees from low-mortality stands (Hoff et al. 1994), and that more than 40 percent of the progeny of survivors in high-mortality stands display resistance to blister rust (Hoff et al. 2001). The long-term persistence of whitebark pine in the presence of blister rust will require a

dramatic increase in the frequency of rust-resistant alleles within populations, which is now estimated at only 1-5% (Hoff et al. 1994).

In high-mortality forests (e.g., > 80% tree mortality) the mature, phenotypically rust-resistant *P. albicaulis* that remain have the potential to function as seed trees and thereby make use of the selective advantage created by the blister rust epidemic (Hoff et al., 1994). Under such a scenario, the frequency of rust-resistant alleles would greatly increase in the offspring generation relative to the parental generation that was first exposed to the rust (Hoff et al., 1994). However, because of the profound changes in these high mortality forests, habitat conditions may favor predispersal cone predation by vertebrates or disfavor seed caching by nutcrackers, or both. Hence the potential selective advantage of the few rust resistant individuals may not be realized if their seeds do not survive to be dispersed by nutcrackers. Our fundamental question, then, is whether coarse scale differences in *Pinus albicaulis* forest attributes equate to differences in the rate, variation, and scale dependence of predispersal cone survival.

We hypothesize that an ecosystem with greater *P. albicaulis* abundance will have (1) greater habitat similarity between cone-tree sites and random locations in the surrounding forest; (2) a greater rate of predispersal cone survival; (3) lower within site variation in cone survival; and (4) broad scale variables (e.g., topographic features) that are more important than fine scale variables (e.g., conditions around cone trees) to cone survival when compared to an ecosystem with lesser *P. albicaulis* abundance. To evaluate these hypotheses, we (1) documented and compared *P. albicaulis* abundance and health status in two subalpine forest ecosystems in the Rocky Mountains U.S.A. that are distinct in *P. albicaulis* health conditions (rust infection and mortality) and abundance;

(2) explored the connection between *P. albicaulis* abundance at a coarse (ecosystem) and fine (cone tree site) scale; (3) evaluated the relationship between coarse scale abundance and the rate of predispersal cone survival; and (4) linked variation in cone survival and the scale of factors most important to cone survival with coarse scale abundance. This information can be used by the U.S. Department of Agriculture, Forest Service, and Department of Interior, Park Service to implement conservation and restoration strategies for whitebark pine in the Rocky Mountains.

Methods

<u>Study Area</u>

We conducted research from June to September, 2004-2006. Research within the Northern Divide Ecosystem (NDE) of northwestern Montana took place in Glacier National Park and the adjacent Flathead National Forest (48.8°N to 48.3°N, 113.3°W to 114.4°W) (Fig.1). Elevation of research sites ranged from 1 928 m to 2 209 m above sea level. In the Greater Yellowstone Ecosystem (GYE) of southwestern Montana and northwestern Wyoming, research was conducted within Yellowstone National Park and the adjoining Gallatin and Shoshone National Forests (45.1°N to 44.8°N, 109.5°W to 110.6°W) (Fig.1). Elevation of sites ranged from 2 529 m to 2 970 m above sea level. Forest communities at research sites were comprised of *P. albicaulis*, *P. contorta* (lodgepole pine), *Abies lasiocarpa* (subalpine fir), *Picea engelmannii* (Engelmann spruce), and *Pseudotsuga menziesii* (Douglas-fir) in various combinations and relative abundances.

<u>Ecosystem Comparison</u>

We established multiple research sites in *P. albicaulis* habitat within each ecosystem (NDE $n = 10$, GYE $n = 8$) by delineating rectangular boundaries that were 100 m wide by ≥ 200 m long (min 2 ha, max 7 ha; mean = 2.6 ha). Sites were subdivided into 1-ha squares (100 m $\times$ 100 m) to provide better control over vegetation sampling. We established two 10 m x 50 m (500 m^2) belt transects along random azimuths within each hectare of each research site (e.g., a 3 ha site would have six transects). All trees with diameter at breast height (dbh, 1.4 m) ≥ 7 cm were recorded by species and dbh (± 0.1 cm). We calculated basal area (BA, m^2 ha^{-1}) from the dbh for each tree and summed BA by transect, species, and research site. We surveyed all living *P. albicaulis* trees ≥ 7 cm dbh for the presence of ovulate cones and coded a tree as with (1) or without (0) cones. Each *P. albicaulis* tree was also inspected for blister rust infection and identified as infected (1) if they exhibited active or inactive branch or bole cankers (Hoff 1992), and uninfected (0) if not. Standing dead *P. albicaulis* also had dbh recorded. Uncertainty associated with determining the primary mortality agent prevented us from ascribing cause of death. All *P. albicaulis* seedlings ≤ 50 cm height were tallied on each transect with a handheld counting device. We estimated elevation (± 10 m) with a Global Positioning System receiver (Garmin, ± 10 m) and measured site slope (± 1 degree) with a clinometer at each transect midpoint.

We grouped *P. albicaulis* trees into two size classes based on dbh (trees ≥ 7 but < 15 cm and trees ≥ 15 cm) and used independent sample t-tests to determine if ecosystems were different in population mean values for the density of trees in each size class and for seedlings (number ha^{-1}). The absolute (m^2 ha^{-1}) and relative (% total) amounts of *P.*

albicaulis basal area in each ecosystem were also compared by independent sample t-tests. We calculated the proportion of transects with at least one living *P. albicaulis* tree for each ecosystem and compared the values with a Z-test for proportions. To determine whether the ecosystems were different with respect to forest health parameters, we compared the mean percentage of standing dead and rust infected trees with independent sample t-tests.

Cone Tree Plots and Habitat Similarity with Forests

We generated random numbers for azimuth degree and distance at a corner of each one-ha square and followed them until we encountered a *P. albicaulis* tree bearing ovulate cones. Selected cone trees were ≥ 25 m apart with up to four sampled trees ha^{-1}. We marked cone trees with metal identification tags and logged tree coordinates with a handheld Global Positioning System receiver (Garmin, ± 10 m) for later relocation. We attached four 7 mm diameter by 11.5 m length ropes to each cone tree and extended them out in each of the four cardinal directions. The ropes were marked with bright flagging at 5 m and 11.3 m from the center (i.e., the cone tree), thus creating two circular plots, each subdivided into quadrants. The smaller plot, with a 5-m radius (78.5 m^2), was nested within the 11.3 m radius (401 m^2) plot. We measured a suite of variables at each of three levels: 78.5 m^2, 401 m^2, and topographic. We recorded bare ground (± 10 %), canopy height (± 1 m), and canopy cover (± 5 %) within the 78.5 m^2 plots. Bare ground was visually estimated as the percentage of ground cover that was comprised of mineral soil or rock relative to all other ground cover types < 50 cm in height. Canopy height was determined by selecting a live tree that represented the average canopy level and measuring its height with a clinometer. Canopy cover was determined by taking readings

102

with a convex forest densitometer in four cardinal directions each 5 m out from the cone

tree. The four canopy cover readings were averaged and converted into percent canopy

cover. Within the 401 m^2 plot, we recorded total tree density (trees^{-1} 401 m^2), and

calculated relative (%) and absolute (m^2 ha^{-1}) abundances of *P. albicaulis*. Tree density

was the sum of all trees in a plot with dbh ≥ 7 cm, and *P. albicaulis* relative abundance

was the proportion of the total represented by that species. Absolute abundance was

obtained by measuring all *P. albicaulis* with dbh ≥ 7 cm and calculating BA. We

measured three topographic variables: slope (± 1 degree), elevation (± 10 m), and aspect

(± 5 degrees). We determined the steepest slope (i.e., the fall line) and measured its angle

12 m away from the cone tree with a clinometer. The aspect of this slope was measured

with a compass, and elevation was derived using a Global Positioning System receiver.

We calculated the relative difference (%) between *P. albicaulis* BA within cone

tree sites and belt transects for each research site to determine whether coarse scale *P.

albicaulis* abundance related to the degree of similarity between *P. albicaulis* BA at cone

tree sites and random locations in the surrounding forest. Site values were then used in an

independent sample t-test to test the hypothesis that greater *P. albicaulis* abundance at the

ecosystem level results in a higher degree of habitat similarity between cone tree sites and

the surrounding forest. We further explored these relationships by calculating a Pearson's

correlation coefficient (*r*) for cone tree site and transect *P. albicaulis* BA in each

ecosystem (NDE and GYE). We used Fisher's exact Z-test to test the hypothesis that this

correlation would be significantly greater where coarse scale *P. albicaulis* abundance was

greater.

Predispersal Cone Survival – Rate, Variation, and Scale Influence

Predispersal cone survival was calculated for each tree as the proportion of cones surviving 45 days of predation pressure. Initial ovulate cone counts (initial cones, C_i) were conducted for each cone tree between 29 June and 15 July of each year (NDE $n = 153$ trees, GYE $n = 116$ trees). We used tripod-mounted Leica spotting scopes with 10x to 60x zoom eyepieces and handheld tally devices to count cones. Two to three marked observation points that allowed for unobstructed views of a tree's canopy were used to census cones on each tree. We returned to the same observation points between 19 August and 4 September of each year and counted the remaining cones (final cones, C_f). The range of dates for the final cone count was determined by two factors. First, Clark's Nutcracker does not begin to disperse seeds until seed coats harden (Tomback, 1998), and in our experience hardening occurs by the end of August in this region (McKinney and Tomback, 2007). Thus, we selected the August 19th date as a reasonable estimate for the onset of seed dispersal. Second, we wanted to compare cone survival consistently across all cone bearing trees and therefore we made a strong effort to return to a cone tree for the final count 45 days after the initial count. Thus cone survival was equal to the proportion of cones remaining ($C_f\ C_i^{-1}$) when the interval between counts was 45 days. When this was not possible, we used the following correction equation:

Cone survival $= \{C_i - [(C_i - C_f)\ \text{no. days}^{-1}] * 45\ \text{days}\}\ C_i^{-1}$

where no. days is the number of days between C_i and C_f. Because the number of days was only rarely a few days more or less than 45, the correction factor was typically negligible.

We used simple linear regression to estimate the slope and intercept for the relationship between C_i and C_f for each ecosystem as a first step in comparing

predispersal cone survival between the two ecosystems. We compared the two slope coefficients (b_1) by calculating a Student's t-test statistic to detect differences. Second, we compared the population proportion of cones surviving in each ecosystem with an independent samples t-test. Initial *P. albicaulis* cone production estimates were calculated as the product of the mean number of cones tree^{-1} and the number of cone-bearing trees ha^{-1} for each ecosystem.

We calculated the within-site variation in cone survival for each ecosystem and used the ratio of the two ecosystems' variances to calculate a F_{MAX}-statistic to determine whether greater *P. albicaulis* abundance is associated with lower within-site variation in cone survival. We used generalized linear models with normal error distribution to estimate the influence of variables taken at three spatial levels on predispersal cone survival for each ecosystem. The 78.5 m^2 level model (5-m radius plot) consisted of the variables bare ground, canopy cover, and canopy height. The 401 m^2 level model (11.3-m radius plot) was represented by the variables total tree density and *P. albicaulis* relative abundance. The topographic model variables were slope, aspect, and elevation. Akaike's Information Criterion corrected for small sample sizes (AIC_c) was then used to rank the relative support for each of the three models in each ecosystem (Burnham and Anderson 2002).

S-Plus 7.0, SPSS 10.0, and Microsoft Excel were used for all statistical analyses and computations, with an assumed study-wide significance level of $P = 0.05$ established prior to all analyses.

Results

<u>Ecosystem Comparison</u>

      Pinus albicaulis abundance was higher and health status better in the Greater

Yellowstone compared to the Northern Divide Ecosystem with significant differences

detected between the two populations in all parameters considered (Table 1). There were

4.5 times more live *P. albicaulis* trees (dbh $\geq$ 7 cm) per unit area in the GYE with 7.6

times more basal area relative to the NDE (Table 1). Hence, *P. albicaulis* constituted

more than 50% of GYE subalpine forests but less than 20% of NDE forests based on BA

(Table 1). The greater abundance in the GYE equated to a much higher probability of

encountering a *P. albicaulis* tree randomly compared to the NDE. In the GYE, 31 out of

32 (0.97) random transects contained at least one *P. albicaulis* tree with dbh $\geq$ 7 cm,

while only 18 out of 34 (0.53) NDE transects contained one or more trees (Table 1).

Likewise, our two measures of health status documented better conditions in GYE

forests. Nearly 70% of all *P. albicaulis* trees encountered in the NDE were dead, almost

five times more relative to the GYE (Table 1). And of the live trees in the NDE,

proportionally 1.7 times more were rust-infected compared to the GYE (Table 1).

<u>Cone Tree Plots and Habitat Similarity with Forests</u>

      Greater abundance of *P. albicaulis* at the ecosystem level corresponded to a

greater similarity between cone tree sites and random locations in the surrounding forest.

A significantly greater amount of *P. albicaulis* (number of trees, absolute BA, and

proportional BA; Table 1) at the ecosystem level in the GYE translated into a lower

relative mean difference in *P. albicaulis* BA between cone tree sites and random transects

in this ecosystem (41% $\pm$ 7.5; mean difference $\pm$ SE) compared to the NDE (65% $\pm$ 10.1;

$t_{16} = 1.874$, $P = 0.04$). Similarly, there was a significant correlation between *P. albicaulis* BA in cone tree sites and transects in the GYE ($r = 0.57$, $P < 0.05$) while essentially no correlation existed in the NDE ($r = -0.02$, $P > 0.05$). Thus the correlation between *P. albicaulis* BA in a cone tree site and in a random transect within the surrounding forest was significantly greater in the GYE compared to the NDE ($Z = 2.01$, $P < 0.05$).

Predispersal Cone Survival – Rate, Variation, and Scale Influence

Greater abundance of *P. albicaulis* at the ecosystem level corresponded to a higher rate of predispersal cone survival ($C_f C_i^{-1}$), with the GYE having a significantly greater cone survival slope than the NDE (Fig. 2). The number of initial cones was a strong predictor of the number of final cones in the GYE, explaining 96% of the variation in final cone number. While in the NDE, the number of initial cones explained only 50% of the variation in final cone number (Fig. 2). Likewise, the GYE had a greater proportion of cones surviving 45 days of predation pressure compared to the NDE ($t_{267} = 7.233$, $P < 0.05$). In the GYE, 73% of the initial cones were left by the final cone count, nearly 1.8 times more proportionally than the 41% remaining in the NDE. Furthermore, we estimated that 3,635 cones (± 651) were produced per hectare in the GYE compared to 641 cones ha^{-1} (± 241) in the NDE. Following predation, roughly 10 times more cones were available per unit area for nutcracker dispersal in the GYE relative to the NDE (GYE 3,635 cones x 0.73 = 2,654 cones, NDE 641 cones x 0.41 = 263 cones).

There was significantly less within-site variation in predispersal cone survival in the GYE compared to the NDE (GYE within-site mean square = 3.64 x 10^{-2}, NDE within-site mean square = 8.48 x 10^{-2}; $F_{104,69} = 2.32$, $P < 0.05$). Thus, greater *P. albicaulis* abundance at the ecosystem level translated into lower tree-to-tree variation in

cone survival within research sites. Likewise, fine-scale (78.5 m^2 and 401 m^2 plots) variables were not important to cone survival in the GYE. The topographic scale received the most support from the GYE cone survival data with a probability ≈ 1.0 that it was indeed the best representation in the set (Table 2). Variables in the finer scale 401 m^2 and 78.5 m^2 plots received essentially no support from the GYE data and could be ruled out based on their large ΔAIC_c values (Table 2). In contrast, scale ranking based on AIC_c for the NDE came out opposite of the GYE. The finest scale (78.5 m^2) plots ranked first in the NDE with a probability $= 0.57$ of being the best representation in the set (Table 3). The 401 m^2 plots ranked second, and the topographic scale received the least support from the data with a probability $= 0.12$ of being the best representation in the set (Table 3). However, all three NDE models were poor predictors of cone survival, and none could be ruled out based solely on their ΔAIC_c values (Table 3).

Discussion

Measurable changes in many subalpine ecosystems have occurred over the last century, often with anthropogenic influences implicated as a factor. In western North America, there are none more apparent than in *Pinus albicaulis* forests, where an introduced species (*Cronartium ribicola*), upsurges in insect populations (mountain pine beetle), and an absence of disturbance (cyclical burning) threaten to reduce many *P. albicaulis* populations to the point where they may no longer be self sustaining or ecologically viable (Tomback and Kendall, 2001). Genetic resistance to blister rust provides some hope that populations of *P. albicaulis* will survive and adapt to threats posed by the rust epidemic. Yet our results demonstrate that coarse scale differences in *P. albicaulis* forest attributes between the Greater Yellowstone and Northern Divide

ecosystems correspond to profound differences in rate, variation, and scale dependence of predispersal cone survival, suggesting restraint in this optimism.

We originally hypothesized that greater *P. albicaulis* abundance at the ecosystem level would be associated with (1) greater similarity between cone tree sites and the surrounding forest; (2) higher predispersal cone survival; (3) lower tree-to-tree variation in cone survival; and (4) greater influences of broad scale (topographic) variables to cone survival relative to an ecosystem with low abundance. All four of these hypotheses were supported by sample data collected at three scales from the Greater Yellowstone and Northern Divide ecosystems. The GYE, with significantly greater *P. albicaulis* both absolutely and relative to other species (Table 1), demonstrated greater similarity between cone tree sites and the surrounding forests; a higher cone survival rate (Fig. 1); and lower tree-to-tree variation in survival relative to the NDE. Furthermore, the order of importance of scale on the variables influencing cone survival is reversed in the two ecosystems (Tables 2 and 3). In the GYE, cone survival was influenced by topographic variables with essentially no support for the influence of the finer scale 78.5 m^2 and 401 m^2 plot variables. Conversely, topographic variables had the least influence on cone survival in the NDE, while the 78.5 m^2 and 401 m^2 plot variables were more important. Thus, the same ecological process is shaped by fundamentally different influence on *P. albicaulis* forests in the two ecosystems.

Increasing *P. albicaulis* tree mortality was strongly correlated with decreasing live basal area ($r = -0.78$) at the stand level. And as live basal area declined within stands, cone production declined in a linear fashion ($r = 0.88$). The results of our study demonstrate that reduced *P. albicaulis* abundance is associated with lower cone

production at the stand and ecosystem level, and a lower chance of a tree's cones

surviving 45 days of predation pressure. When few cones are produced and a low

proportion of them survive, still fewer are available for nutcracker seed dispersal.

Moreover, our results suggest that ecosystem-wide declines in *P. albicaulis* forests

reported elsewhere throughout the Northern Rocky Mountain Region (e.g., Keane and

Arno 1993; Keane et al., 1994) may also be influencing predispersal cone survival at the

individual tree level within these forests.

Clark's Nutcrackers are sensitive to rates of energy acquisition and adjust their

foraging behavior to account for changes in available food (Tomback, 1978; Vander

Wall, 1988). In a complementary study, we have identified a threshold of cone

production in Rocky Mountain *P. albicaulis* forests that is necessary for nutcrackers to

remain within an area until seeds ripen and seed dispersal behavior initiates. Below this

threshold, the probability of nutcracker seed dispersal becomes extremely small

(McKinney, Fiedler, and Tomback, *in prep*). Similar relationships were identified in

small forest stands in the Bitterroot Mountains of Montana and Idaho; when blister rust

damage and mortality increased, cone production and predispersal survival decreased,

and the likelihood of nutcracker seed dispersal diminished (McKinney and Tomback,

2007). These blister rust-cone production relationships may explain why there was nearly

five times more regeneration (seedlings $\leq$ 50 cm height) per unit area in the GYE than in

the NDE (Table 1).

White pine blister rust is exerting strong selection pressure in many *Pinus

albicaulis* forests. Trees that are rust resistant should have a selective advantage in these

forests, leaving greater numbers of offspring relative to trees that die rapidly following

rust exposure. The paradox is that the very process that should afford a selective advantage–extreme differential mortality of non-resistant trees–also creates forest conditions that are unfavorable to predispersal cone survival. These results cast doubt on whether the potential selective advantage of rust resistant trees will be realized in forests with high levels of rust damage and mortality. In these conditions, which are common across the U.S. Northern Rocky Mountains, growing and outplanting rust-resistant seedlings may be the most promising way to combat rust-induced declines in *P. albicaulis* forests.

Acknowledgments

Literature Cited

Baker, B. B., and Moseley, R. K., 2007: Advancing treeline and retreating glaciers: Implications for conservation in Yunnan, P.R. China. *Arctic, Antarctic, and Alpine Research*, 39: 200-209.

Brown, J. K., Arno, S. F., Barrett, S. W., and Menakis, J. P., 1994: Comparing the prescribed fire program with presettlement fires in the Selway-Bitterroot Wilderness. *International Journal of Wildland Fire*, 4: 157-168.

Burnham, K. P., and Anderson, D. R., 2002: *Model selection and multi-model inference: a practical information theoretic approach.* Second edition. New York: Springer-Verlag.

Camarero, J. J., and Gutiérrez, E., 2007: Response of *Pinus uncinata* to climate warming and changes in grazing pressure in an isolated population of the Iberian system (NE Spain). *Arctic, Antarctic, and Alpine Research*, 39: 210-217.

Hoff, R. J. 1992. How to recognize blister rust infection on whitebark pine. *USDA Forest Service Research Note*, INT-406.

Hoff, R.J., Hagle, S.K., and Krebill, R.G., 1994: Genetic consequences and research challenges of blister rust in whitebark pine forests. *In* W.C. Schmidt and F.K. Holtmeier (eds.), *Proceedings—International Workshop on Subalpine Stone Pines and Their Environment: the Status of Our Knowledge. USDA Forest Service General Technical Report,* INT-309: 118-126.

Keane, R.E., and Arno, S.F. 1993: Rapid decline of whitebark pine in Western Montana: Evidence from 20-year remeasurements. *Western Journal of Applied Forestry*, 8: 44-47.

Keane, R. E., Morgan, P., and Menakis, J. P., 1994: Landscape assessment of the decline of whitebark pine (*Pinus albicaulis*) in the Bob Marshall Wilderness Complex, Montana, USA. *Northwest Science*, 68: 213-229.

Little, E. L. Jr., 1971: Atlas of United States Trees. Volume 1. Conifers and important hardwoods. USDA Forest Service Misc. Publ. No. 1146. Washington, D.C.

Logan, J. A., and Powell, J. A., 2001: Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). *American Entomologist*, 47: 160-172.

McDonald, G. I., and Hoff, R. J., 2001: Blister rust: An introduced plague. *In* Tomback, D. F., Arno, S. F., and Keane, R. E. (eds.), *Whitebark Pine Communities: Ecology and restoration*. Washington, D.C.: Island Press: 193-220.

McKinney, S. T., and Tomback, D. F., 2007: The influence of white pine blister rust on seed dispersal in whitebark pine. *Canadian Journal of Forest Research*, 37: 1044-1057.

Murray, M. P., Bunting, S. C., and Morgan, P., 2000: Landscape trends (1753-1993) of whitebark pine (*Pinus albicaulis*) forests in the west Big Hole range of Idaho/Montana, U.S.A. *Arctic, Antarctic, and Alpine Research*, 32: 412-418.

Tomback, D. F., 1978: Foraging strategies of Clark's nutcracker. *Living Bird*, 16: 123-161.

Tomback, D. F., 1998: Clark's nutcracker (*Nucifraga columbiana*). *In* Poole, A., and Gill, F. (eds.), *The birds of North America*. Philadelphia, Pennsylvania: The Birds of North America Incorporated: number 331.

Tomback, D. F., and Kendall, K. C., 2001: Biodiversity losses: the downward spiral. *In* Tomback, D. F., Arno, S. F., and Keane, R. E. (eds.), *Whitebark Pine Communities: Ecology and restoration*. Washington, D.C.: Island Press: 243-262.

Tomback, D. F., Arno, S. F., and Keane, R. E., 2001: The compelling case for management intervention. *In* Tomback, D. F., Arno, S. F., and Keane, R. E. (eds.), *Whitebark Pine Communities: Ecology and restoration*. Washington, D.C.: Island Press: 3-25.

Vander Wall, S. B., 1988: Foraging of Clark's Nutcrackers on rapidly changing pine seed resources. *The Condor*, 90: 621-631.

Table 1. Comparison of ecosystem mean values (±SE) of *Pinus albicaulis* forest conditions, Rocky Mountains, USA.

	Ecosystem		Comparison	
Forest parameter	Greater Yellowstone	Northern Divide	Test statistic	*P* value
Size class (no. ha^{-1})				
Seedling ($\leq$ 50 cm ht.)	296.5 (30.15)	61.9 (7.8)	$t_{16} = 2.91$	0.005
Trees (7-15 cm dbh)	90.4 (15.5)	36.3 (21.5)	$t_{16} = 1.94$	0.035
Trees (> 15 cm dbh)	191.5 (27.1)	26.8 (10.2)	$t_{16} = 6.18$	<0.001
Abundance				
Absolute (BA, m^2 ha^{-1})	14.5 (2.4)	1.9 (2.0)	$t_{16} = 2.75$	0.007
Relative (% total BA)	53.6 (10.5)	19.4 (7.3)	$t_{16} = 5.02$	<0.001
Frequency (% transects)	96.9	52.9	$Z = 4.08$	<0.05
Health status				
Mortality (%)	14.5 (4.4)	68.4 (4.1)	$t_{16} = 8.77$	<0.001
Rust infected (%)	49.3 (7.6)	82.2 (6.7)	$t_{16} = 3.22$	0.002

Note: Values are for *P. albicaulis* trees only; dbh is diameter at breast height ($\approx$1.4 m); BA is basal area; Frequency is the percentage of all transects in an ecosystem with $\geq$ 1 *P. albicaulis* tree of $\geq$ 7 cm dbh.

Table 2. Model results and selection statistics from maximum likelihood analysis testing the influence of variables at three spatial scales on *Pinus albicaulis* predispersal cone survival in the Greater Yellowstone Ecosystem, Rocky Mountains, U.S.A.*

Rank	Scale	Variables	K	Residual sums of squares	AIC_c	Δ_i	w_i	R^2
1	topographic	slope, elevation, aspect	5	2.608	-259.815	0.000	1.000	0.635
2	401 m^2	tree density, *P. albicaulis* relative abundance	4	5.467	-203.114	56.700	0.000	0.236
3	78.5 m^2	bare ground, canopy height, canopy cover	5	5.707	-199.515	60.300	0.000	0.202

* K is the number of parameters estimated from the data; AIC_c is the Akaike information criterion corrected for small samples; Δ_i is the difference in AIC_c for model i and the best model; w_i is the AIC_c weight interpreted as the probability of being the best model in the total combined model set.

Table 3. Model results and selection statistics from maximum likelihood analysis testing the influence of variables at three spatial scales on *Pinus albicaulis* predispersal cone survival in the Northern Divide Ecosystem, Rocky Mountains, U.S.A.*

Rank	Scale	Variables	K	Residual sums of squares	AIC_c	Δ_i	w_i	R^2
1	78.5 m^2	bare ground, canopy height, canopy cover	5	8.045	-301.714	0.000	0.574	0.139
2	401 m^2	tree density, *P. albicaulis* relative abundance	4	8.147	-300.423	1.291	0.301	0.128
3	topographic	slope, elevation, aspect	5	8.260	-298.664	3.050	0.125	0.116

* K is the number of parameters estimated from the data; AIC_c is the Akaike information criterion corrected for small samples; Δ_i is the difference in AIC_c for model i and the best model; w_i is the AIC_c weight interpreted as the probability of being the best model in the total combined model set.
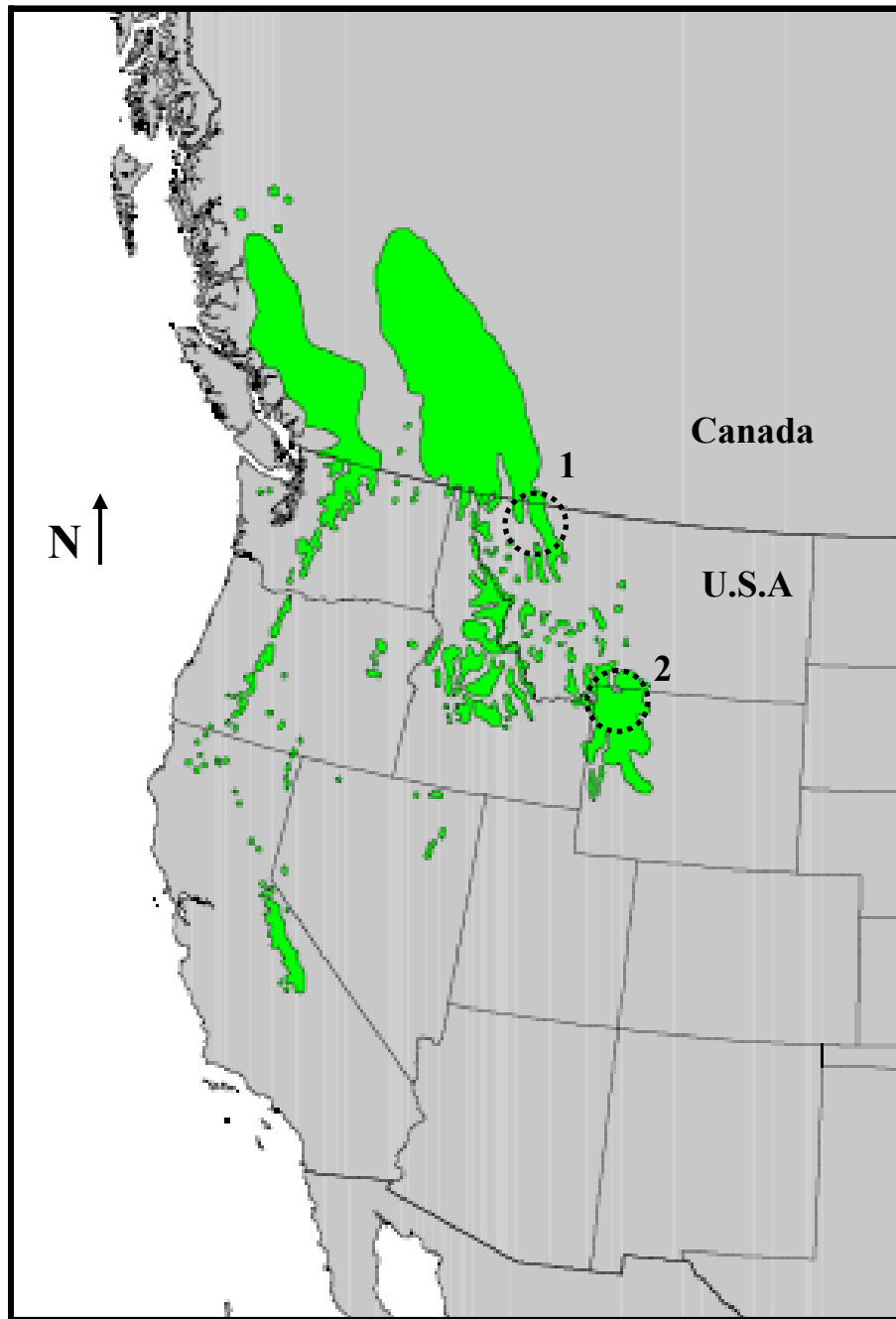
Figure 1. Geographic distribution of *P. albicaulis* (from Little, 1971) including the location of the two study ecosystems: (1) the Northern Divide in northwestern Montana, and (2) the Greater Yellowstone in southwestern Montana and northwestern Wyoming.
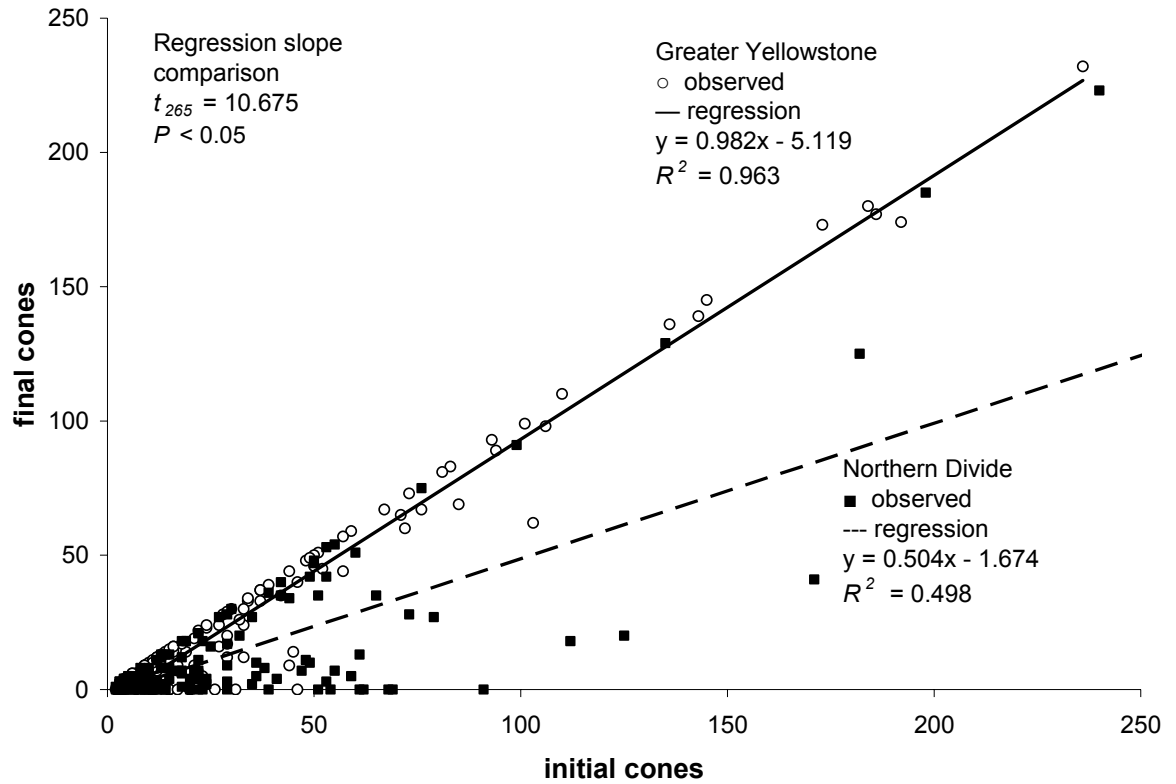
Figure 2. Simple linear regression analysis and slope comparison of cone survival (the number of final cones against the number of initial cones) for the Greater Yellowstone and Northern Divide ecosystems in 2004-2006. Initial cones refers to the number of ovulate cones counted on each tree in July and final cones to the number remaining in August (~45 days later).

Chapter 5

Conclusions

I present three manuscripts of original research within this dissertation that demonstrate the influence of whitebark pine's (*Pinus albicaulis*) decline on species interactions and ecological processes within subalpine forest ecosystems in the Rocky Mountains, USA. These interactions revolve around the capacity of whitebark pine forests – at both the stand and ecosystem levels – to produce ovulate cones. As blister rust infection and rust-induced tree mortality increased, whitebark pine abundance declined; cone production in turn declined with declining abundance.

The first manuscript shows that Clarks' Nutcracker (*Nucifraga columbiana*) responds to the amount of cones available within forest stands. The frequency of nutcracker occurrence and numbers of birds per hour declined as cone production declined. Moreover, a threshold of cone production was identified below which the probability of nutcracker seed dispersal declined sharply. The birds presumably were able to gauge the amount of food available in forest stands, and either foraged locally in other forest types, or were absent altogether from areas with low cone production. When cone production was below a threshold of approximately 1,000 cones ha^{-1}, there was not enough food to attract and maintain birds in these forests into the late summer and early fall seed dispersal period. As whitebark pine trees continue to die, the threshold levels of cone production will be met in fewer forests, which means that fewer areas will be potential sources for nutcracker seed dispersal.

In the second manuscript, I present results that show the interactions between red squirrels (*Tamiasciurus hudsonicus*) and whitebark pine were dependent upon the

abundance (relative and absolute) of whitebark pine within forest stands. Red squirrel

cone predation increased when whitebark pine abundance decreased. Red squirrels were

less likely to be residents in nearly-pure stands of whitebark pine. If squirrels did not

maintain residential status, their impact on the cone crop was diminished. As blister rust

continues to kill mature whitebark pine, as regeneration declines, and as succession

advances, mixed conifer forest stands in whitebark pine habitat will have a lower

component of whitebark pine. These conditions comprise more optimal red squirrel

habitat, and thus the likelihood of red squirrel residence increases. Remaining whitebark

pine trees growing in mixed species forests containing residential red squirrels will suffer

greater relative rates of cone predation, leaving fewer seeds available for nutcracker seed

dispersal.

Surviving trees in high-mortality forests are more likely to possess rust-resistant

alleles than trees in low-mortality forests. Therefore, it is important to understand how

coarse scale declines of whitebark pine are influencing conditions and processes at the

individual tree level, and this idea was investigated in the third manuscript. I found that

conditions surrounding whitebark pine cone trees in high mortality/low abundance forests

are less similar to the surrounding forest, have lower rates of predispersal cone survival,

greater variability in cone survival, and cone survival that is more influenced by

conditions around individual trees than in forests with low whitebark mortality and high

abundance. The implication of these results is that the very process that should afford a

selective advantage for rust-resistant trees–extreme differential mortality of non-resistant

trees–also creates forest conditions that are unfavorable to predispersal cone survival.

These results cast doubt on whether the potential selective advantage of rust resistant

trees will be realized in forests with high levels of rust damage and mortality, and also show that the effects of blister rust are manifest at multiple levels in whitebark pine communities.

The results presented in this dissertation were obtained by sampling from multiple forest stands located within three distinct ecosystems in the Rocky Mountains. At the ecosystem level, the effect of whitebark pine mortality is very clear; cone production declines, rates of cone predation increase, the amount of seeds available for bird dispersal declines, and the probability of seed dispersal by Clark's Nutcracker diminishes. The Northern Divide Ecosystem (NDE) had the highest levels of rust infection and mortality and lowest whitebark pine abundance and cone production of the three ecosystems studied. In addition, cone predation was highest, while the frequency of nutcracker occurrence, average number of birds per hour, and percentage of sites with seed dispersal were lowest in the NDE. All of these comparisons were at intermediate levels in the Bitterroot Mountains Ecosystem. Rust infection and mortality were lower than the NDE but higher than the Greater Yellowstone (GYE). Likewise, cone production, nutcracker occurrence and abundance, and the percentage of sites with nutcracker seed dispersal were higher than the NDE but lower than the GYE, while red squirrel predation was lower than the NDE but higher than the GYE. Whitebark pine forest conditions were best in the GYE, where rust infection and mortality were the lowest and whitebark pine abundance and cone production the highest of the three ecosystems evaluated. In the GYE, nutcrackers were present in almost all sampled hours (96%), and 100% of research sites had nutcrackers dispersing seeds. Both of these measures of nutcracker habitat use, along with nutcracker abundance (birds hr^{-1}), were highest in the GYE of the three

ecosystems. Furthermore, the impact of cone predation by red squirrels was lowest in the GYE.

The findings of this dissertation point to a diminishing capacity of whitebark pine to sustain itself in the Northern Divide Ecosystem. In 80% of the site-years (i.e., a given research site on a given year) in the NDE, I failed to record a single nutcracker seed dispersal event. Moreover, regeneration (seedlings < 50 cm height ha^{-1}) in the NDE was five times lower than the next comparable ecosystem. Results strongly suggest that growing and outplanting rust-resistant seedlings over a broad area and for an extended period of time will be needed in the NDE to conserve and restore whitebark pine. However, because 20% of the site-years did have nutcracker seed dispersal, and because regeneration was much higher than average in some forests, the potential to utilize the natural regeneration process still exists under certain conditions in the NDE. Managers can identify potential seed source areas based on the cone production threshold presented in chapter two and utilize natural or prescribed burning to create nutcracker caching habitat and make use of natural seed sources. Furthermore, areas that are not likely to serve as functional seed sources can be given priority in restoration planting activities.

Both blister rust infection and mortality are high enough to be of concern within the Bitterroot Mountains ecosystem. The greatest variability among forest stands in both of these health measures as well as with nutcracker habitat use occurs there also. There is greater opportunity to utilize the natural regeneration process in the BME than in the NDE, but since many seeds will not possess resistant alleles, much of the future regeneration will likely succumb to blister rust. It is important for managers in the BME

to be proactive and plant rust-resistant seedlings and maintain nutcracker populations before conditions deteriorate to those of the NDE.

The Greater Yellowstone Ecosystem was used effectively as a standard for comparison in the research of this dissertation. Unfortunately, however, rust infection levels are climbing in the GYE and the levels reported in this dissertation portend future declines. Because whitebark pine seeds are an important dietary staple for grizzly bears in this ecosystem, a decline of whitebark pine to levels observed in the NDE could pose real barriers to the long term sustainability of grizzly bear populations. Managers there need to be ahead of the whitebark pine decline curve by anticipating declines and initiating restoration activities.

Future directions

The main body of questions remaining following this research involves the long-term response of nutcracker populations to declines in whitebark pine. We need to know what other forest types, if any, nutcrackers are utilizing in an area when they are not in whitebark pine forests. What is the spatial extent over which nutcrackers emigrate and return to an area to reassess the cone crop of a stand with low whitebark pine abundance; and how long will individuals continue to return to low productivity areas? Where there is natural regeneration resulting from nutcracker caching, what is the level of resistance in this next generation; is it higher than the original generation that was exposed to the rust and; can we detect the effects of natural selection favoring resistant genotypes in the generation following blister rust introduction? Developing answers to these questions will be essential in the long-term strategy to conserve and restore whitebark pine ecosystems in the Rocky Mountains.