CHAPTER 3

EDGE EFFECTS FOR ALIEN AND NATIVE PLANT SPECIES ARE RELATED TO EDGE TYPE:

A COMPARISON OF FIRE, ROAD AND CLEARCUT EDGES IN *Pinus contorta* FORESTS IN WEST YELLOWSTONE, MONTANA.

ABSTRACT

Forest edges are key elements in the percolation of alien plant species into forest interiors. However, little research has been conducted to understand the role of forest edge type in controlling edge effects on invasive species. In the Northern Rocky Mountains of the United States, forest edges are a common feature in the landscape with anthropogenic (roads, clearcuts) and natural (burns) edge types. High elevation *Pinus contorta* (lodgepole pine) forests are no exception. In this paper we aim to test for differences in patterns of alien species invasion and native communities among three forest edge types in the *P. contorta* forests around West Yellowstone, Montana. We also explore the role of forest structure, edge type and distance from the edge in these patterns. Six transects were located in each of five edge types: 1) highway in Gallatin National Forest, 2) highway in Yellowstone National Park, 3) a burn forest of the 1988 fires in Yellowstone National Park, 4) a burned forest in Gallatin National Forest and 5) clearcuts of Gallatin National Forest. Edge-transects consisted of 5 plots of 2 by 20 m, distributed from the adjacent matrix to 40 m inside the forests. We found a significant effect of edge type and the interaction of edge type and distance on native species richness and native species cover ($p<0.05$, ANOVA). Alien species richness was significantly related to edge type, distance and interaction between both variables ($p<0.01$, ANOVA), with higher values in highway matrices and edge plots. Burn and clearcut edges had, on average, less than one alien species per plot. Overall, alien species richness was negatively correlated with native species richness in plots with at least one alien species ($R^2=0.30$, $p<0.001$). Patterns in the distribution of native and alien species in forest edges appear to be not only affected by physical changes in relation to proximity to the edge, but also by the pool of propagules that is able to reach them. Our study suggests that patterns of native and alien plants are related to both the physical effects of creating a forest edge and also to the landscape context in which these edges occur. These results should help to prioritize management efforts to control invasive alien species into edges adjacent to human corridors.

INTRODUCTION

Increasing evidence suggest that landscape structure and land-use are key elements in influencing alien species invasion processes (Hobbs 2000). At the landscape scale, forest edges are recognized as a potential starting point for invasions, acting as facilitators of the percolation of alien species into less disturbed environments (Saunders et al. 1991, Brother and Spingarn 1992, Cadenasso and Pickett 2001, Honnay et al. 2002). However, little research has been conducted to understand the role of forest edge type in controlling edge effects on invasive species and their implications for landscape invasions.

Most of the evidence of edge effects in forests on native and alien species comes from road and clearcut edges (Chen et al. 1992, Murcia 1995, Euskirchen et al 2001). Other natural and anthropogenic forest edges, which have been less studied, may show distinct responses due to their unique characteristics including landscape context and causal agent. This may prove particularly critical in the case of alien species invasion where landscape processes influence smaller scale phenomena. For example, clearcut edges may appear physically similar to road edges, but the dispersion of alien species may be significantly lower than in road-forest edges that are continuously receiving propagules carried by vehicles from other distant areas that act as sources (Spellerberg 1998, Parendes and Jones 2000).

While changes in physical environment along edges have been intensively studied (Cadenasso et al. 1997, Matlack et al. 1993, Young and Mitchell 1994), these physical factors may actually play a secondary role in alien plant invasion, whereas propagule availability may represent the main constraint for invasion (Cadenasso and Pickett 2001, Honnay et al. 2002, D'Antonio et al 2001).

Edge types (e.g road, cleacuts, burned forests) provide natural experiments to compare invasion processes in relation not only to distance from the edge, but to other variables including the nature of the matrix (landuse adjacent to the forest edge sensu Lindermayer and Franklin 2002). By comparing edge effects through several types of edges, it may be possible to examine the relative importance of propagule flow as compared to physical factors in invasions of forest edges.

In the Northern Rocky Mountains of the United States, forest edges are a common feature in the landscape. Road and clearcut forest edges are the dominant anthropogenic edge types (Reed et al. 1996), while edges in burned forests are a naturally abundant edge type (Turner et al. 1994). Even though edges are important landscape elements in high elevation *Pinus contorta* (lodgepole pine) forests, edge effects have been scarcely studied and most of the emphasis has been in the effects of fire on overall forest dynamics (Turner et al. 1994; Turner et al. 1997). Studying these forests may provide important information about invasion processes in high elevation forest edges and their relation to edge type. The results may further help to identify generalities in edge-effects and alien invasions.

Pinus contorta forests around West Yellowstone, Montana provide a unique opportunity to study the influence of edge type in invasion processes. In a relatively small and homogeneous forested area it is possible to find highways, burned forests, and clearcut forest edges. In addition, these edges occur both in the managed areas of Gallatin National Forest and in undeveloped areas of Yellowstone National Park. All these edge types can be found in the Madison Plateau area on one habitat type with similar soil, elevation, and topographic conditions.

In this paper we aim to test for differences in patterns of alien species invasion and native communities among three forest edge types (burned forests, clearcuts and highways). We also explore which variables may be related to these patterns including forest structure, edge type and distance from the edge. We hypothesize that alien species invasion will be related to edge type as a function of propagule availability. We expect that edges located closer to dispersal corridors or in a matrix with high presence of alien species will show higher levels of infestation. We also hypothesized that distance from the edge will influence the presence of alien by modifying available resources and competition. However, we expect that alien species will only colonize an area given sufficient propagule pressure. We expect that changes in native communities will be more related to physical conditions modified by proximity to the edge.

Study Site

The study area (Fig. 1) is located in the West Side of Yellowstone National Park and adjacent Gallatin National Forest (44˚48'N, 111˚12'W and 44˚37'N, 111˚00'W). The area represents a strong contrast between landuse outside and inside the park, but the entire study area has an almost constant elevation, soil type and habitat type (Despain 1990).

The geomorphology of the study area is primarily a product of glacial erosion and deposition. These factors determined the formation of the Madison valley (slopes less than 5%), which extends along the Madison River from Mount Jackson to the Hebgen Lake. The majority of soils are Typic Cryochrepts with obsidian sand alluvial parent material (Gallatin NF, soil survey). These soils are coarse textured, well drained and have low organic matter content.

Climate in the study area is strongly influenced by its high elevation (2000 m) and protected valley topography. Precipitation in the area averages 550 mm/year, with peaks in the months of December, January, and June. During the winter, snow accumulation averages 100 cm for March. The snow cover may last from November to April. Mean temperature ranges from a low of –11.1 ˚C during January to a high of 15.2 ˚C in July (Climate data from Western Regional Climate Center, 2001).

Pinus contorta forests and *Artemisia tridentata* shrublands are the dominant vegetation types. Forests are classified as lodgepole pine / bitterbrush habitat type for most of the area (Pfister et al. 1977). These forests have a low productivity, with heights around 20 m (Pfister et al. 1977; Despain 1990). Understory species include *Purshia tridentata*, *Lupinus* spp, *Antennaria rosea*, *Oryzopsis exigua* and *Sixtry histranion*. Forests are open and tree seedlings occur only in more protected areas, drought being the most limiting factor (Despain 1990). This habitat type

(PICO/PUTR) has been found only for West Yellowstone and it is associated with this alluvial soil type (Pfister et al. 1977).

Disturbances in the area include fire, logging, and road development. Fire is the main natural disturbance, but low rates of fuel accumulation in these low productivity forests limits their intensity and thereby the frequency of catastrophic fires. Fire average return intervals range from 400 to 600 years, but frequency may increase in more productive sites (Despain 1990). Gallatin NF has been subjected to great logging pressure, with clear-cutting and selective cutting as the major extractive techniques (Susan LaMont, Personal communication 2000). Road development for both local transportation and regional transportation has fragmented the area, especially in Gallatin National Forest.

Grazing, logging and transportation have facilitated the introduction of aggressive weeds. Among the most invasive are *Centaurea maculosa*, *Linaria vulgaris*, *Linaria dalmatica*, *Melolitus officinalis*, *Circium vulgaris* and *Verbascum thapsus* (Ollif et al. 2001, Whipple 2001). The harsh, high elevation climate restricts the intensity of weed invasion, especially those adapted to more temperate agricultural conditions (Forcella and Harvey 1983; Sax and Brown 2000). Nevertheless, human disturbed areas (e.g. roads, clearcuts) have been already modified by plant invaders. Furthermore, weeds are progressively colonizing riparian habitats and other pristine environments (See Chapter 4 and 5).

METHODS

We established a total of 30 edge-transects in south facing forest edges. Six transects were located randomly in each of five edge types: 1) highway 93 in Gallatin NF (GNF-hwy), the west entrance park highway (YNP-hwy), burned forests of 1988 in YNP (YNP-burns), a burned forest in Gallatin NF (GNF-burns) and clearcuts of Gallatin NF (CC). GNF-hwy is a high traffic highway with wide roadsides (15 to 20 m) cleared of forest or shrubs. YNP-hwy has lower traffic than GNF-hwy and forest edges occur around 5 m from the road surface. The YNP-burns were caused by high intensity fire and no machinery was used to limit the fire perimeter. Instead, the GNF burn also occur in 1988, but have a perimeter built by heavy machinery and salvage logging was conducted after the fire. Finally, clearcuts were logged between 1978-1982 and edges were sharply delimited.

Edge-transects were composed of 5 plots of 2 by 20 meters. Plots were located at –10, 0, 10, 20 and 40 m from the end of the road surface (plots E1, E2, E3, E4, and E5 respectively). YNP-hwy transects lacked of plot E1 due to the <5m distance from the edge to the road. Each 40 m^2 plot was divided in two 10 m by 2 m subplots to make cover estimation more accurate. In each subplot cover class for every species (native and alien) present in the subplot was recorded using Braun-Blanquet cover classes (Mueller-Dombois and Ellemberg 1974). Nomenclature followed Hitchcock and Cronquist (1973). For each subplot, we visually estimated canopy cover for all strata, dominant height and DBH for all trees inside the plot. In each subplot, we also recorded seedlings by tree and height class (<0.5m, 0.5-1.0 m, 1.0-1.5m, 1.5-2.0m, >2.0m).

Analyses

For analytical purposes, we averaged the data from the two adjacent subplots of $200m^2$ into one plot of $400m^2$. We characterized vegetation structure in each edge type by calculating mean canopy cover, mean dominant height and mean basal area at each plot. We used ANOVA to test for the effects of distance and edge type on seedling density.

Using ANOVA, we tested for the effects of 1) distance from the edge and 2) edge type on the following plot variables: a) alien species richness, b) alien species cover, c) native species richness, b) native species cover, d) total species richness and e) total species cover. Normality was tested in the model studentized residuals using Wilcox index ($p<0.05$).

Linear regression models were used to test the relationship between native species and alien species richness for all plots (20x2 m). The relationship was also tested for plots stratified by distance from the edge and for plots stratified by edge type.

For all understory species, we recorded a relative decrease or increase in cover of each species from the matrix to forest interiors. For this purpose, a ratio between the mean cover of each species in the matrix (E0) to that in the interior (E4) was calculated. Similarly, we recorded increase or decrease to the interior in mean cover of species grouped in life form types (annuals grasses, annual herbs, perennial grasses, perennial herbs, shrubs and trees; based on Grime 1977). For all statistical analyses we used SPSS 10.0.

Using PC-ORD 4.0, we ran a Detrended Correspondance Analysis (DCA, Hill and Gauch 1980) of all plots (n=144) with all species present in more than one plot (n=65). We plotted DCA diagrams to visually assess variations in community composition in relation to distance from the edge and edge types. Differences among groups were tested using MRPP ($p<0.05$) (McCune and Mefford 1999).

RESULTS

Patterns of native species

We found a significant effect of edge type and the interaction of edge type and distance on native species richness and native species cover ($p<0.05$, ANOVA), however distance by itself was not a significant factor (Table 1). When edge types were contrasted, plots in GNF-hwy had the lowest mean native species richness ($p<0.01$, t-test; Fig. 2), the other edge types were not significantly different.

Within each edge type, native species richness varied by distance from the edge, but it was significantly different only in YNP-hwy, where E1 plots had the highest mean number of native species for that type ($p<0.01$, t-test). When comparing plots located right in the edge (E1) among types, YNP-hwy had the higher native species richness ($p<0.01$, ANOVA). For all other distances, we found no significant differences among edge types.

Native cover, when analyzed within each edge type, was lower in E0 for GNF-hwy ($p<0.05$, t-test). Within all other edge types, no significant differences were found among distances (Fig. 2).

Patterns of alien species

Alien species richness was significantly related to edge type, distance and interaction between both variables ($p<0.01$, ANOVA, Table 1). When contrasting edge types, the highest mean alien species richness by plot occurred at GNF-hwy and the lowest at YNP-burns (Fig. 2). Within edge types, alien species richness responded to distance from the edge, with significantly higher values for plots E0 and E1 in the GNF-hwy and E1 in the YNP-hwy ($p<0.001$, t-test). In clearcuts, a slight difference was found in mean alien species richness between E0 and E4 ($p<0.05$, t-test). For burned edges, both in Gallatin and Yellowstone, no consistent difference was found.

When comparing positions between edge types, GNF-hwy had the higher alien species richness for E0, and burns had the lowest ($p<0.001$, t-test). For position E1, YNP-hwy and GNF-hwy, both had significantly more alien species than the other edge types ($p<0.001$, t-test). For all other distances, no significant differences were found among edge types. The mean alien species richness for E2, E3 and E4 was less than 1 species per plot for all edge types (Fig. 2).

Alien species richness was negatively correlated with native species richness for all plots with at least one alien species ($R^2=0.30$, $p<0.001$) (Fig. 3). When plots were classified by edge type, the relationship was significant only for GNF-hwy ($R^2=0.69$, $p<0.001$) and YNP-hwy ($R^2=0.33$, $p<0.01$) (Fig. 3). However, slope was negative in GNF-hwy and positive in YNP-hwy. No correlation was significant when plots of all edge types combined were classified by distance from the edge.

Alien species total cover followed a similar trend to alien species richness (Fig. 2). However, differences among cover values were stronger than for richness. Highest alien species cover was found in GNF-hwy (plots E0 and E1) and YNP-hwy (E1) ($p<0.001$, t-test). All other edge types and distances showed mean alien cover lower than 5% with no significant differences (Fig. 2).

Total species pattern

Total species richness was significantly related to edge-type and distance from the edge, while total species cover was only related to distance from the edge ($p<0.05$, ANOVA, Table 1). Most of the variation in total richness occurred in YNP-hwy where E1 showed a significantly higher number of species compared to interior plots ($p<0.001$, t-test, Fig. 2).

As expected in all edge types, height of the upper stratum was lower in the matrix (E0, test, $p<0.01$), but showing no significant variation within interiors (Fig. 1). Canopy cover was lower in the matrix for all edge types (t-test, $p<0.01$), but considerable variation occurred over the transect depending on the edge type with peak values on E1 and E2 (Fig. 1). Basal area followed a similar distribution to canopy cover (Fig. 1). Seedlings of *Pinus contorta* showed a complex pattern with higher mean densities in plots E2 and E3 in all edge types (Fig. 1).

Distance and edge type were significant factors determining *Pinus contorta* seedling densities ($p<0.001$ and $p<0.05$ respectively, ANOVA). However, the interaction between both variables was not significant in explaining *P. contorta* seedling density. Considering all edge types, density in E2 and E3 was significantly higher than in other distances ($p<0.05$, t-test). We found no significant correlation between *P. contorta* seedling density and canopy cover.

Species-specific responses

Species showed individualistic responses to distance from the edge (Table 2). Most native species increased in abundance in forest interiors in GNF-hwy (Table 3). However, no clear trend was observed in YNP-hwy, mainly because this edge type lacked E0 plots and therefore the contrast was less intense. In all other edge types, the majority of native species decrease their cover in forest interiors. The vast majority of alien species in all edge types decreased in the interior (Table 2, Table 3). Only *Taraxacum officinale* was found from E0 to E4, and *Lactuca serriola* and *Agropyron repens* were found in from E0 to E3 plots.

The cover of understory species, grouped in life form types, showed group-specific trends from edges to interiors (Table 2). The cover of annual grasses and annual herbs decreased, in most cases, into forest interiors. Perennial grasses increased to the interiors in highways and YNP-hwy. Shrubs showed a mixed response, increasing in YNP-burn, clearcuts and GNF-hwy. Finally, trees increased to the interiors with the exception of GNF-fire.

Ordination gradients

Axis 1 of the DCA ordination (Eig=0.717) discriminated those plots located in E0 and E1 of the two highways edge types from the rest of plots (Fig. 4). All other plots appeared similar in Axis 1 with variation in Axis 2 (Eig=0.288). MRPP tests showed a significantly lower than expected variation within groups compared to overall variation for both edge types and distance from the edge ($p<0.0001$, Euclidean distance).

DISCUSSION

Alien and native species patterns in relation to edge type

Patterns in the distribution of native and alien species in forest edges are not only affected by physical changes in relation to proximity to the edge but also by the pool of propagules that is able to reach them (Cadenasso and Pickett 2001). Therefore, both distance from the edge and edge type should determine variation in plant community, especially for the distribution of alien species. In our study that included three anthropogenic (highways and clearcut) and two natural (forest burns) edge types, we expected to find a relationship between alien species distribution and edge type, in addition to the well-documented relationship to distance from the edge. We found that both edge type and distance from the edge significantly influenced alien species patterns and native community composition.

Edges located along highways show the highest number of alien species, while the other edge types show only traces of alien species. Interestingly, high cover of alien species coincided with low cover of native species in the E0 and E1 plots of highway edges. This inverse relationship may be the product of long history of disturbance in the matrix (roadside) and continuous propagule introduction due to high vehicular traffic (Trombulak and Frissell. 2000, Spellerberg 1998).

In highway matrices of our forest edges, the complete destruction of the native community due to road construction allows the dominance of a combination of alien annual grasses and annual herbs (as reviewed by Trombulak and Frissell 2000). These edges are also the oldest in our study, thus alien plants have had more time to colonize the edge (E1) and displace native species. In addition, roadsides are mowed annually in the middle of the summer to decrease fire risk, which has been shown to increase the chances for alien species (Spellerberg 1998).

Contrary to the results for GNF-hwy that show high richness of alien species but low levels of native species richness, the E1 plots in YNP-hwy show both a high richness of alien species and a high richness of native species. This may indicate that highways act as corridors for both native and alien plant propagules, increasing overall diversity, at least in areas less developed like Yellowstone National Park.

In interior plots of highway edges, only *Taraxacum officinale* has established, suggesting that most alien species cannot survive in less disturbed and more shaded *P. contorta* forests (Table 2). Brother and Singarn (1992) reported a similar exponential decline in abundance and richness of alien species for old growth forests in Indiana, United States. Interior plots may be less susceptible to invasion because of a combination of factors including less soil disturbance, less light availability and less propagule arrival (Brother and Singarn 1992, Parendes and Jones 2000).

The DCA analysis supports the trend found in our previous analyses, that most changes in native and alien species abundance occur in the matrix and edges (E0, E1) of highways and that all other plots show a similar community composition independent of edge type and distance from the edge.

The low number of alien species in clearcuts compared to highways may be associated with both lower disturbance frequency and lower propagule availability. Edges in clearcuts have also suffered intense disturbance in the matrix, but less constant over time. Additionally, these areas have not been under heavy propagule pressure by alien species, because most clearcuts have not been heavily invaded (See Chapter 4), which has allowed for the recovery of the native perennial herb and perennial grass community.

The presence of only one alien species (*Taraxacum officinalis*) in forest burns edges suggests that disturbance by itself does not trigger invasion process in *Pinus contorta* forest edges. Turner at al. (1997) only found two alien species in 1988 burn areas of Yellowstone NP. In our case, the YNP-burn edges are located more than 2 km away from roads and other corridors, limiting the possibility of alien propagules dispersal. However, the GNF-burn edges are less than 0.5 km away from secondary roads and heavy machinery was used to control the fire, but they still show little invasion by alien species. These results suggest that for alien species to get established in matrices and edges it is necessary for a propagule source sufficiently close to the area to generate a frequent and intense seed shadow.

Structural differences

Structural attributes in the forest edges studied follow the trends observed in previous edge research (Murcia 1995). Height, canopy cover and basal area, in general, increase toward forest interiors as has been shown for other forest types (Chen et al. 1992). However, we observed considerable variation in canopy cover and basal area, variability that may be related to the intrinsic heterogeneity in the spatial distribution of *Pinus contorta* forests. Overall, tree canopies appeared highly sparse with mean cover around 20%.

Most studies that have found a linear negative or positive relationship between distance from the edge and seedling density, which depends mainly on the species light requirements (e.g. Chen et al. 1991). These studies have usually been conducted in closed forests where light availability is a constraint for regeneration of shade intolerant species. However, our results, which suggest a non-linear response of seedling density to distance from the edge, denote the complexity of edge effects and the difficulty in making generalizations (Murcia 1995). *Pinus contorta*, in these sites, is probably achieving a higher recruitment in environments that are more protected from drought than forest edges, but that are not overly shaded as interiors.

Implications for edge ecology and management

Much emphasis has been put into understanding and measuring forest edge effects and trying to find generalities among forest ecosystems. However, the interaction of physical edge effects with other landscape processes such as dispersal is often overlooked. Studying patterns of distribution of native and alien plants across several edge types can increase our understanding of the importance of landscape factors in determining the magnitude and nature of edge effects.

Our study suggests that patterns of native and alien plants are related to both the physical effects of creating a forest edge and also to the landscape context within which the edge occurs. Highway or road edges should have a much higher chance of being invaded by alien species, due to the frequent propagule introduction by human and animal vectors (Forman and Alexander 1998), than edges occurring in areas with which are isolated from propagule sources. This principle of propagule pressure as a limiting factor should hold both for natural created edges, such as burn forest edges, and for anthropogenic edges, such as clearcuts. Our results contribute to understand the interactions between landscape context and edge effects, but generalizations from these results are limited by the uniqueness of the area studied and the lack of the replicates in other ecosystems. Further, studies should try to capture these processes over larger scales to increase the inference power.

Management efforts to diminish the impact of edge-effects in native forest communities should emphasize the control of alien species along human corridors. Also, the dispersal of alien species into edges should be avoid by limiting the extent and amount of source populations in heavy disturbed areas such as clearcuts or other logged areas. These preventive actions may limit the percolation of alien species into interior forests and reduce their negative effects on native communities.

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Table 1. ANOVA for species richness and cover percentage variables for all edge plots (n=144). Variables were recorded for each plot. Edge type includes 5 categories (GNF-highway, YNP-highway, GNF-burns, YNP-burns and clearcuts). Distance represents distance from the edge (-10, 0, 10, 20 and 40 m).

Dependent Variable	Source	df	SS	F	p
Alien species richness	Edge Type	4	125	73.02	0.000
	Distance	4	115	67.13	0.000
	Type*distance	15	212	32.93	0.000
	Error	120	52		
Alien species cover %	Edge Type	4	5995	27.92	0.000
	Distance	4	6010	27.99	0.000
	Type*distance	15	17075	21.21	0.000
	Error	120	6441		
Native species richness	Edge Type	4	335	8.69	0.000
	Distance	4	84	2.18	0.075
	Type*distance	15	360	2.49	0.003
	Error	120	1159		
Native species cover %	Edge Type	4	21270	7.51	0.000
	Distance	4	667	0.24	0.918
	Type*distance	15	22322	2.10	0.014
	Error	120	84919		
Total species richness	Edge Type	4	134	2.97	0.022
	Distance	4	311	6.90	0.000
	Type*distance	15	248	1.47	0.128
	Error	120	1351		
Total species cover %	Edge Type	4	6467	2.13	0.081
	Distance	4	7606	2.51	0.045
	Type*distance	15	14151	1.25	0.249
	Error	120	90950		

Table 2. Variation in the distribution of species and life form groups from E0 to E4 in relation to edge type (for YNP-Hwy comparison is between E1 and E4). Native species include only those present in more than 10 plots. Alien species include only those present in more than 3 plots. Life form=1) annual grasses, 2) annual herbs, 3) perennial grasses, 4) perennial herbs, 5) shrubs, 6) trees. Signs indicate: += an increase in cover, - = a decrease in abundance and () indicates that the species was present in both plots E0 and E4. Nomenclature followed Hitchcock and Cronquist (1973).

Species \ Type	Life form	T. Count	GNF-Hwy	YNP-Hwy	YNP-Burns	GNF-Burns	Clearcuts
Natives							
Collomia linearis	2	15	(-)	-	a	-	-
Crepis acuminata	2	15	+	a	a	(-)	+
Arabis holboeli	2	33	-	-	-	(-)	-
Gayophytum diffusum	2	34	(-)	-	-	-	-
Agoseris glauca	2	94	(+)	()	(+)	(-)	(-)
Danthonia sp.	3	11	a	a	a	(-)	a
Danthonia intermedia	3	13	a	-	(-)	a	a
Stipa nelsonii	3	28	a	(-)	(-)	-	(-)
Oryzopsis exigua	3	71	+	a	(+)	(+)	(-)
Poa nervosa	3	73	+	+	(-)	(+)	(-)
Festuca idahoensis	3	79	+	(+)	(-)	-	(-)
Sitanion hystrix	3	85	(-)	(+)	(-)	(-)	(+)
Agropyron spicatum	3	105	(+)	(+)	(+)	(-)	(+)
Phacelia hastata	4	13	-	-	a	a	-
Lupinus sericeus	4	15	a	(+)	-	a	a
Castilleja occidentalis	4	16	a	()	(+)	a	a
Erigeron speciosus	4	16	+	-	(-)	-	a
Erigeron compositus	4	19	-	-	-	a	-
Eriogonum ovalifolium	4	20	a	-	(-)	-	(-)
Ivesia gordonii	4	25	a	a	a	(+)	a
Hieracium albiflorum	4	29	+	+	-	+	+
Senecio canus	4	32	-	-	()	(-)	-
Achillea millefolium	4	39	(-)	-	(-)	-	(-)
Penstemon procerus	4	45	+	(+)	(-)	(+)	+
Epilobium angustifolium	4	48	+	+	(-)	(-)	+
Geum triflorum	4	59	+	(+)	(+)	(-)	(+)
Arenaria capillaris	4	84	+	(+)	(+)	(-)	(+)
Eriogonum umbellatum	4	88	+	(-)	(+)	(-)	(-)
Phlox multiflora	4	106	+	(-)	(+)	(-)	(-)
Lupinus argenteus	4	112	+	(+)	(+)	(-)	(+)
Carex rossii	4	129	+	(+)	(+)	(-)	(+)
Antennaria rosea	4	132	(+)	(+)	(-)	(-)	(-)
Artemisia tridentata	5	15	a	-	a	+	(-)
Arctostaphylos uva-ursi	5	38	+	+	(+)	+	a
Purshia tridentata	5	85	+	a	(-)	(+)	(+)
Pinus albicaulis	6	11	+	a	+	a	a
Pinus contorta	6	128	+	(+)	(-)	(+)	(+)
Aliens							
Poa pratensis	1	7	-	-	a	a	a
Lactuca serriola	2	7	-	-	a	a	a
Melilotus officinalis	2	10	-	a	a	a	a
Berteroa incana	2	15	-	-	a	a	a
Tragopogon dubius	2	16	-	-	a	a	-
Taraxacum officinale	2	66	()	(+)	()	(-)	(-)
Bromus inermis	3	13	-	-	a	a	a
Centaurea maculosa	4	4	-	-	a	a	a
Mentha arvensis	4	7	-	-	a	a	a
Life form groups							
Annual Grasses			-	-	a	a	a
Annual Herbs			182.50	4.00	0.19	4.11	2.54
Perennial Grasses			2.15	1.88	1.54	2.22	1.61
Perennial Herbs			0.60	0.85	0.74	1.47	1.16
Shrubs			0.00	2.25	4.36	0.83	0.34
Trees			0.00	0.08	1.51	0.92	0.95

Table 2. Total number of species that decreased or increased their percentage cover, by edge type, when comparing their cover in E0 to E4 (YNP-hwy considers E1 to E4). Hwy= highway and burns= forest burns. ()= number of alien species. YNP= Yellowstone National Park and GNF= Gallatin National Forest.

Edge type	Increase	Decrease	No-change
GNF-hwy	24	12 (11)	(1)
YNP-hwy	15(1)	18 (8)	4
YNP-burns	14	22	2
GNF-burns	10	24	-
GNF-Clearcuts	13	18 (1)	-

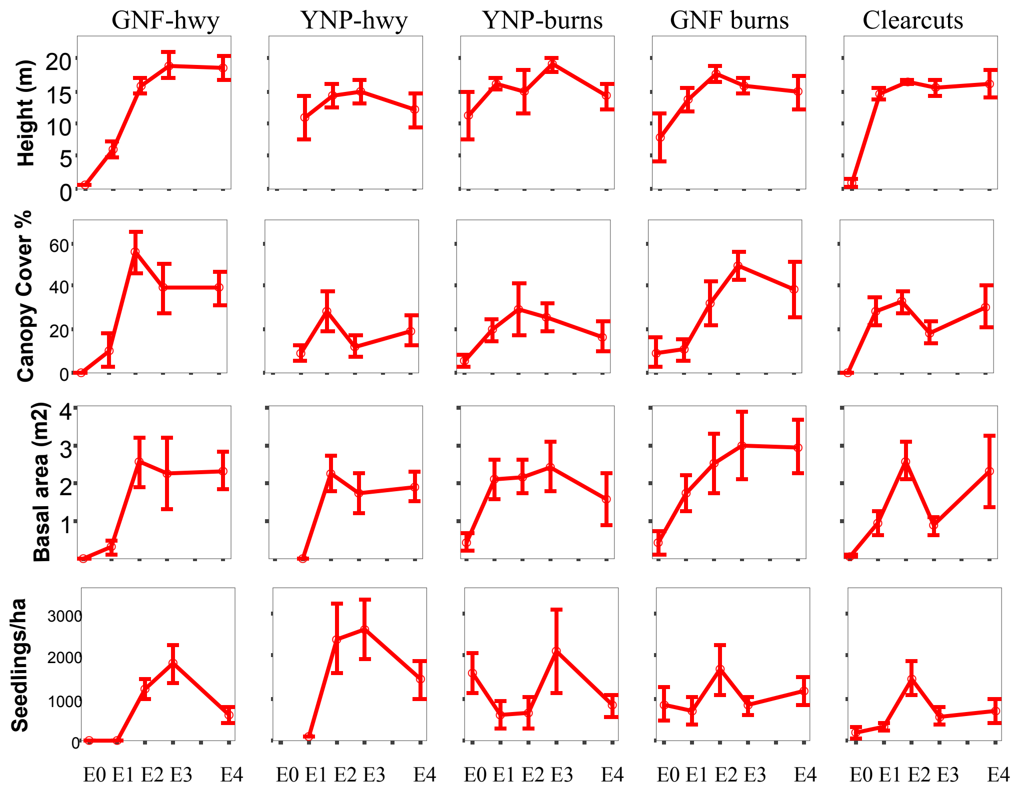

Fig. 1. Structural attributes by edge type: height of the higher stratum, canopy cover percentage, basal area, and *Pinus contorta* seedling density per ha. E0, E1, E2, E3 and E4 represent distance from the edge (-10, 0, 10, 20, 30 and 50m respectively). YNP-hwy does not have an E0 location. Means ± SE are for 6 plots for each location and each edge type (total n=144).

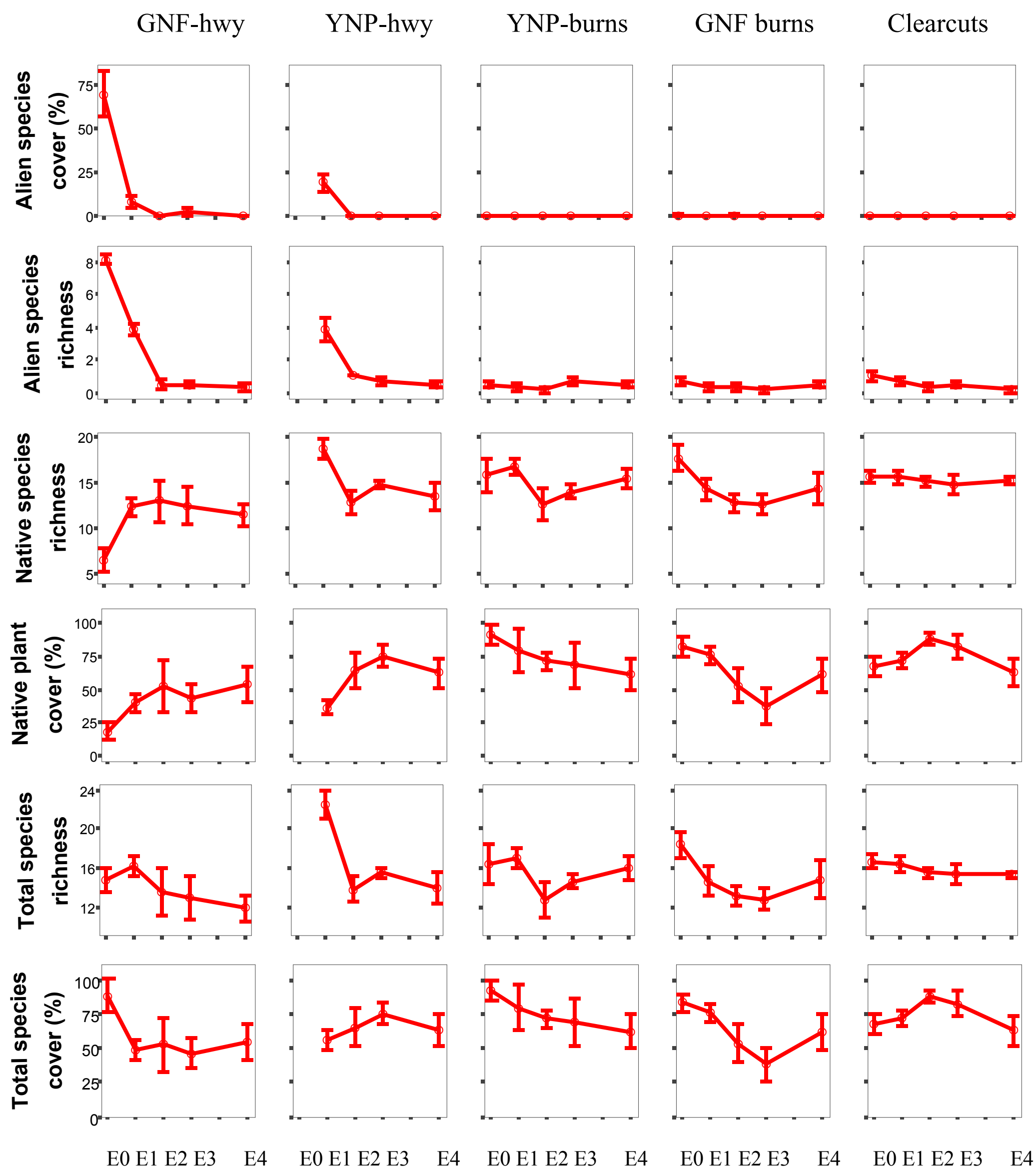

Fig. 2. Species richness and cover percentage by edge type, for alien species, native species and all species. E0, E1, E2, E3 and E4 represent distance from the edge (-10, 0, 10, 20, 30 and 50m respectively). YNP-hwy does not have an E0 location. Means ± SE are for 6 plots for each location and each edge type (total n=154).

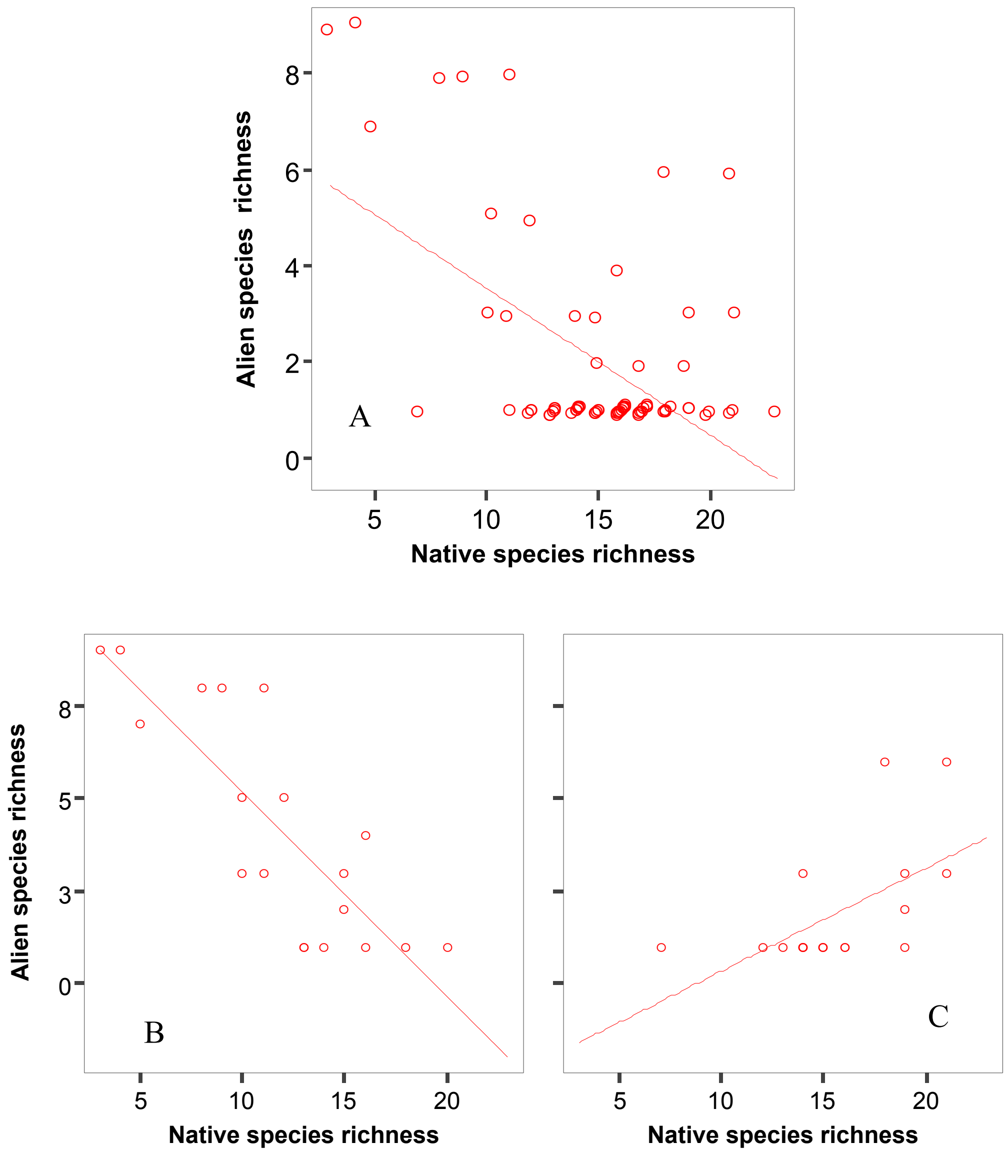

Fig. 3. Alien vs. native species richness for plots, in edge transects, with at least one exotic species. A) all plots (R^2=0.30, p<0.001), B) Gallatin National Forest highway (R^2=0.69, p<0.001), C) Yellowstone National Park highway (R^2=0.33, p<0.01). Notice that Yellowstone NP highway has a positive slope. All other edge types show no significant correlation.

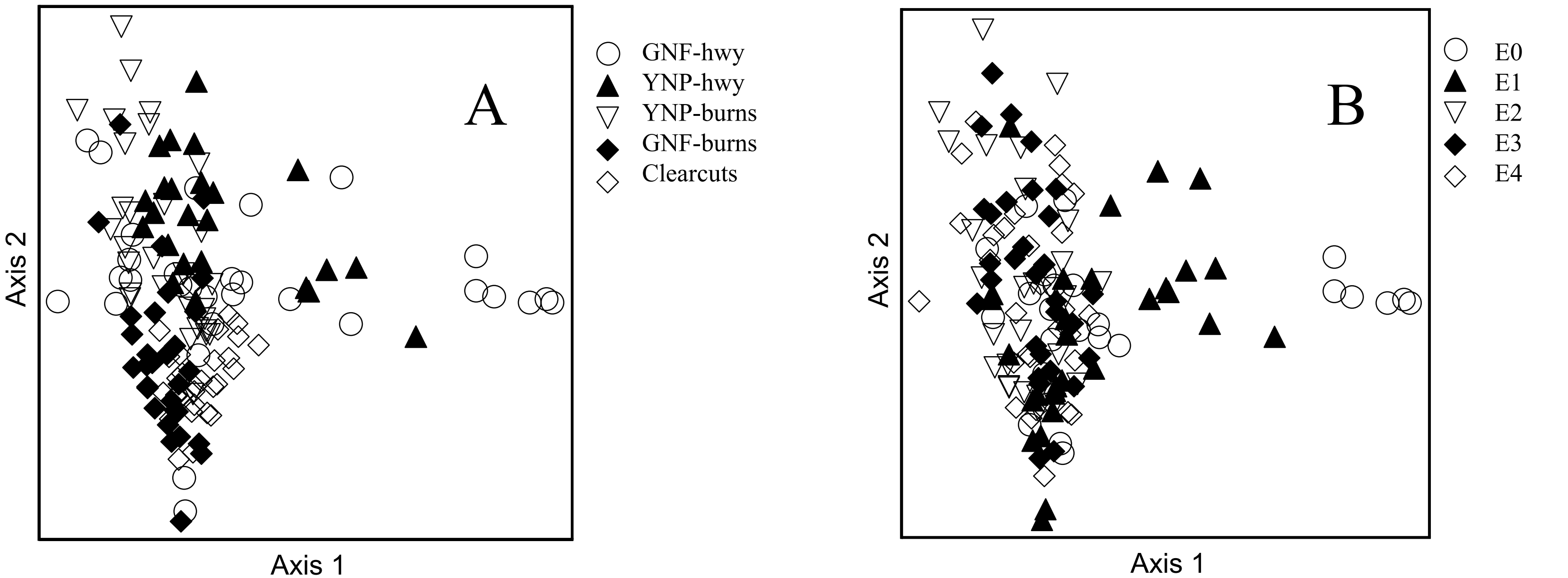

Fig. 4. DCA diagram of edge plots (Total n=144). Plots classified by A. Forest type and B. distance from the edge. E0, E1, E2, E3 and E4 represent distance from the edge (-10, 0, 10, 20, 30 and 50m respectively). YNP-hwy does not have an E0 location.