

Edge type defines alien plant species invasions along *Pinus contorta* burned, highway and clearcut forest edges

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Abstract

Forest edges have been long recognized as the first landscape elements to be invaded by alien plant species in forest ecosystems. However, little is known about the role of forest edge type in invasive species patterns. In the Northern Rocky Mountains of the United States, disturbance-caused forest edges are a common feature in the landscape with anthropogenic (e.g. roadside, clearcut) and natural (e.g. burned, windthrown) edge types. In this paper we examine patterns of alien species invasion and native community structure across three forest edge types in *Pinus contorta* forests including contrasts between undeveloped landscapes in Yellowstone National Park (YNP), and developed (roaded and logged) portions of the adjacent Gallatin National Forest (GNF). Six sets of transects were located in each of five study sites, including clearcut, burn and highway edge types. When burn and highway edges were compared between GNF and YNP, landscape matrix did not have a significant effect on either alien species richness or cover. In both landscapes, highway edges had higher alien species richness and cover than burn edges. For burn and highway edges, alien species richness and cover were significantly related to edge type, distance from edge and the interaction between both variables. In Gallatin NF, alien species were concentrated along highway edges, while burn and clearcut edges are significantly less invaded. Overall, alien species richness was negatively correlated with native species richness in plots with at least one alien species ($R^2 = 0.30$, $p < 0.001$). We were able to explain from 23 to 68% of the variation in alien species richness from simple measures of vegetation structure within each of the edge types. Our study suggests that at least for high elevation conifer ecosystems such as West Yellowstone, alien plant invasion into interior forest is significantly enhanced by disturbance edges only along roadsides. Further studies are needed to determine causal mechanisms that explain the high degree of invisibility of roadside edges. Our results highlight the need for careful planning and management of roads, as they may become a primary conduit of alien plant invasions.

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1. Introduction

While much work has been done on understanding how alien invasive species interact with native species at the individual plant or patch scale, increasing evidence suggests that landscape structure and land-use are also key elements influencing alien species invasion processes across a range of spatial scales (Hobbs, 2000; With, 2002; Pauchard and Alaback, 2004; Pauchard and Shea, 2006). At the landscape scale, forest edges are recognized as a potential starting point for invasions of alien plant species into less disturbed environments (Saunders et al., 1991; Brothers and Spingarn,

1992; Cadenasso and Pickett, 2001; Honnay et al., 2002). Invasive species often are unable to percolate deeply into forested environments (Honnay et al., 2002; Watkins et al., 2003; Pauchard and Alaback, 2004). While many of these species have high light, nutrient or energy requirements that are best met in edge environments, it is unclear what role native species and ecosystem structure plays in affecting “invasibility” in forest habitats (Gilbert and Lechowicz, 2005; Stohlgren and Barnett, 2003).

Most of the evidence of edge effects in forests on native and alien species comes from clearcut logged and agricultural edges (e.g. Chen et al., 1991; Honnay et al., 2002; Murcia, 1995; Euskirchen et al., 2001). Other natural and anthropogenic edges types such as forest road edges or burn forest edges would be expected to show distinct edge responses due to their unique structure and landscape context, yet few studies have directly

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compared edge types (Mullen et al., 2003; Watkins et al., 2003). The influence of edge type is particularly important in the case of alien species invasions where landscape dispersal processes may influence stand scale phenomena (With, 2002). While changes in physical environment along edges have direct implications to growth, competition and population dynamics of many native species, there is growing evidence that for alien species propagule pressure may be an equally important factor (Matlack, 1993; Young and Mitchell, 1994; Cadenasso et al., 1997; Cadenasso and Pickett, 2001; D'Antonio et al., 2001; Honnay et al., 2002).

Edge types (e.g., roads, clearcuts, burned forests) provide natural experiments not only to compare invasion processes in relation to distance from the edge, but also to examine other factors such as landscape matrix influences (sensu Lindenmayer and Franklin, 2002). Since edge types are generally associated with unique matrix conditions and thereby specific alien species propagule pressure, comparing edge effects of several types of edges within contrasting landscape matrices may be useful to examine the role of landscape phenomena on alien species invasions.

In the Northern Rocky Mountains of the United States, disturbance-caused forest edges are a common feature in the landscape. Roadside and clearcut forest edges are the dominant anthropogenic edge types (Reed et al., 1996), while edges of burned forests are the dominant edge type in protected areas (Turner et al., 1997; Parmenter et al., 2003). *Pinus contorta* forests in the vicinity of West Yellowstone, Montana provide a unique opportunity to study the influence of edge type and landscape matrix on invasion processes. A relatively small and homogeneous forested area contains highways, burned forests and clearcut forest edges. In addition, these edges occur on both human-disturbed (logged and high density roads) landscapes of Gallatin National Forest (GNF) and in undeveloped landscapes of Yellowstone National Park (YNP) (low density roads and burn edges only). All these edge types can be found in the Madison Plateau area on one habitat type with similar soil, elevation and topographic conditions (Despain, 1990).

In this paper we examine differences in patterns of alien species invasion and native community structure among three forest edge types (burned forests, clearcuts and highways) in the Madison Plateau of West Yellowstone to determine: (1) are there differences in patterns of alien plant invasions along edges between the landscape matrices of GNF and YNP?, (2) are there differences in alien species between edge types (highway, burn, clearcut) within the developed landscape matrix of GNF? and finally (3) what structural attributes of the vegetation are most closely associated with alien species invasion within each edge type?

2. Methods

2.1. Study sites

The study area 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 land use history inside and outside of the park, but the entire study area has a similar elevation, soil type and habitat type (Despain, 1990). Soils are dominated by Typic Cryochrepts with obsidian sand alluvial parent material (USDA Forest Service, Gallatin NF, unpublished). These soils are coarse textured, well drained, and have low organic matter content.

Climate is continental and montane, and is strongly influenced by its high elevation (2000 m) and protected valley topography. Precipitation in the area averages 550 mm/year, with peaks in December–January, and June. During the winter, snow accumulation averages 100 cm. Snow cover usually persists 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 (Western Regional Climate Center, 2001). Frosts are common throughout the year.

P. contorta forests and *Artemisia tridentata* shrublands are dominant vegetation types. Forests are classified as *P. contorta*/*Purshia tridentata* habitat type for most of the area (Pfister et al., 1977). These forests have a low productivity, with mature tree heights around 20 m (Pfister et al., 1977; Despain, 1990). Understory species include *P. tridentata*, *Lupinus* spp., *Antennaria microphylla*, *Oryzopsis exigua* and *Sitanion hystrix*. Forests are open and tree seedling establishment is limited by drought (Despain, 1990; Stohlgren and Bachard, 1997). This habitat type has been found only in West Yellowstone and it is associated with alluvial soils (Pfister et al., 1977).

Disturbances in the area include fire, windthrow, logging and road development (Parmenter et al., 2003). Fire is the main natural disturbance, but is infrequent due to low rates of fuel accumulation and the rarity of extended droughts (Turner et al., 1997, 2003; Schoennagel et al., 2003). Fire average return intervals range from 400 to 600 years, but frequency may increase in more productive sites (Romme and Despain, 1989; Turner et al., 1994). GNF has been subjected to significant logging pressure, with clear-cutting and selective cutting as the major extractive techniques (Susan LaMont, USDA Forest Service, Gallatin National Forest, Personal communication 2000). Logging effected approximately 800 ha/year from the 1970s to the 1990s, with peaks in the early 1970s and mid 1980s (Gallatin National Forest, unpublished). Road development associated with logging has fragmented the area. Grazing, logging and transportation have facilitated the introduction of aggressive weeds into the area of West Yellowstone (Stohlgren et al., 1999; Olliff et al., 2001; Whipple, 2001). Among the most invasive are *Centaurea maculosa*, *Linaria vulgaris*, *Linaria dalmatica*, *Melilotus officinalis*, *Cirsium arvense* and *Verbascum thapsus* (Olliff 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 (Pauchard et al., 2003).

2.2. Sampling design

Thirty edge-transects were established in south facing forest edges. Six transects were randomly located in each of the five combinations of edge type (highway, burned forest, clearcut) and landscape matrix (GNF, YNP): highway 93 in GNF (GNF-hwy), the west entrance park highway (YNP-hwy), burned forests in YNP (YNP-burns), a burned forest in GNF (GNF-burns) and clearcuts (GNF-CC). GNF-hwy is a high traffic highway with wide roadsides (15–20 m) cleared of forest or shrubs and sustain yearly weed mowing. 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 in 1988 and no machinery was used to limit the fire perimeter. The GNF burn also occurred in 1988, but had a perimeter built by heavy machinery and salvage logging was conducted after the fire. Clearcuts were logged between 1978 and 1982 and edges were sharply delimited.

2.3. Data collection

Edge-transects were composed of five 2 m × 20 m plots. Plots were located at –10, 0, 10, 20 and 40 m from the edge (E0, E1, E2, E3 and E4, respectively). YNP-hwy transects lacked plot –10 due to the <5 m distance from the edge to the road. Each 40 m² plot was divided into two 10 m × 2 m subplots to increase the accuracy of cover estimation. In each subplot, cover class for every species (native and alien) was recorded using Braun-Blanquet cover classes (Mueller-Dombois and Ellemberg, 1974). Nomenclature followed Hitchcock and Cronquist (1973). For each subplot, the percentage overstory canopy cover was visually estimated (Mueller-Dombois and Ellemberg, 1974). Tree height and DBH were measured for all trees greater than 5 cm in DBH. Seedlings were tallied by species and height class (<0.5, 0.5–1.0, 1.0–1.5, 1.5–2.0, >2.0 m).

2.4. Analyses

Vegetation structure in each edge type and at each distance from the edge was characterized by calculating mean and standard error for (a) overstory cover, (b) overstory height and (c) basal area. For analytical purposes, data from the two adjacent subplots of 20 m² were averaged into one plot of 40 m². The effects of distance and edge type on seedling density were tested using MANOVA. We tested for the effects of (1) landscape context (GNF, YNP), (2) edge type (burns, highways, clearcuts), (3) distance from the edge (E1–E4 plots) and their interactions on the following dependant variables at the 40 m² scale: (a) alien species richness, (b) alien species cover (%), (c) native species richness and (d) native species cover (%). Normality was tested in the model using studentized residuals and the Wilcox index ($p < 0.05$). To have a balanced sampling design, analyses were run (1) for burns and highway edge types of both YNP and GNF and (2) for burns, highway and clearcut edge types of GNF.

The relationship between native and exotic richness was tested using a linear relationship for plots stratified by distance from the edge and for plots stratified by edge type. In addition, the relationship between alien species richness and structural variables and native species were assessed using stepwise regression (in, $p = 0.05$ and out, $p = 0.10$). Regressions were run for each combination of landscape and edge type: highway, burn and clearcut edges of GNF and YNP. Plots considered for the regression were E1–E4 ($n = 24$ for each site). Variables incorporated in the stepwise procedure were: maximum tree height, percent overstory canopy cover, forest basal area/ha, *P. contorta* seedling density/ha, tree seedling density/ha, native species cover (%) and native species richness.

For the most common alien species, the relative decrease or increase in cover of each species from the matrix to forest interior was calculated using a ratio between the mean cover of the species in the matrix (–10 m) to that of the interior (40 m). Similarly, an increase or decrease to the interior in mean cover of species grouped in life form types was estimated (annual grasses, annual herbs, perennial grasses, perennial herbs, shrubs and trees; based on Hitchcock and Cronquist, 1973). The software SPSS 10.0 was used for statistical analyses.

General patterns of community composition were assessed using detrended correspondance analysis (DCA, Hill and Gauch, 1980). The composition matrix was developed using all plots ($n = 144$) and those species present in more than one plot ($n = 65$). DCA diagrams were used to visually assess variation in community composition in relation to distance from the edge, edge types and landscape matrices. Differences among groups were tested using multi-response permutation procedures (MRPP) ($p < 0.05$) (McCune and Mefford, 1999). The software PC-ORD 4.0 was used for multivariate analyses.

3. Results

3.1. Effects of landscape matrix and edge type on alien and native species cover and richness

Contrary to our expectations landscape matrix did not have a significant effect on either alien species richness or cover. In both landscapes, highway edges had higher alien species richness and cover than burn edges (Table 1; Fig. 1). For burn and highway edges, alien species richness and cover were significantly related to edge type, distance from edge and the interaction between both variables ($p < 0.01$, MANOVA, Table 1).

Distance from edge was a significant factor in modeling alien species distribution ($p < 0.01$, MANOVA, Table 1). In highway edges, plots at 0 m had significantly greater number of alien species than interior plots ($p < 0.001$, *t*-test), with little difference between landscapes (Fig. 1). In burn edges, alien species are evenly distributed from the edge to the forest interior, for both landscapes.

There was a significant interaction between edge type and distance on alien species richness ($p < 0.01$, MANOVA, Table 1). For plots in the edge and in the matrix (E0, E1), highway edges had significantly more alien species than burn edges ($p < 0.001$, *t*-test). For all other distances, no significant

Table 1
MANOVA for the effects of landscape matrix, edge type, and distance from edge on vegetation composition and structure in Gallatin NF and Yellowstone NP burn and highway edges ($n = 96$)

Dependent variable	Model				Factors (p)						
	R^2	d.f.	F -value	p -Value	Landscape	Edge	Distance	L × E	L × D	E × D	L × E × D
Composition											
Alien richness	0.760	15	16.880	0.000*	0.308	0.000*	0.000*	0.662	0.861	0.000*	0.659
Alien cover	0.637	15	9.369	0.000*	0.214	0.000*	0.000*	0.156	0.029*	0.000*	0.030*
Native richness	0.258	15	1.855	0.041*	0.006*	0.480	0.042*	0.283	0.139	0.432	0.739
Native cover	0.195	15	1.295	0.225	0.040*	0.109	0.965	0.910	0.286	0.052	0.974
Structure											
Basal area/ha	0.258	15	1.851	0.041*	0.161	0.037*	0.006	0.858	0.738	0.145	0.836
Seedlings/ha	0.344	15	2.802	0.002*	0.155	0.385	0.000*	0.113	0.406	0.152	0.194
<i>P. contorta</i> seedlings/ha	0.340	15	2.752	0.002*	0.145	0.403	0.000*	0.103	0.375	0.164	0.207
Overstory cover	0.355	15	2.931	0.001*	0.001*	0.812	0.001*	0.272	0.079	0.242	0.695
tree height	0.338	15	2.724	0.002*	0.540	0.062	0.002*	0.243	0.062	0.067	0.213

Landscape has two levels: Yellowstone NP and Gallatin NF. Edge type has two levels: burns and highways. Distance includes four levels E1–E4 (0, 10, 20 and 40 m from the forest edge).

* $p < 0.05$.

differences were found among edge types. Few alien species percolated into forest interiors with mean alien species richness less than one species per plot for all edge types at 10–40 m (Fig. 2).

Alien species cover followed a similar trend to alien species richness (Fig. 2). However, differences among cover values were more consistent than for richness. Highest alien species cover was found at E0 and E1 on the highway–forest edges ($p < 0.001$, t -test). All other edge types and distances showed mean alien cover less than 5% with no significant differences between them (Fig. 2).

Native species richness was only marginally explained by the model (MANOVA, $R^2 = 0.26$, $p < 0.05$, Table 1) while variation in native cover was not significantly explained by the

model (MANOVA, Table 1). Native species richness was significantly related to landscape matrix and distance from edge (Table 1). Only in YNP-hwy did native species richness vary significantly by distance, where 0 m plots had the highest mean number of native species for that type ($p < 0.01$, t -test). Within all other edge types, no significant differences were found among distances (Fig. 1).

3.2. Effects of edge type and distance from the edge on alien species in the developed landscape matrix (GNF)

In Gallatin NF, alien species were concentrated along highway edges, while burn and clearcut edges significantly less invaded (MANOVA, Table 2). At highways alien species

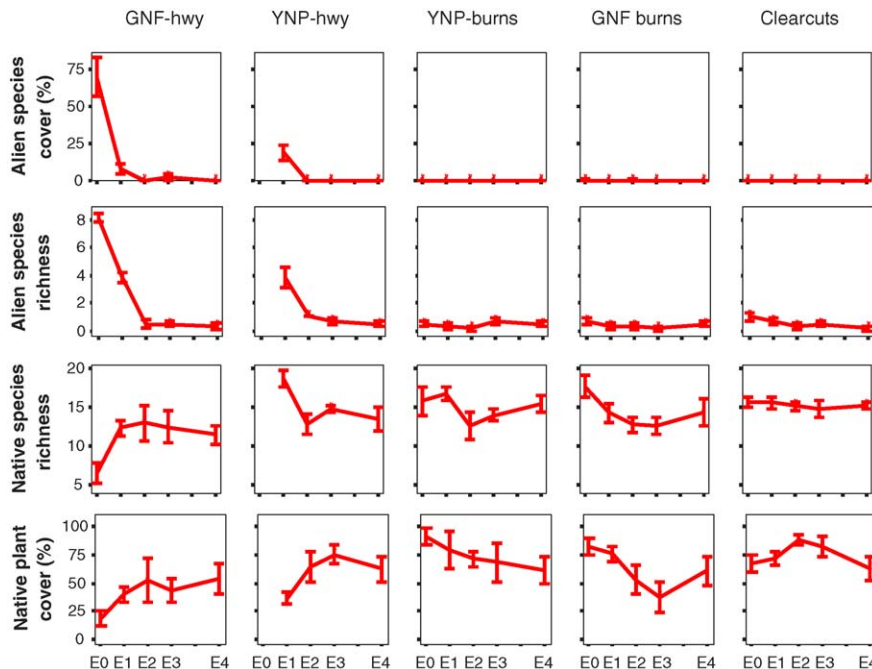


Fig. 1. Species richness and cover percentage by edge type, for alien and native species. E0, E1, E2, E3 and E4 represent distance from the edge (–10, 0, 10, 20, 30 and 50 m, respectively). YNP-hwy does not have an E0 location. Means \pm S.E. are for six plots for each location and each edge type (total $n = 154$).

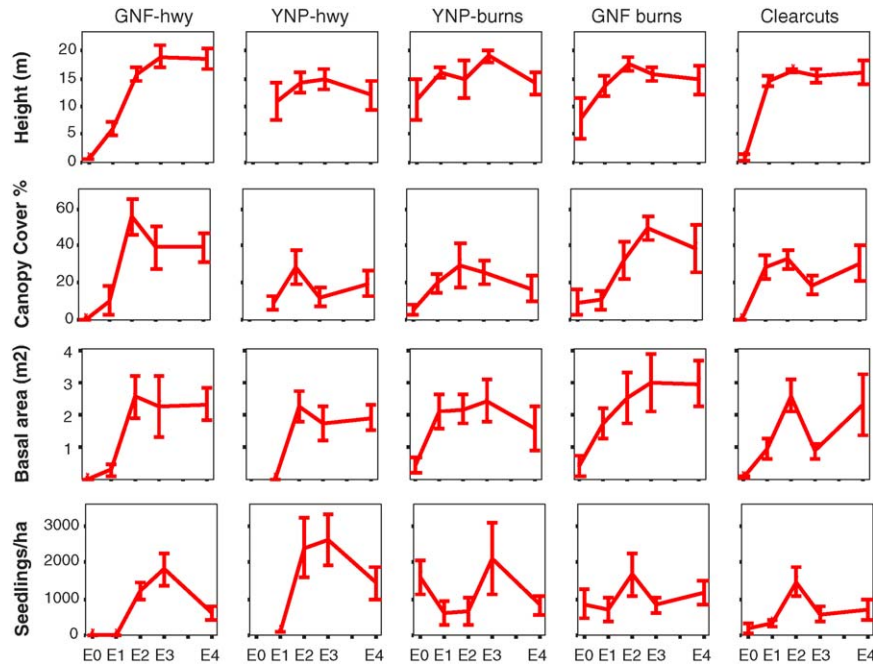


Fig. 2. Structural attributes by edge type: maximum height of vegetation, overstory canopy cover percentage, tree basal area and *Pinus contorta* seedling density per hectare. E0, E1, E2, E3 and E4 represent distance from the edge (–10, 0, 10, 20, 30 and 50 m, respectively). YNP-hwy does not have an E0 location. Means ± S.E. are for six plots for each location and each edge type (total $n = 144$).

concentrated in edge plots (E1) and had lower alien richness and cover in interior plots. A similar trend occurred in burn and clearcut edges. Clearcuts showed lower values for alien species richness and cover than highways and were similar to those of burn edges, but they also showed an effect of distance from the edge ($p < 0.05$, t -test, Fig. 2; Table 2).

3.3. Correlation between native and alien species diversity

Alien species richness was negatively correlated with native species richness for all plots with at least one alien species ($R^2 = 0.30$, $p < 0.001$). When plots were classified by edge type, the relationship was significant only for the highway–forest

edges (GNF-hwy: $R^2 = 0.69$, YNP-hwy: $R^2 = 0.33$). 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.

3.4. Species distribution and community patterns

Ordination analysis suggested a strong compositional uniqueness for edge plots (E0 and E1) at highway edges (Fig. 3). Axis 1 of the DCA ordination (Eigen = 72%) discriminated those plots located at E0 and E1 of the GNF and YNP highways edges from the rest of the plots. All other plots do not show a clear segregation in Axis 1 but show more

Table 2
MANOVA for effects of edge type and distance from edge on vegetation composition and structure in Gallatin NF burn, highway and clearcut edges ($n = 72$)

Dependent variable	Model				Factors (p)		
	R^2	d.f.	F -value	p -Value	Edge Type	Distance	E × D
Composition							
Alien richness	0.759	11	17.133	0.000*	0.000*	0.000*	0.000*
Alien cover	0.420	11	3.947	0.000*	0.004*	0.029*	0.004*
Native richness	0.168	11	1.099	0.378	0.011	0.911	0.933
Native cover	0.284	11	2.161	0.029*	0.002*	0.726	0.197
Structure							
Basal area/ha	0.250	11	1.82	0.070	0.145	0.015*	0.595
Seedlings/ha	0.373	11	3.245	0.002*	0.329	0.000*	0.061
<i>P. contorta</i> seedlings/ha	0.358	11	3.047	0.003*	0.341	0.001*	0.088
Overstory cover	0.328	11	2.667	0.007*	0.361	0.006*	0.053
Tree height	0.450	11	4.458	0.000*	0.718	0.000*	0.002*

Edge type has three levels: burn, highway and clearcut. Distance includes four levels E1 to E4 (0, 10, 20 and 40 m from the forest edge).

* $p < 0.05$.

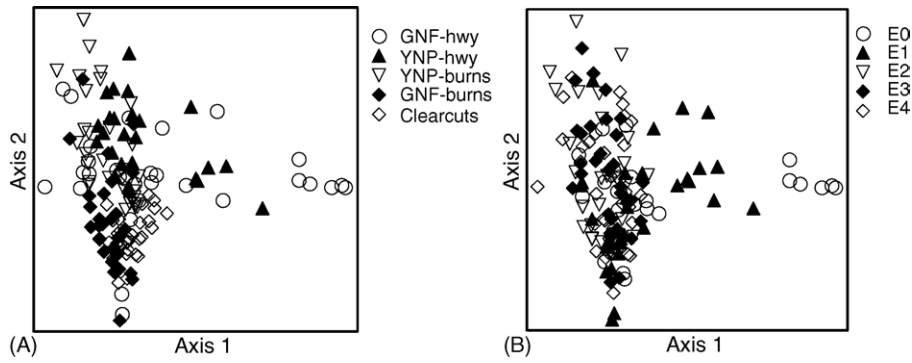


Fig. 3. DCA diagram of edge plots (total $n = 144$). Plots classified by (A) forest type and (B) distance from the edge. E0, E1, E2, E3 and E4 represent distance from the edge (–10, 0, 10, 20, 30 and 50 m, respectively). YNP-hwy does not have an E0 location.

Table 3
Effects of edge type and landscape matrix on the abundance of the most common alien species

Alien species	Life form ^a	Total count	GNF-hwy	YNP-hwy ^b	YNP-burns	GNF-burns	Clearcuts
<i>Poa pratensis</i>	1	7	–	–	a	a	a
<i>Lactuca serriola</i>	2	7	–	–	a	a	a
<i>Melilotus officinalis</i>	2	10	–	a	a	a	a
<i>Berteroa incana</i>	2	15	–	–	a	a	a
<i>Tragopogon dubius</i>	2	16	–	–	a	a	–
<i>Taraxacum officinale</i>	2	66	()	(+)	()	(–)	(–)
<i>Bromus inermis</i>	3	13	–	–	a	a	a
<i>Centaurea maculosa</i>	4	4	–	–	a	a	a
<i>Mentha arvensis</i>	4	7	–	–	a	a	a

Data represents the ratio of the abundance from E0 edge plots to the E4 interior plots. For each species symbols indicate: a, absence; –, decrease to forest interior; +, increase to forest interior; (), presence in both E0 and E4.

^a 1, annual grasses; 2, annual herbs; 3, perennial grasses; 4, perennial herbs; 5, shrubs; 6, trees.

^b Comparison is between E1 and E4.

variation in Axis 2 (Eigen = 29%). MRPP tests revealed a significant overall effect of edge type and distance from the edge on community composition considering both native and exotic species together ($p < 0.001$, Euclidean distance). Alien species in all edge types were less common in interior plots (Table 3). *Taraxacum officinale* was the only species found at all distances, and was the only common alien species in burn edges.

3.5. Variation in edge structure

As expected in all edge types, mean overstory height was lower in the E0 (Fig. 2, t -test, $p < 0.01$), but showed no significant variation from E1 to interior plots (Fig. 2). Overstory height was associated with distance, but no significant landscape matrix or edge type effects were detected (Table 1).

Table 4
Linear regression models predicting alien species richness from vegetation structure in highway, burn and clearcut edges of Gallatin NF and Yellowstone NP

Site	R^2	d.f.	F -value	p -Value	Predictors	Slope	p -Value
Dependent variable: alien species richness							
GNF-hwy	0.678	2	22.155	0.000*	Maximum height Canopy cover	– –	0.001* 0.013*
YNP-hwy	0.543	2	12.4999	0.000*	Basal area Native cover	– –	0.000* 0.037*
GNF-burns	0.660	2	20.413	0.000*	Native richness Maximum height	+ –	0.000* 0.018*
YNP-burns	0.230	1	6.57	0.018*	Canopy cover	–	0.018*
GNF-clearcuts	0.390	1	14.064	0.001*	Maximum height	–	0.001*

Plots considered for the regression were E1–E4 ($n = 24$ for each site). Variables incorporated in the stepwise procedure were: maximum tree height, overstory canopy cover, tree basal area/ha, *Pinus contorta* seedlings density/ha, tree seedlings density/ha, native species cover, and native species richness.

* $p < 0.05$.

Overstory cover was lower at the edge (E1) than interior (E2–E4) for all edge types in both GNF and YNP (*t*-test, $p < 0.01$). However, considerable variation occurred over the transect depending on the edge type with peak values at 0 and 10 m (Fig. 1). GNF had overall higher cover values for burns and highways edges compared to YNP (MANOVA, $p < 0.001$, Table 1). Basal area by contrast showed no landscape effect but was significantly related to both edge type and distance from edge (Fig. 1; Table 1). Seedlings of *P. contorta* showed a general trend towards higher mean densities at 10 and 20 m in all edge types (Fig. 1). Distance was significantly associated with variation in most structural variables between GNF and YNP edges and among GNF edges ($p < 0.01$, MANOVA, Tables 1 and 2). Considering all edge types, seedling density in at 10 and 20 m was significantly higher than other distances ($p < 0.05$, *t*-test). We found no significant correlation between *P. contorta* seedling density and canopy cover.

3.6. Effects of vegetation structure on variation in alien species

Vegetation structure was closely associated with alien species richness in all edge types. Linear regression models to predict alien species richness from vegetation structure were significant for all combinations of landscape and edge types, explaining 23–68% of the variation (Table 4). However, the best predictors change for each site. In general, maximum tree height and overstory canopy cover were the most closely associated with variation in alien species richness.

4. Discussion

4.1. Alien and native species patterns along edges in relation to edge type and landscape matrix

In our study both edge type and distance from the edge were significantly related to alien species patterns. Edges located along highways show the highest number of alien species, while the other edge types show only traces of alien species. 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 (–10, 0 m) of highways and that all other plots show a similar community composition independent of edge type and distance from the edge. 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 a long history of disturbance in the matrix (roadside) and continuous propagule introduction due to high vehicular traffic (Trombulak and Frissell, 2000; Spellerberg, 1998), which represent an opportunity for generalist alien plant species to invade (Pauchard and Alaback, 2004).

In highway matrices of our forest edges, intense disturbance 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 (0 m) 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 invasion by 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 *T. officinale* has established, suggesting that most alien species cannot survive in less disturbed and more shaded *P. contorta* forests (Table 2). Brothers and Spingarn (1992) reported a similar exponential decline in abundance and richness of alien species for old growth deciduous forests in the eastern United States. Interior plots may be less susceptible to invasion because of a combination of factors including competition with native species, fewer safe sites for seed germination, less solar radiation and less propagule dispersal (Brothers and Spingarn, 1992; Parendes and Jones, 2000; Cadenasso and Pickett, 2001).

Our results are consistent with the notion that patterns in the distribution of native and alien species in forest edges are not only affected by well documented 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). Both distance from the edge and edge type should determine variation in plant community, especially for the distribution of alien species. 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 been subjected to intense disturbance in the matrix, but are less frequently disturbed over time than roadside edges. Additionally, clearcuts have lower propagule pressure by alien species than roadsides (Pauchard et al., 2003), 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 burn edges suggests that disturbance by itself does not trigger invasion process in *P. contorta* forest edges. Turner et 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 efficacy of alien propagule dispersal. However, the GNF-burn edges are less than 0.5 km away from secondary roads and areas where heavy machinery was used to control the fire, but they still show little invasion by alien species.

It appears that propagule dispersal is a key constraint to alien species invasion, even after resource liberation caused by large scale disturbances such as fire. In the study sites, most alien species are located along highways (Table 3), even though they are mostly generalist species adapted to highly disturbed areas. This pattern suggests a propagule limitation for them to expand into more pristine environments. For alien species to get established along edges, it may be necessary to have a propagule source sufficiently close to the area to generate a

frequent and abundant seed rain, or alternatively an efficient dispersal vector (e.g. machinery, cattle).

4.2. 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., 1991). 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 *P. contorta* forests. Overall, tree canopies are quite open with mean cover around 20%.

Most studies that have found a linear relationship between distance from the edge and seedling density have been conducted in closed forests where light availability is a constraint for regeneration of shade intolerant species (e.g. Chen et al., 1991). 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). *P. contorta*, in these sites, appears to be achieving a higher recruitment in environments that are more protected from drought than forest edges, but that are less heavily shaded than forest interiors (Despain, 1990).

4.3. Landscape effects on alien invasions across edges

While much experimental and theoretical work has emphasized the potential role of landscape structure and processes on phenomena like alien plant species invasion, in our study we were unable to detect a significant effect at this scale. This is especially surprising as the contrast in land-use and forest management between Yellowstone and surrounding national forests is well-known and dramatic (e.g. Parmenter et al., 2003). In our system it appears that the alien invasion is at an early stage where smaller scale phenomena such as edge structure and local propagule availability are playing a larger role than general dispersal processes at the landscape scale. It will be important to continue to monitor alien species in this study system to see if and when landscape-scale patterns begin to play a larger role in determining rates and patterns of alien invasions. In a harsh climate such as this it will also be important to establish the role of spatial and temporal climatic variation on alien invasions. Preliminary data suggests that droughts in the winter and early spring can constrain invasion patterns in this system (Pauchard, unpublished data). Further work is needed to establish the role of spatial microclimatic variations in smaller scale processes like alien invasions along forest edges.

4.4. Conclusion

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. 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 processes such as seed dispersal and disturbance, which are influenced by edge type. 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 large propagule sources. This principle of propagule pressure as a limiting factor should hold both for naturally created edges such as burned forest edges, and for anthropogenic edges such as clearcuts. Further work comparing multiple edge types is needed to determine the generality of this result for other forest types and climatic settings.

Management efforts to diminish the impact of edge-effects on native forest communities should emphasize the control of alien species by limiting the extent and amount of source populations in heavily disturbed areas. These preventive actions may limit the percolation of alien species into interior forests and reduce their impacts on native communities. Our results highlight the need for careful planning and management of road networks, as they may become the primary conduit of alien plant invasions.

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