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Plant invasion at landscape and local scales along roadways in the mountainous region of the Greater Yellowstone Ecosystem

Fredric Pollnac · Tim Seipel · Charles Repath · Lisa J. Rew

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Abstract Roadways are increasingly recognized as common points of entry for non-native species into natural habitats in mountainous areas. Studies were conducted within the Greater Yellowstone Ecosystem from 2003 to 2007 to evaluate (1) landscape scale patterns of non-native plant richness along roadways, and (2) local scale factors influencing native and non-native plant richness and cover, and surrogate non-native plant (SNP) emergence in an invaded habitat. At the landscape scale, non-native plant richness decreased with increased elevation and increased distance from the road, and was positively correlated to the proportion of plots with signs of disturbance. Non-native plant richness also varied by habitat type: sagebrush steppe had the highest and alpine the lowest. At the local scale, in sagebrush steppe, SNP emergence was negatively associated with increased distance from the road, and percent cover of litter was positively associated with SNP emergence. The proportion of non-native plant cover and richness decreased, while the proportion of native cover and native species richness increased with distance from road. Our study suggests that landscape scale variables such as elevation and habitat type influence non-native plant success, and that while local conditions adjacent to the road may be favorable for non-native plants, factors which vary at the local scale can also effect non-native plant establishment away from the roadside. This highlights the need for studies to evaluate multiple scales when assessing patterns and processes driving non-native plant invasions, and suggests that sagebrush steppe may be resistant to invasion as long as it remains undisturbed.

Keywords Invasion resistance · Non-native plants · Roads · Elevation gradient · Ecological filtering · Yellowstone

Introduction

Roadways often serve as dispersal vectors within a region at both landscape and local scales (Arevalo et al. 2010; Kosaka et al. 2010; Paiaro et al. 2011; Parendes and Jones 2000; Spellerberg 1998; Trombulak and Frissell 2000) and several studies have shown that plant propagules can be transported on vehicles (Hodkinson and Thompson 1997; Pickering and Mount 2010; Schmidt 1989; Von der Lippe and Kowarik 2007; Zwaenepoel et al. 2006). Consequently, roadways are

F. Pollnac (✉) · L. J. Rew
Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, MT 59717, USA
e-mail: fpollnac@montana.edu

T. Seipel
Institute of Integrative Biology, ETH Zurich, Universitätsstrasse 16, 8092 Zürich, Switzerland

C. Repath
Yosemite National Park, PO Box 577, Yosemite, CA 95389, USA

believed to be a large source of non-native plant introductions via vehicular transport (Von der Lippe and Kowarik 2007). Roadsides have different environmental conditions in terms of altered light availability, soil texture, compaction and chemistry, increased water runoff, and repeated disturbance from maintenance and off road driving when compared with adjacent native vegetation (D'Antonio and Vitousek 1992; Gelbard and Belnap 2003; Hobbs 1991; Rejmánek 1989). In addition, non-native plants may respond better than indigenous species to the alien substrates and altered disturbance, water, and nutrient regimes found on roadsides (Mack and Thompson 1982; Tyser and Worley 1992). Once established, roadside non-native plant patches can then serve as sources for the spread of non-native plants into the interiors of natural areas, as suggested by Tyser and Worley (1992) and Pauchard and Alaback (2004).

Whether a non-native plant will be able to spread into the surrounding habitat away from roadsides depends on several biotic and abiotic factors. These include, but are not limited to, poor soil conditions (Williamson and Harrison 2002), large amounts of plant litter (Fowler 1988), shading (Parendes and Jones 2000), seed predation (Maron and Vila 2001), and more stressful climatic conditions (Baker 1986; Hautier et al. 2009; Laughlin and Abella 2007; Ross et al. 2008). Habitats away from roadsides are also often composed of co-evolved and environmentally adapted groups of native species, and such communities may have more potential to resist invasions by non-native plants (Maron and Marler 2007; Naeem et al. 2000; Prieur-Richard et al. 2000). Thus, habitats may vary in the amount that they are invaded depending on their proximity to a road. However, the exact processes that reduce non-native plant abundance at the local scale remain unclear. Does the native vegetation farther away from the roadside resist invasion, or does decreased propagule pressure farther away from roadside seed sources result in the decreased richness and abundance of non-native plants? In addition to the variability in invasibility imposed by proximity to a road, elevation gradients may impose additional sources of variability. Climatic conditions change as elevation increases (Körner 2003), which leads to increased habitat and climatic heterogeneity over a given distance as compared to an area without a steep elevation gradient. Non-native plant richness has been shown to decline as elevation increases in mountain regions (Alexander et al. 2011; Arevalo et al. 2005; Becker et al. 2005; McDougall et al. 2005; Pauchard et al. 2009), and directional ecological filtering has been proposed as an explanation of the pattern of non-native plant species richness in mountain systems in general, whereby non-native plant communities are assembled from nested sets of plants with broader and broader environmental tolerances as elevation increases (Alexander et al. 2011). All this suggests that elevation gradients in mountain systems are an additional source of variability in invasibility. For example, in addition to differences in invasibility in a habitat due to proximity to a road, invasibility may be lower in general at the higher elevation limit of a particular habitat due to differences in climatic conditions there.

Non-native plant abundance tends to decrease away from roadsides (Arevalo et al. 2010; Timmins and Williams 1989), and this pattern has been shown to be exacerbated along an elevation gradient within the GYE (Seipel et al. 2012). In order to better understand the process of non-native plant invasion along roadways in the GYE, we examined the relationship of elevation and distance from road to non-native plant richness at the landscape scale. Here, we hypothesized that non-native plant richness would decrease with both increased distance from the roadside and increased elevation. We then focused on the most invaded habitat, sagebrush steppe, at the local scale. We added equal numbers of seeds of a surrogate non-native plant (SNP) species to the environment at varying distances from a road. This tested the null hypothesis that decreased propagule pressure is solely responsible for decreased non-native species abundance and/or presence farther away from roadsides. If the null hypothesis were true, emergence would not vary with distance from the roadside. The alternative hypotheses were that other factors, such as native plant cover, available bare ground, litter abundance, and SNP seed predation would be associated with variability in surrogate non-native plant species emergence.

Methods

Landscape scale non-native plant abundance: effects of elevation and distance from road

Site description

Three roads (elevation transects) were chosen for sampling during summer 2007 within the GYE. Roads were chosen in the area based on presence of vehicle traffic and suitable elevation ranges. The elevation transects were located within the GYE in the states of Montana and Wyoming, USA, centered around 45 N 110 W. These included two transects in Yellowstone National Park (YNP) and another outside the park. The transect outside of YNP (Beartooth Pass) ascended the east side of the Beartooth Pass, Highway US 212 between Red Lodge, Montana and Cooke City, Montana, with an elevation range of 1,803–3,307 m. The first transect in YNP (Mt. Washburn) ascended Mount Washburn from Tower Junction to the summit travelling south, with an elevation range of 1,936–3,065 m. The second transect in YNP (Craig Pass) ascended Craig Pass to the continental divide moving south from the Old Faithful visitor area, with an elevation range of 2,232–2,513 m. All elevation transects were paved roads, except for the final 3.6 km of the Washburn transect, which was an unpaved road subject to infrequent vehicle traffic. The bottom of each transect represents a valley bottom where the road leveled out: it does not represent the lowest area within the region.

Habitats in this area ranged from sagebrush steppe at low elevations to alpine at high elevations. Sagebrush steppe was characterized by *Artemisia tridentata* (the major shrub) and the bunchgrasses *Festuca idahoensis* and *Agropyron spicatum* along with a diverse complement of forbs. The alpine habitat was characterized by small forbs and grasses as well as *Salix* sp. shrubs in protected areas, and some *Phyllodoce* spp. Habitats at the intermediate elevations were typically montane conifer forests which have been subject to infrequent forest fires.

Sampling

To examine non-native plant frequency on the landscape, 10 m × 2 m plots were sampled at the roadside and at an increased distance from the roadside along the three elevation transects. This ensured that we captured diverse habitats and abiotic conditions. For each transect, the elevation range of the road was divided into 19 equal portions prior to sampling, providing 20 evenly-spaced contour lines starting at the lowest point and ending at the highest point. T-plots were then placed at the intersection of the road and each contour line (transect point). At each transect point, the side of the road on which to place the T-plot was randomly selected. Each T-plot consisted of two parts, one parallel to the road edge and the other perpendicular. Each part of the T-plot was divided into 10 m × 2 m sampling units (plots) giving a total length of 50 m along the road edge (five plots) and 100 m perpendicular to the road (10 plots). The outside edge of the roadside section of the T-plot was placed at the first occurrence of the roadside vegetation. The perpendicular part was placed abutting the middle of the roadside transect. Within each 10 m × 2 m plot, the presence of non-native plants was recorded on a scale of 0–3, with 0 = absent; 1 = 1–10; 2 = 11–100; 3 = >100 individuals or ramets. Habitat type, local disturbance (0 = none, 1 = low, 2 = moderate, 3 = high), disturbance context (“mowing”, “grazing”, “logging” “regular/recent fire”, “flooding”, or “other (specified)”), and canopy openness (measured as percent bare ground and percent total canopy cover) were also measured within each plot. Finally, the elevation in meters above sea level and location of each T-plot was recorded using a Trimble XT global positioning system (GPS).

Local scale non-native plant abundance: effects of habitat characteristics

Site description

To examine local scale patterns of native and non-native plant species cover near roads, and how distance from a road affected the emergence and seed predation of a SNP, four transects were established perpendicular to a road west of Yellowstone National Park on United States Forest Service land. The site was located just west of Hebgen Lake at 44°47′ 44″ N, 111°16′ 43″ W, 2,008 m altitude. The site was on a wide bench in a large meadow in sagebrush steppe habitat. Site slopes were gentle, from 2 to 4%, except for the first 1–2 m along the road shoulder where slopes were 60–70%, as measured with a clinometer. Soils were loams and sandy loams. Observed disturbance at this site came from off-road vehicles, elk, deer and cattle grazing and small animal burrowing.

Sampling

Four transects were placed randomly within the study area in spring 2003. Each transect measured 100 m and was placed perpendicular to the road. Seven sampling stations were located along each transect, at 1.5, 3, 6, 12, 24, 48, and 96 m away from the road. At each sampling station on both sides of each transect, a 0.1 m^2 sample ring was placed randomly at either 0.5 m or 1 m away from the transect for a total of 28 plots per transect. Within each ring, 50 seeds of a SNP, *Raphanus sativa* (radish), were sown on May 26, 2003 by scattering the seeds on the surface without disturbing the extant vegetation. Radish was used as a SNP because it was approved and permitted by the United States Forest Service. Prior to sowing, seeds were tested for germination which was observed to be 99%. Any germinating radishes that were visible within the ring were counted, recorded, and then removed on a weekly basis until mid July. In late June 2003, data on the percent cover of each species present was collected for each plot. In September of 2003, transects were shifted to avoid previously sown areas, and the study was repeated with weekly counts continuing until the first significant snowfall. Fall germination trials were repeated in 2004, 2005, and 2007, with the location of transects changing each year. A second spring germination trial and summer vegetation survey was conducted in 2007.

During the first 3 years (2003–2005) of the study, seed loss was evaluated along another two transects established as described above. Fifty radish seeds were placed on top of sand in a dish placed flush to the soil surface at each sampling station on each side of the transect. The dishes were 10 cm in diameter and had two holes in the bottom, of which one was used to fix the dish to the ground with a nail, and the other to provide drainage in case of precipitation. A filter paper was placed at the bottom of the dish under the sand and seed to prevent loss through the holes. Dishes were placed in the field during the first week of September and collected after 3 weeks to assess the magnitude of seed predation.

Data analysis

Landscape analysis

Most of the landscape scale data presented here were originally collected for a study examining global and regional patterns of non-native plants along elevational gradients at different distances from roads in mountainous regions (Seipel et al. 2012). The effect that habitat type and local disturbance intensity had on non-native species richness and individual species occurrence within the GYE was not analyzed in that study, despite the indication that habitat and resistance of native vegetation were important factors affecting local patterns of non-native plant abundance. Here, we extend the analysis of these data within the GYE to habitat and disturbance intensity in addition to elevation and distance from road because changes in habitat and disturbance intensity influence non-native species richness.

We used an information criterion approach (Burnham and Anderson 2002) to compare generalized mixed-effects models using the response of non-native plant richness in plots to the fixed effects of elevation, distance from roadside, habitat type, and disturbance intensity. We iteratively added and removed fixed effects to determine the model with the lowest Akaike's information criterion (AIC) score (Venables and Ripley 2002). We compared both elevation and a second order polynomial expression of elevation to allow for hump shaped patterns. The different roads and transect points were fitted as random factors to account for the nested structure of the data. The models used a poisson error distribution and logit link. We assessed correlations between habitat type and elevation, and non-native plant richness and disturbance intensity. To understand the fluctuations in disturbance intensity along the elevation gradient, the proportion of plots with at least moderate human disturbance was fitted in response to elevation using a general additive model.

Finally, to understand the variation in the response of the five most common species, we fitted the presence-absence of those individual species to elevation, distance from road, habitat type and disturbance intensity using generalized linear models (GLMs) with a binomial error distribution (logistic regression). All analyses were performed in R (R-Development-Core-Team 2009).

Local scale analysis

The local scale data were analyzed using a GLM approach to help elucidate some of the processes responsible for non-native plant spread away from roads and into interior habitats. Data were pooled at each distance along each transect, yielding four replicates per year (i.e. transect level) for each distance from the road. Dependent variables analyzed were native and non-native cover, *Bromus inermis* cover, bare ground, litter cover, native and non-native plant species richness, SNP emergence, and SNP seed predation. The primary independent variable for analysis was distance from road. This variable was natural log transformed prior to analysis so that the data could be modeled in a linear fashion. Preliminary models were fitted by regressing each dependent variable against distance from road, year, and the interaction between distance and year. Although some interactions were found between year and distance, none of these interactions indicated that the general trend changed from year to year for any of the dependent variables except SNP seed predation. Additional analysis with data separated by year confirmed that while intercepts and slopes changed slightly from year to year, the general trends were consistent. Thus data from different years were pooled prior to final analysis for all dependent variables except SNP seed predation. All models were fitted using a GLM with the appropriate error distribution. Results were examined for evidence of overdispersion and models were re-fitted with a quasi-error distribution if overdispersion was evident.

Results

Landscape scale variability in non-native plant abundance

Overall, 34 different non-native plant species were recorded at the landscape scale. Two separate models best characterized non-native species richness along the elevation gradient (Table 1). The more parsimonious model contained elevation, distance from road, and their interaction (ΔAIC = −984.3 from the intercept only model; Fig. 1). The best-fit model of non-native species richness was a model that contained elevation, distance from road, their interaction, habitat type and disturbance intensity (ΔAIC = −960.7 from the intercept only model; Fig. 2). In plots away from the roadside (i.e. natural habitat), the sagebrush steppe and Douglas fir habitats had the highest number of non-native plant species, with means of 2.06 and 1.03 non-native plant species per 20 m^2, respectively. The lowest numbers of non-native plant species were found in the alpine (0.08 per 20 m^2), followed by closed conifer forest (0.14 per 20 m^2). Although the sub-alpine has a higher median elevation, it contained more non-native plant species on average (0.42 per 20 m^2) than the rocky talus (0.30 per 20 m^2). Elevation and habitat type co-varied because habitats were stratified by elevation (Fig. 2b, r = 0.837). Non-native plant richness was positively correlated to proportion of plots with obvious signs of disturbance (r = 0.368), which declined sharply in closed conifer forests but increased again in sub-alpine forests (Fig. 2a).

Table 1 Generalized mixed-effects models predicting non-native species richness ranked from lowest Akiake's information criterion (AIC) to highest

Mixed-effect model formula: fixed effects	AIC	Number of model parameters
~Habitat + dist to road × poly(elev, 2) + disturb intensity	1,017.0	12
~Poly(elev, 2) × dist to road	1,040.6	8
~Habitat + disturb intensity + dist to road	1,057.3	10
~Poly(elev, 2) + dist to road	1,135.0	6
~Disturb intensity + dist to road	1,322.2	5
~Dist to road	1,364.4	4
~Habitat × disturb intensity	1,388.2	14
~Disturb intensity + poly(elev, 2)	1,535.5	6
~Habitat + poly(elev, 2)	1,730.6	10
~Habitat	1,762.4	8
~Poly(elev, 2)	1,771.9	5
~Disturb intensity	1,789.3	4
~Elevation	1,792.7	4
~1	2,001.3	3

Road and transect were fit as random effects because 900 plots were grouped in 3 roads each with 20 transects consisting of 15 plots at different distances to road. Fixed effects were habitat type (habitat; 5 levels), distance to road (dist to road; continuous variable of ranging from 2 to 100 m), elevation (elev) and elevation as a second order polynomial expression (poly(elev,2)), and disturbance intensity (disturb intensity; 3 levels)

The most common non-native species varied in relation to elevation and distance from road (Fig. 3). The ruderal species *Bromus tectorum* and *Verbascum thapsus* declined sharply as elevation increased (Fig. 3a). Alternatively, the perennial grasses *Poa pratensis, Phleum pratense*, and *B. inermis* declined more slowly, which likely reflects intentional plantings at the lowest elevations and subsequent spread. The ruderal species had no significant relationship with

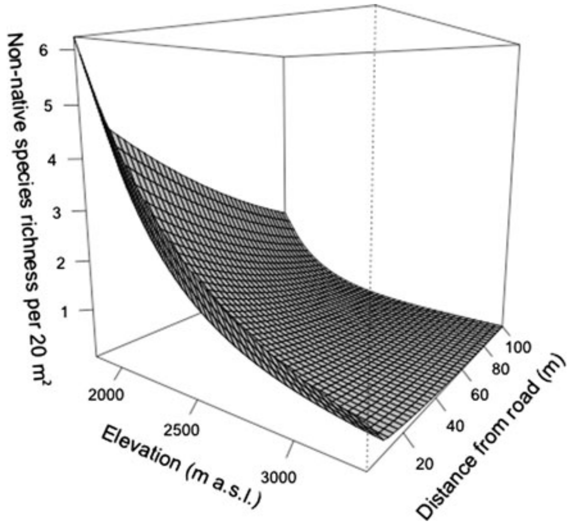


Fig. 1 The 3-D relationship of non-native plant species richness, elevation and distance to roadside fitted as a generalized linear mixed model

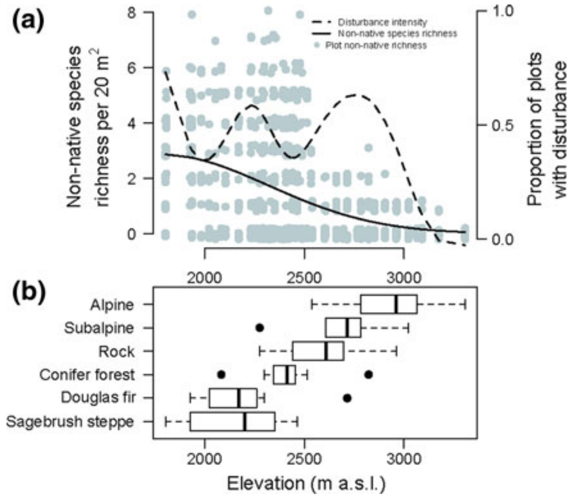


Fig. 2 **a** The covariation of non-native plant species richness to disturbance as a function of elevation. **b** *Boxplots* indicate the elevational distribution of habitats. *Grey circles* are richness of non-native species in plots along the elevation gradient (jittered for clarity) with the fitted trend as the *black solid line*. The *dashed line* is a generalized additive model of the proportion of plots with at least moderate disturbance

distance from road, which reflects their scattered distribution at low elevations, and the high number of absences in plots. In contrast, the perennial grasses showed a significant decline as distance away from the roadside increased, but still had a probability of occurrence of 0.1 at 100 m from the road (Fig. 3b). The highest predicted occurrence of four of the five species was in the sagebrush steppe, with the more ruderal species, *B. tectorum* and *V. thapsus,* having very low predicted occurrence in all other habitats (Fig. 3c). Only *P. pratense* reached a maximum in a different habitat (Douglas fir), which was also low on the elevation gradient. Occurrence of all five species significantly increased with increasing disturbance intensity (Fig. 3d).

Local scale patterns in non-native plant abundance

The local scale study displayed the same type of trend in non-native plant richness and cover with distance from road as in the landscape scale study. At the local scale plots, decreases in non-native plant richness ($P < 0.01$) and the proportion of non-native plant cover ($P < 0.01$) were associated with increased distance from road (Fig. 4).

Local scale vegetative community characteristics away from the roadside

Increased distance from road was associated with increases in native plant species richness ($P < 0.01$) and the proportion of native plant cover ($P < 0.01$, Fig. 4). Plant litter cover decreased with distance from road ($P = 0.011$) and bare ground cover showed no significant trend with distance from the road ($P = 0.14$, Fig. 4). *B. inermis* cover decreased with increased distance from the road ($P < 0.001$) and increased litter was positively associated with the presence of *B. inermis* ($P < 0.001$) though these data are not shown.

Surrogate non-native plant emergence at the local scale

Fall radish seed emergence was found to be negatively associated with increased distance from the road ($P < 0.01$) for all years combined (Fig. 5). In 2003 (the only year in which site attributes were collected along with radish emergence data), percent cover of litter was found to be positively associated with fall radish emergence, after accounting for distance from road ($P = 0.003$), but there was no evidence of an association between native cover and SNP emergence.

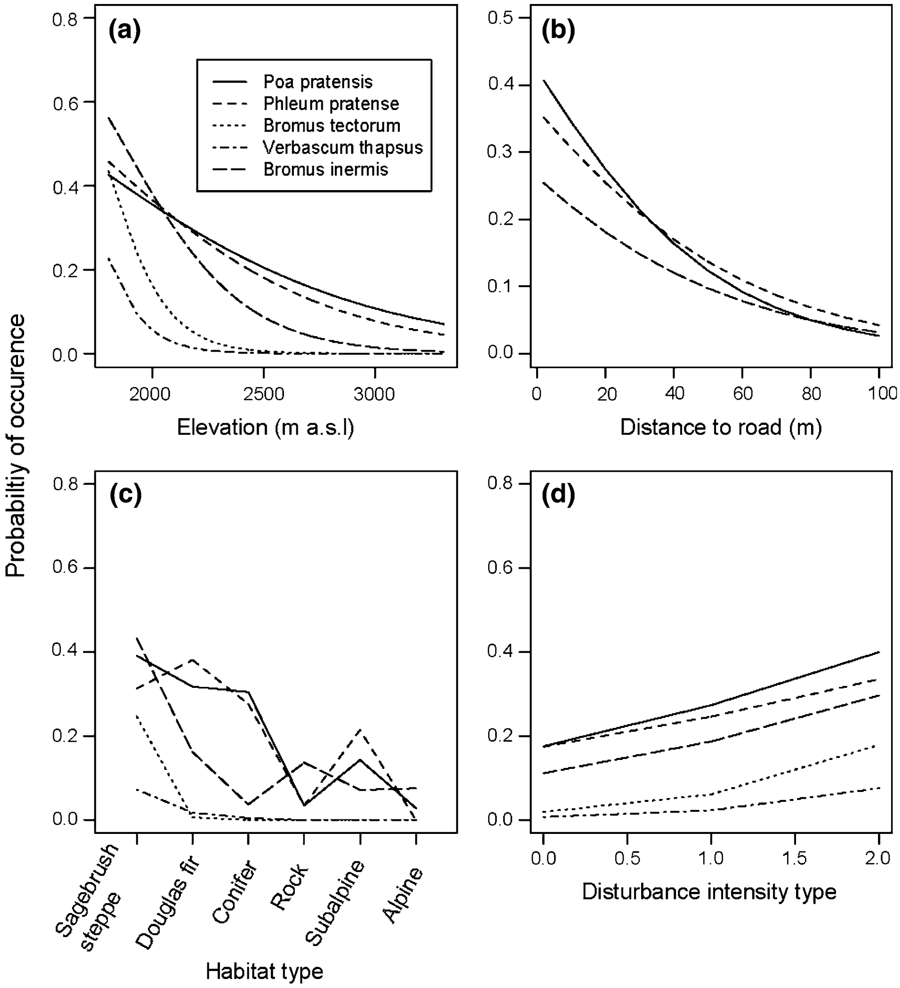


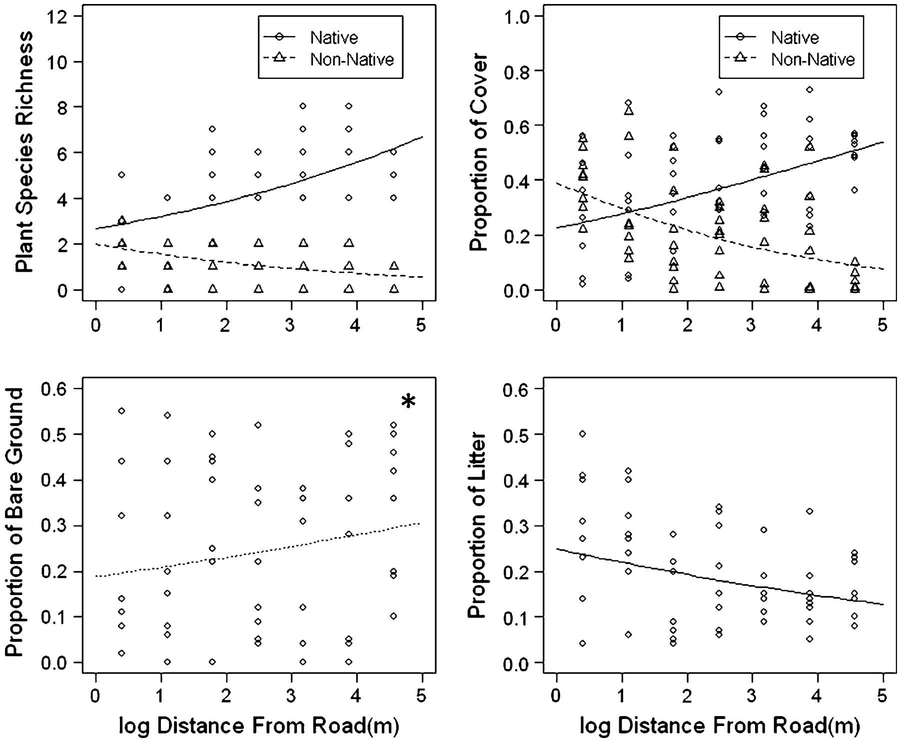
Fig. 3 Fitted probability of occurrence models of common species in relation to (**a**) elevation, (**b**) distance to road, (**c**) habitat type shown in the order they occurred along the elevation gradient, and (**d**) the estimated disturbance intensity within plots

Few radish seeds emerged during the spring trials, and there was no significant relationship between radish emergence and distance from road in the spring. There was no consistent pattern in radish seed predation. In 2003 there was a weak negative association with increased distance from road ($P = 0.09$), no association in 2004 ($P = 0.27$), and a positive association in 2005 ($P = 0.04$).

Discussion

Within the study area, the abundance of non-native plants close to roadways in the sagebrush steppe indicated that this was the most heavily invaded habitat. With increased elevation and changes in habitat, non-native plant species richness was reduced beginning in the closed conifer forest. The general decrease in non-native plant richness with increasing elevation is probably due to directional ecological filtering, where species are introduced into the low elevations and spread to higher elevations (Alexander et al. 2011). The result of the ecological filtering is that only species with broad environmental tolerances establish and survive across the gradient from low to high elevations (Alexander et al. 2011). In the case of the GYE, these were perennial rhizomatous grasses (*P. pratensis, P. pratense* and *B. inermis*), that were intentionally introduced to the region for livestock. In addition, increasing canopy closure presumably played a part in decreasing non-native plant richness with increased elevation and should be recognized as a filter of species, as has been theorized elsewhere (Martin et al. 2009). Similar findings, whereby non-native plant species richness was associated with both climate and habitat factors, have been noted by Haider

Fig. 4 Species richness, and proportion of cover, bare ground, and litter with distance from road in local scale plots. * This trend was not statistically significant ($P = 0.14$)



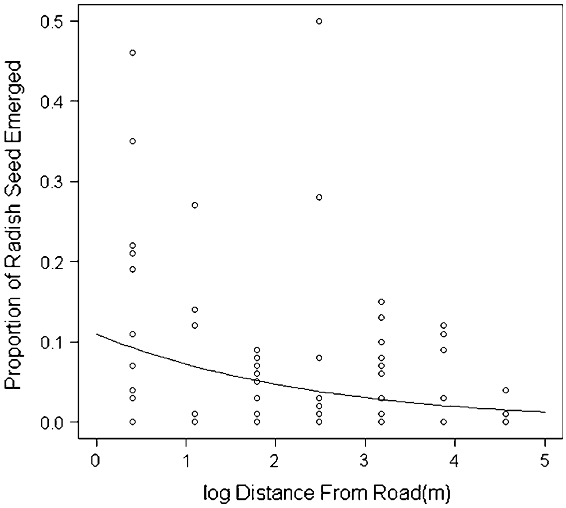


Fig. 5 Proportion of surrogate non-native plant seedlings that visibly emerged in soil during the fall field trials along a distance from road gradient

et al. (2010). Our results confirmed this, since the best fit model to explain non-native plant species richness also included habitat type. Thus, perhaps directional ecological filtering should include both biotic and abiotic factors as filters. With the possible movements of non-native plants in mountain systems divided into either vertical (along the elevation gradient) or horizontal (across the landscape within a limited elevation range) vectors, it seems that biotic factors would be more likely than abiotic factors to act as filters in the horizontal vector. However, it is possible that they could also act in conjunction with, or independently of, the abiotic factors that limit the vertical vector of movement under the current model of directional ecological filtering (i.e. less invasible biotic communities could also inhibit non-native plant movement upslope), as is suggested by our findings and the findings of Haider et al. (2010).

In contrast to higher elevation habitats, sagebrush steppe had comparatively favorable growing conditions due to lower elevation, relatively open canopy, greater frequency of human disturbance, and use by domestic and wild animals. All of these factors should make it easier for non-native plants to establish, and the increased level of non-native plant richness and abundance in this habitat, as shown by our data, support the concept of a less severe ecological filter in this area. As elevation increases, this region is subject to strong biotic and abiotic filters at the landscape scale. In our landscape scale data, there was a negative interaction between elevation and distance from road, indicating that non-native species richness declined away from the roadside more sharply as elevation increased. In general, this suggests that local scale invasion processes are influenced by local habitat, landscape context, and the interaction of the two. More specifically, as elevation increases, the abiotic/biotic environment may pose more challenges to successful establishment of non-native species, which may require more disturbance and/or more propagule pressure to overcome.

Examination of local scale SNP emergence specifically within the sagebrush steppe revealed that fall emergence decreased with increasing distance from the road. Since propagule pressure was constant, we can reject the null hypothesis of decreased propagule pressure as the sole factor resulting in a decrease in non-native plant species abundance/presence with increasing distance from roadsides. Thus, some other process related to the characteristics of the invaded habitat is responsible for limiting the presence of non-native species away from the roadside. Seed predation showed no consistent trend from year to year, and thus did not indirectly affect emergence with distance from the road via differential removal of propagules. Bare ground increased with distance from the road, but the decrease in SNP emergence with increasing distance from the road suggests that bare ground was not the limiting factor either. Several studies have shown positive associations between disturbance intensity and invasibility (Belote et al. 2008; Eschtruth and Battles 2009; Hendrickson et al. 2005; Hierro et al. 2006; Larson et al. 2001; Von Holle and Simberloff 2005), and negative associations between native species abundance and invasibility (Maron and Marler 2007; Naeem et al. 2000; Prieur-Richard et al. 2000, 2002; van Ruijven et al. 2003; Von Holle and Simberloff 2005). In our study, native plant species cover increased with distance from the road, possibly due to less disturbance intensity. This more intact and established native vegetative community could be making more complete use of the available resources (Davis et al. 2000; Grime 2002; Tilman et al. 1997), and thus limiting invasibility at increased distance from the roadside. This is supported by a study conducted in sagebrush steppe which found that non-native plant species cover was negatively associated with increased native plant cover, and that increased cover of perennial species appeared to increase resistance to invasion (Anderson and Inouye 2001). However, the increased emergence of the SNP species in areas closest to the road where the presence of other non-native species was greatest suggests that the sagebrush steppe in the GYE is only resistant to invasion as long as it remains relatively undisturbed, and is consistent with the fluctuating resource theory of Davis et al. (2000).

The amount of plant litter decreased with increased distance from the road. Most of this litter appeared to be from the non-native grass, *B. inermis,* which also decreased in cover with increasing distance from the road in the landscape study. It is impossible to say what is responsible for this trend, but increased moisture availability at the roadside (Hillel and Tadmor 1962) might have contributed to this phenomenon. We did not examine soil moisture extensively at this site, but a limited investigation of soil moisture from June through July of 2003 revealed that soil moisture decreased with distance from the road (Repath 2005). Thus, it is possible that increased soil moisture could increase plant biomass and consequently plant litter, and that the increased litter at the roadside could act as a protective layer (Schramm and Ehrenfeld 2010) conserving soil moisture in the relatively dry sagebrush steppe. While this could help to explain the increased emergence of the SNP closer to the road, the links between SNP emergence, soil moisture, *B. inermis* cover, and plant litter warrant further investigation if the drivers behind non-native plant invasions in the GYE are to be fully elucidated.

The presence of processes limiting the emergence of a SNP species which were associated with the biotic community at the local scale, coupled with the presence of similar trends across the habitats observed in the landscape scale study suggest that invasibility may be similarly influenced by biotic factors across the landscape. The interaction between elevation and distance from road in limiting the presence of non-native species further suggests that both abiotic and biotic factors influence the invasibility of habitats in mountain systems. Thus, while climatic factors may be primarily limiting the abundance of non-native plant species as elevation increases, other local scale biotic factors are also operating which further limit the presence of non-native plant species as distance from anthropogenic disturbances increases. Although the results of this study are context specific, if data are made available from similar studies conducted in different regions of the world, it will be possible for such data to be evaluated for the presence of general trends. Inclusion of local scale data would allow the concept of directional ecological filtering in mountain systems to be assessed and eventually modeled at multiple scales. Therefore, considering both landscape and local scale invasion processes in the future will provide a more complete picture of the phenomenon of non-native plant invasions in mountain systems.

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