

Life after establishment: factors structuring the success of a mountain invader away from disturbed roadsides

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Abstract Climate change and increased anthropogenic activity may both alter the current ranges of non-native plant species in mountainous areas, and could result in increased success of such species at higher elevations in the future. However, the course that management should take is often unclear due to a lack of information about the dynamics of how successful mountain invaders spread away from roadsides. The goals of this study were to determine if patterns of growth of a successful mountain invader, *Linaria dalmatica* (L.) Mill., (as measured by species cover) were: (1) similar to those of establishment (as measured by probability of occurrence), and (2) structured by the extant plant community. Study sites were established throughout the current elevation range of *L. dalmatica* in the Greater Yellowstone Ecosystem, and cover of the species was measured along with several vegetative community characteristics. Elevation influenced probability of occurrence

(i.e., chance of establishment) for *L. dalmatica*, but not cover (which represents growth after establishment). *L. dalmatica* cover was negatively associated with several vegetative community characteristics which did not appear to be influenced by the presence of *L. dalmatica*. These results suggest that *L. dalmatica* establishment may be limited by climate, but that spread of established populations away from roadsides is most influenced by properties of the vegetative community. They further suggest that the resident vegetative communities structure the abundance of this invader, and that to limit spread of this species in mountainous areas, disturbance to the existing vegetative communities should be minimized.

Keywords Climate change · Disturbance · Directional ecological filtering · Elevation gradient · Invasion resistance · Invasive species

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Introduction

The spread of non-native plant species in mountain systems has become a topic of increasing interest over the last decade due to the fact that these systems are not yet as heavily impacted by non-native plants as are lowland systems (Pauchard et al. 2009). The steep environmental gradients, and the recent nature of many plant species introductions, present mountain systems as a unique opportunity to examine the dynamics of non-native plant invasions (Becker et al. 2005;

Pauchard et al. 2009), and the anticipated changes to these areas in the near future add some urgency to elucidating the causes and effects of non-native plant spread. Climate change has the potential to alter the current range of non-native plants (Becker et al. 2005; Marini et al. 2009; McDougall et al. 2005; Pauchard et al. 2009) and could potentially result in increased success of non-native plants at higher elevations (Crimmins et al. 2009; McDougall et al. 2005). In addition, the increased use of mountainous areas by humans could result in more opportunities for non-native plant establishment due to an increase in dispersal vectors and suitable habitat (Hansen and Clevenger 2005; McDougall et al. 2009; Pauchard et al. 2009). However, there is currently no consensus related to the potential long term dynamics for non-native plants which have established in disturbed habitats, such as roadsides, in mountainous areas.

Although interest is generally focused on the effects of non-native plants on native plants (Brewer 2011; Chen et al. 2007; Collier et al. 2002; Ens et al. 2009; Flory and Clay 2010; French et al. 2011; Galbraith-Kent and Handel 2008; Vila et al. 2010), the direction of impact may be the opposite, in that native vegetation may affect non-native plant abundance. The concept of invasibility (i.e., how easily invaded by non-native plants a habitat is) as a property of native plant communities has been discussed extensively (Belote et al. 2008; Brown and Peet 2003; Davis et al. 2000; Lonsdale 1999; Maron and Marler 2007; Naeem et al. 2000; Prieur-Richard et al. 2000; Rejmánek 1989; van Ruijven et al. 2003; Walker et al. 2005; Wardle 2001). However, despite all of the interest in the concept of invasibility, studies quantifying the effects of the native community on individual non-native plant species abundance are less common than studies of the opposite relationship. If one is interested in patterns of non-native plant spread, determining if or how individual non-native plant species are influenced by extant plant communities and environmental characteristics can provide valuable insights which not only help to advance our knowledge of invasion dynamics in general, but help guide management as well.

A common trend seen in plant invasions in mountainous areas is that as one moves upslope, fewer and fewer non-native plant species are encountered (Alexander et al. 2011; Arevalo et al. 2005; McDougall et al. 2009; Pauchard et al. 2009; Pollnac

et al. 2012; Tassin and Riviere 2003). The theory of directional ecological filtering (DEF, Alexander et al. 2011) has described the general process underlying the observed trends in non-native plant species richness in these areas. DEF states that as elevation increases, the number of individual species from the lowland non-native plant species pool which can survive decreases due to different individual tolerances to climatic filters (Alexander et al. 2011). One of the main concepts of this theory is that, aside from the special case of introduced alpine species, individual non-native plant species that are successful invaders in mountain systems will be broadly adapted and capable of surviving in many different microclimates, occurring from low to high elevations along the corridor of introduction (Alexander et al. 2011).

Roadways have been described as ideal corridors for non-native plant species introductions (Gelbard and Belnap 2003; Pauchard et al. 2009; Pollnac et al. 2012), and DEF currently only addresses non-native plant species in disturbed roadside habitats. Exclusively examining roadsides allows for reliable quantification of the effects of climatic variables influenced mainly by elevation (Alexander et al. 2011). However, to gain a better understanding of non-native plant invasions at the landscape scale, it is necessary to consider how extant vegetative communities may or may not affect the growth of individual non-native plant species as they spread away from highly disturbed roadsides in mountainous areas (Pollnac et al. 2012). For example, can we assume that a non-native plant species will flourish in the surrounding environment if it has established along the roadside? Some studies suggest that this is not the case (Pollnac et al. 2012; Seipel et al. 2012), especially if there are additional sets of filters which come into play after establishment and movement away from roadsides. Thus, we need to determine if the dynamics of non-native plant species *after* moving away from the roadside are associated only with the same climatic filters structuring roadside establishment as discussed in Alexander et al. (2011); or, if growth after establishment is also related to plant community factors which could be more easily impacted by land use/management. To our knowledge, no other study has investigated the relationship between the extant plant community and the success of a species fitting the profile of a successful mountain invader as defined by DEF.

Several studies support the idea of climatic limitations to non-native plant establishment (Ansari and Daehler 2010; Griffith and Loik 2010; Ross et al. 2008). Other studies suggest that invader performance in both mountain and non-mountain environments can be influenced by properties of the plant community (Badano et al. 2007; Cavieres et al. 2007; Cavieres et al. 2008; Knight and Reich 2005; Larson et al. 2001; Maron and Marler 2007; Naeem et al. 2000; Pollnac et al. 2012; Prieur-Richard et al. 2000; Reinhart et al. 2006). However, since successful mountain invaders (i.e., those which are abundant at high elevations) are likely to be the most broadly adapted species (Alexander et al. 2011), perhaps they will not be as influenced by extant plant communities as a result of their broad adaptation to a variety of conditions. We focused on a species fitting the profile of a successful mountain invader as defined by DEF, *Linaria dalmatica* (L.) Mill., to determine what the fate of these types of species may be once they move beyond the roadside environment in mountain systems. Our objectives were: (1) to determine if patterns of growth (as measured by species cover) were similar to those of establishment (as measured by probability of occurrence) for this species, and (2) to determine if the growth of this species is structured by the extant plant community.

Methods

Study area and site selection

Three networks of linked roads were chosen as replicate elevation gradients (elevation transects) within the Northern Range of Yellowstone National Park (YNP), in the vicinity of Gardiner, MT (45°01'60"N, 110°42'33"W, 1,598 m elevation). During the growing season of 2008, the three elevation transects were surveyed for the presence of *L. dalmatica*, and an effort was made to identify every distinct population of *L. dalmatica* present within ~250 m of the elevation transects (roads) from the lowest to the highest elevation of occurrence of the species in the study area. Six *L. dalmatica* survey sites were then selected on each elevation transect to evenly represent the elevation range of the species from the lower limit of its range to the upper limit of its range. Six 1/4 m² vegetation survey plots were randomly

established within *L. dalmatica* populations at each one of the study sites. At each site, four additional 1/4 m² vegetation survey plots were randomly placed outside of but within 25 m of *L. dalmatica* populations. Within each of the vegetation survey plots, the percent of bare ground (including rocks), litter (including mosses and lichens), species richness, and percent cover of each plant species were recorded by a single observer during the growing season of 2011. Since individual species occurred in different layers of vegetation, total cover of each plot was not bounded at 100 %.

To investigate the patterns of establishment (i.e., probability of occurrence) of *L. dalmatica* along elevation gradients within the study area in general, data from the vegetation survey plots could not be used because plots were all selected in areas where *L. dalmatica* was established. Therefore, data from a comprehensive survey of the Northern Range of Yellowstone National Park (YNP) were used instead, where 379 transects (2,000 m by 10 m) beginning at and running perpendicular to roads or trails were surveyed for the presence of non-native plant species during four summers (2001–2004, Rew et al. 2005). The presence of non-native plant species was recorded using a global positioning system (GPS) unit and these data were then converted to occurrence (presence/absence) information for every 10 m by 10 m section of each transect. More detailed methods are described in Rew et al. (2005). Here, we selected only transects that started from roads (164 transects). For each of the 164 transects, 10 plots (10 m by 10 m) were randomly sampled from the 25 plots within 250 m of the road, in order to keep the survey area (near roads) consistent with the finer scale study.

Invasion patterns at the study site

Since the goal of this study was to investigate relationships between the extant vegetative community and a non-native plant species which would be classified as a successful mountain invader based on the ideas put forth by Alexander et al. (2011), it was important that we establish that DEF appeared to be occurring in the study area, and that *L. dalmatica* fit the profile of a successful mountain invader. Based on the methods described in Alexander et al. (2011), we completed an identical analysis of nestedness within *L. dalmatica*'s range in our study area using the

oecosimu function in R (R-Development-Core-Team 2011). We saw patterns of significant nestedness within the non-native plant species community moving from low to high elevations ($P < 0.001$, Nest = 37.2, $Z = 3.4$, Online Resource 1). In addition, *L. dalmatica*'s range width was significantly greater than the mean range width of native species within its current range ($P < 0.001$, $t = -16.4$, data not shown). This confirms that DEF is operating within our study area, and that *L. dalmatica* fits the profile of a successful mountain invader as described in Alexander et al. (2011).

Data analysis

Occurrence of L. dalmatica along the elevation gradient within the study area

R was used for all analyses (R-Development-Core-Team, 2011). Data from the 164 roadside YNP survey transects were used to estimate probability of occurrence in relation to elevation within the study area. Each plot had a binary presence/absence value for *L. dalmatica*, and this variable was regressed against elevation and its 2nd order polynomial term using a binomial generalized linear mixed effects regression with transect as a random factor (using the glmer function in the lme4 package).

Relationship between L. dalmatica cover and the vegetative community

Linaria dalmatica cover was logit transformed and used as the response variable in linear mixed effects regressions with site as a random factor to account for the six plots nested within each site (using the lme function in the nlme package). A simple model regressing *L. dalmatica* cover against elevation and the 2nd order polynomial of elevation was investigated first, based on previously noted trends in stem density for this species along elevation gradients (Pollnac and Rew, *In Prep.*). There was no suggestion that the data needed to be analyzed separately for each elevation transect, based on a lack of main effects of transect identity (ID) or interactions between elevation transect ID and any of the vegetative community predictor variables (Table 1) in preliminary analyses (data not shown). *Linaria dalmatica* was excluded from the data when calculating levels of species

richness, diversity, and cover for the predictor variables. Polynomial relationships between vegetative community variables and *L. dalmatica* cover were also examined for all of the vegetative community variables individually and determined to be unnecessary due to a lack of any statistically significant 2nd order polynomial terms. Hence each model contained only the individual vegetative community variable as a predictor of *L. dalmatica* cover.

Relationship between the vegetative community and L. dalmatica presence

Vegetative community variables listed in Table 1 were used as *response* variables in linear mixed effects models to evaluate if these vegetative community characteristics varied based on the presence of *L. dalmatica* within its current range of invasion. Response variables pertaining to percent cover were logit transformed. For each site, four out of six survey plots within *L. dalmatica* populations were randomly drawn from the dataset to pair with the four survey plots outside of *L. dalmatica* populations to achieve a balanced design. Predictor variables for these models were the type of plot (inside population or outside of population) and elevation, with site as a random factor.

Results

Occurrence of L. dalmatica along the elevation gradient within the study area

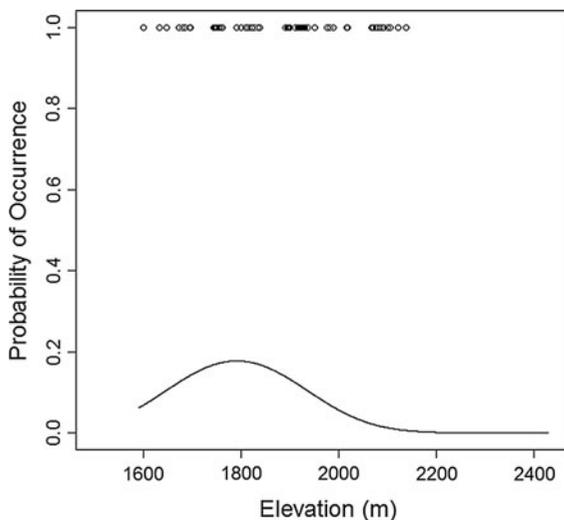
Probability of occurrence for *L. dalmatica* had a polynomial relationship with elevation ($P = 0.009$ and 0.005 , $Z = -2.62$ and -2.81 for elevation and elevation² respectively, Fig. 1). Establishment of this species is not very frequent on the landscape, but establishment rates peaked at $\sim 1,800$ m.

Relationship between L. dalmatica cover and the vegetative community

Native richness, total vegetation cover, and perennial cover were all negatively associated with *L. dalmatica* cover (Table 1). Non-native plant species richness had a positive association with *L. dalmatica* cover (Table 1). Elevation did not describe a significant portion of the variation in *L. dalmatica* cover

Table 1 Results of linear mixed effects models of individual vegetative community predictor variables versus logit *L. dalmanica* percent cover with site as a random effect

Predictor variable	Estimate	SE	df	F value	P value
Elevation	-6.38E-03	3.29E-02	1,15	0.001	0.97
+ elevation ²	1.58E-06	8.16E-06	1,15	0.037	0.85
Elevation	-5.51E-05	1.16E-03	1,16	0.002	0.96
Total richness	-0.11	0.06	1,50	-1.78	0.08
Native richness	-0.19	0.06	1,50	-2.92	<0.01
Non-native richness	0.33	0.14	1,50	2.35	0.02
Vegetation cover	-0.01	5.58E-03	1,50	-2.20	0.03
Perennial cover	-0.02	5.31E-03	1,50	-2.97	<0.01
Annual cover	0.02	0.02	1,50	1.28	0.21
Litter	-0.008	6.56E-03	1,50	-1.15	0.26
BARE ground	2.82E-04	4.81E-03	1,50	0.06	0.95
Diversity	-0.63	0.59	1,50	-1.07	0.29

**Fig. 1** *L. dalmanica* probability of occurrence predicted from Yellowstone National Park survey data collected perpendicular to and within 250 m of a road, within the Greater Yellowstone Ecosystem. *P* value for curve <0.05, *n* = 1,639. Points represent *L. dalmanica* occurrences

(Table 1). Several of these independent variables were also correlated with one another (data shown in Online Resource 2).

Relationship between the vegetative community and *L. dalmanica* presence

There was no evidence that any of the vegetative community variables differed between the type of survey plot (inside vs outside of *L. dalmanica*

population) except for non-native plant species richness (excluding *L. dalmanica*) and plant litter cover. There was weak evidence that mean non-native plant species richness was higher in plots inside *L. dalmanica* populations (Fig. 2a) after accounting for the effects of elevation. Mean native species richness for plots inside vs outside of *L. dalmanica* populations was identical at 4.7 species. There was strong evidence that percent plant litter cover was higher in plots outside of *L. dalmanica* populations (Fig. 2b) after accounting for the effects of elevation.

Discussion

Our preliminary analysis of *L. dalmanica* in the context of the vegetative community confirmed our assumptions that DEF was occurring in the study area (Online Resource 1). These results also showed that the patterns in community assembly which arise from DEF also manifest in areas away from the immediate roadside (between 5 and 250 m from the roadside in our case). This suggests that the patterns of establishment resulting from DEF which have been observed in roadside environments have, in this case, persisted into more intact vegetation communities. Therefore, DEF is also operating to some extent in these areas away from the road, and is not completely obscured or overridden by other additional filters.

Our first objective was to determine if patterns of growth were similar to those of establishment for *L.*

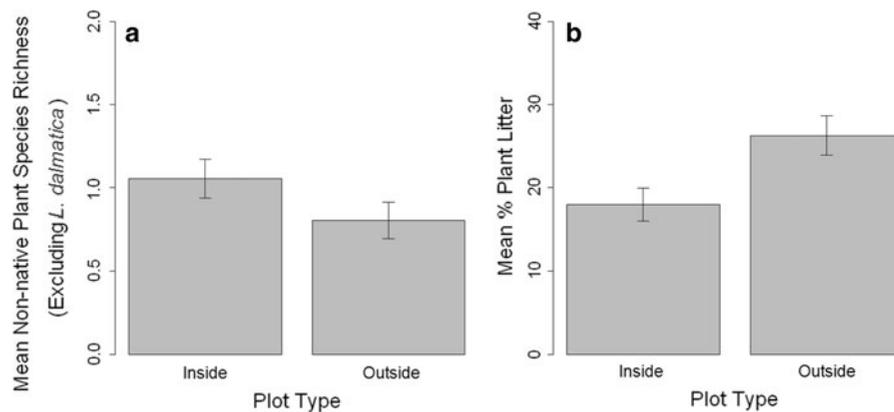


Fig. 2 **a** Mean non-native plant species richness with standard error bars by plot (0.25 m^2). P value for difference in means from model = 0.06, $F = 3.63$, $df (1, 125)$. **b** Mean percent plant litter cover with standard error bars by plot (0.25 m^2). P value

for difference in means from model = 0.001, $F = 10.79$ $df (1, 125)$. Inside = inside of *L. dalmatica* patch ($n = 72$), Outside = outside of *L. dalmatica* patch ($n = 72$)

dalmatica, which would indicate that establishment and growth are both influenced directly or indirectly by the same set of climatic or abiotic filters. The idea that establishment is related to elevation linked factors was confirmed by the significant hump shaped association between elevation and probability of *L. dalmatica* occurrence which indicated that the probability of establishment decreased at both ends of the current elevation range of *L. dalmatica* and peaked at the interior of its current range. Similar trends have been found for the relationship between non-native plant species richness and elevation in the same study area (Alexander et al. 2011; Pollnac et al. 2012), and in other parts of the world (Alexander et al. 2011; Haider et al. 2010; Pauchard et al. 2009), which result from individual non-native plant species having decreasing or hump shaped patterns of probability of occurrence with increasing elevation. However, we did not find that *L. dalmatica* cover was associated with elevation, despite the fact that stem density (Pollnac and Rew *In Prep*) and probability of occurrence were both associated with elevation (the stem density association was hump shaped in some years, and positive in others). This lack of association reinforces the fact that stem density/probability of occurrence and percent cover measure different aspects of success. Stem density provides some measure of establishment/reproductive success, as does probability of occurrence, in that each stem or presence represents the successful establishment of a seedling or a vegetative ramet. Cover is generally related to stem density, but it also

incorporates the growth or vigor of individuals. Thus, we can only hypothesize that the lack of association between *L. dalmatica* cover and elevation is due to differential vigor of individuals along the elevation gradient. More importantly, it suggests that while establishment may be influenced by factors or processes closely related to elevation, as suggested by DEF (Alexander et al. 2011), vigor is influenced by additional factors or processes. Thus, the filters proposed by DEF which limit establishment of non-native plant species are apparently not the only filters operating in this mountainous area away from the roadside. This agrees with the suggestions that: (1) non-native plant species are probably influenced by both abiotic and biotic factors along elevation gradients (Haider et al. 2010; Pollnac et al. 2012), and (2) that it will be necessary to consider biotic factors if attempts are made to examine DEF in plant communities outside of the immediate roadside environment (Pollnac et al. 2012).

Other studies have shown that biotic factors can either facilitate (Badano et al. 2007; Cavieres et al. 2007, 2008) or hinder (Pollnac et al. 2012; Reinhart et al. 2006) non-native plant invasions in mountainous areas. In the case of *L. dalmatica*, cover of this species was negatively associated with native richness, total vegetation cover, and perennial vegetation cover along the elevation transects. Other studies have shown similar relationships, whereby the success of a single non-native plant species was negatively associated with vegetative community characteristics such as

species richness or diversity (Knight and Reich 2005; Maron and Marler 2007; Ortega and Pearson 2005; Prieur-Richard et al. 2000).

In our observational study, we could not establish the direction of influence from the relations between *L. dalmatica* cover and the vegetation community variables alone (i.e., was *L. dalmatica* cover limited by increases in these variables, or were these variables decreased by increased *L. dalmatica* cover?). Therefore, our last analysis was conducted specifically to test the null hypothesis that the presence of *L. dalmatica* had no effect on mean levels of the vegetative community variables. If the associations described above were structured by the vegetative community, one would expect that the presence of *L. dalmatica* would, for example, have no association with mean perennial cover, indicating that *L. dalmatica* is essentially filling in gaps in the community instead of possibly displacing other species. We found no differences based on *L. dalmatica* presence in the mean levels of any of the vegetative community variables with which *L. dalmatica* cover was negatively associated, lending support to the idea that once *L. dalmatica* spreads beyond the immediate roadside environment, it begins to be subjected to another set of filters associated with the extant plant community.

Both presence and cover of *L. dalmatica* were positively associated with non-native plant species richness, suggesting that either there is a facilitative relationship between *L. dalmatica* and other non-native plant species, or that other non-native plant species are simply responding favorably to the same conditions that promote the presence and growth of *L. dalmatica*. Mean litter cover was higher in plots outside of *L. dalmatica* patches, but litter cover was not associated with *L. dalmatica* cover. The lack of association between litter and *L. dalmatica* cover indicates that while litter is linked to the establishment or presence of this species, it is not influential on, or influenced by, the growth of established individuals. In other studies, plant litter has been shown to decrease establishment (Bartuszevige et al. 2007; Hager 2004) and alternatively to increase survival (Schramm and Ehrenfeld 2010) of non-native plants. Since non-native plant species richness was negatively associated with plant litter in our study area (data not shown), further evaluation of the role of plant litter with native and non-native plant species germination and survival is necessary. However, at present our data

suggest that once species like *L. dalmatica* move beyond the immediate roadside environment, their success may be largely dependent upon how intact the native plant community is, and therefore dependent upon further disturbance (MacDougall and Turkington 2005; Maskell et al. 2006).

Management implications

Linaria dalmatica has proven to be a broadly adapted mountain invader. Dispersal of this species into higher elevation areas is not limited, as it is primarily wind dispersed (Robocker 1970), and the location of this species at roadsides presents additional opportunities for both dispersal on motor vehicles (Clifford 1959; Pickering and Mount 2010; Veldman and Putz 2010; Von der Lippe and Kowarik 2007; Wichmann et al. 2009; Zwaenepoel et al. 2006; Taylor et al. 2012) and establishment in disturbed areas along roadsides (Arevalo et al. 2005; Arteaga et al. 2009; Hansen and Clevenger 2005; Hendrickson et al. 2005; Paiaro et al. 2011; Pollnac et al. 2012; Seipel et al. 2012; Veldman and Putz 2010). Although perennial plants dominate in alpine areas (Körner 2003) and could potentially limit the success of *L. dalmatica*, total vegetation cover in the subalpine/alpine zone was found to be lower than within the current range of *L. dalmatica* within the study area (Pollnac and Rew *In Prep*). Since *L. dalmatica* cover showed a positive association with decreased vegetation cover, this species should be managed at its high elevation limits to prevent spread into alpine areas unless some limitation to its establishment there is quantified in the future. At present, there is no indication that population growth rates for *L. dalmatica* are lower at its high elevation limits (Pollnac et al. 2013), but there is some indication that lower germination rates (Pollnac and Rew *In Prep*) and cold temperatures (Pollnac et al. 2013) could potentially limit establishment at higher elevations. However, perennial and general vegetation cover should be conserved to limit spread of this species.

Because introduced species need time to spread as described by DEF, questions about newly introduced species cannot be addressed by this theory unless their climatic tolerances are already known. However, examining *established* non-native plant species in the context of DEF can be very useful. If a species fits the profile of the broadly adapted mountain invader as

specified by DEF (Alexander et al. 2011), there may be nothing aside from dispersal opportunities constraining the species from spreading higher or lower along the gradient. Without any information indicating dispersal limitations, or that the alpine area is less invulnerable for the species due to biotic or abiotic factors, upper populations should be actively monitored for invasiveness and managed as appropriate, and protocols should be implemented (washing of vehicles and limiting access, see Fleming 2008; Pickering and Mount 2010; Taylor et al. 2012) to prevent further spread into alpine environments. For established non-native plant species which do not fit the wide range pattern and have narrow or comparable range widths in comparison to native species, this suggests very poor dispersal or relatively narrow environmental tolerances, making rapid spread beyond its current range unlikely unless dispersal is augmented or the species undergoes some form of adaptation (Becker et al. 2005; Gaston 2003). Such species should be a lower priority for managers unless dispersal is likely to increase.

Conclusions

Directional ecological filtering has shed light on patterns of declining non-native plant species richness with increased elevation that have been noted in mountainous areas for at least the last decade, and has provided a solid conceptual framework that will facilitate the development of further ideas regarding the dynamics and management of the spread of non-native plants in mountain systems. Most importantly, it has done so in a timely fashion which will hopefully allow us to respond effectively. Our study has shown that the filters associated with DEF operate in areas away from the roadside for a successful mountain invader, but in conjunction with other filters (vegetation cover, native species richness, and perennial cover in our case). In general, discovering what other filters, if any, are limiting non-native plants away from the roadside environment could potentially provide managers with great insights with regard to if or how these non-native plant species can be effectively managed in mountain environments. Although the invasibility of alpine areas is largely unquantified, these areas are not as immune to invasions by non-native plants as they were once thought to be (McDougall et al. 2009, 2011;

Pauchard et al. 2009). Given the value of mountain systems as repositories of plant diversity and endemism (Körner et al. 2011), timely action could be extremely important if these areas are to be protected from degradation associated with the expansion of non-native plant species in the future.

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