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Contrasting distribution patterns of invasive and naturalized non-native species along environmental gradients in a semi-arid montane ecosystem

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Keywords

Community assembly; Disturbance; Elevation gradient; Functional groups; Habitat filtering; Non-native species; Plant invasions; Species turnover

Abbreviations

AWC = available water capacity; DD < 0 = degree days below 0 °C; DD > 5 = degree days above 5 °C; DD > 18 = degree days above 18 °C; MAP = mean annual precipitation; MCMT = mean coldest month temperature; MIREN = Mountain Invasion Research Network; MWMT = mean warmest month temperature; PCCA = partial canonical correspondence analysis.

Nomenclature

Boyle et al. (2013)

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Introduction

Temperature, precipitation and soil fertility change with elevation and are important abiotic factors determining

Abstract

Questions: Mountain systems have high abiotic heterogeneity over local spatial scales, offering natural experiments for examining plant species invasions. We ask whether functional groupings explain non-native species spread into native vegetation and up elevation gradients. We examine whether non-native species distribution patterns are related to environmental variables after controlling for elevation and, thus, driven by niche processes.

Location: The Wallowa Mountains, northeast Oregon, USA.

Methods: We surveyed non-native plant species along three mountain roads and into the native habitat matrix to assess the extent of invasion success along distance from roadside and elevation gradients. We used GLM to predict single species occurrence probabilities, LMM to examine differences in distribution patterns among functional types, and pCCA to examine multivariate responses of the non-native community to ecological variables.

Results: Probability of occurrence of the eight focal invasive species was not significantly related to distance from the road, but declined with elevation. Non-native species with annual life history strategies were more restricted to lower elevations than perennial species. Non-native species considered invasive occurred at lower minimum elevations than naturalized species. Shifts in the species composition of the non-native plant community were related to changes in soil and climate variables.

Conclusions: Our results suggest that invasive species have similar patterns of habitat associations and spread from roadsides to interior vegetation zones, whereas naturalized species partition environmental gradients in this semi-arid montane ecosystem. Furthermore, annual and invasive species groups occupy lower elevations and perennial and naturalized species groups have invaded further up the mountain roads and into the native vegetation. Thus, functional groupings may explain contrasting distribution patterns of non-native species and could be used to inform management strategies for non-native species.

species distribution and function (Raich et al. 1997; Kelly & Goulden 2008). Studies along elevation gradients have enormous potential for understanding processes shaping plant communities and how they may be expected to

change with shifts in temperature and precipitation regimes due to global climate change. For example, species elevational ranges have shifted over the last several decades due to changes in precipitation and temperature regimes (Kelly & Goulden 2008; Harrison et al. 2010; Felde et al. 2012). Furthermore, species richness often peaks at low to mid-elevations and decreases rapidly at higher elevations. Habitat filtering and dispersal limitation may drive rapid species turnover along elevational gradients (Kraft et al. 2011; Swenson et al. 2011; de Bello et al. 2013). Thus, understanding which environmental factors influence species distribution patterns would inform projections for shifts in their distributions, given current climate change scenarios.

Understanding the spread of non-native plant species along elevational gradients also has important implications for mechanisms determining community assembly (Pauchard & Alaback 2004; Pauchard et al. 2009; Alexander et al. 2011; Pyšek et al. 2011). Similar patterns of decreasing species richness with increasing elevation have been documented across sites for non-native plant species (Pauchard et al. 2009; Seipel et al. 2012) and native species (Alexander et al. 2011). Habitat filtering and specialization may drive native plant species composition along elevation gradients, whereas 'directional ecological filtering' (*sensu* Alexander et al. 2011) has been identified as a key process in determining compositional changes with elevation for non-native species. Generally, non-native species pools are highest near lowland anthropogenic sources, with species dropping out of the community with increasing elevation (Alexander et al. 2011). Species found at higher elevations were a subset of those found at lower elevations, suggesting that species with wider ecological tolerances were those found at higher elevations, rather than high-elevation specialist species (McDougall et al. 2010).

The Willowa Mountains in northeast Oregon has a high representation of globally successful invaders (McDougall et al. 2010; Alexander et al. 2011; Seipel et al. 2012), allowing the examination of habitat preferences and patterns of invasion of these species at a common site. Here, non-native plant species richness is relatively high and declines as a function of the interaction between elevation and linear distance to the road (Alexander et al. 2011; Seipel et al. 2012). Most non-native species are restricted to the lower half of the elevational gradient (Alexander et al. 2011) and near roadsides (Seipel et al. 2012). However, the distribution patterns of the most common invaders and the mechanisms behind this filtering process have not been previously explored.

Performance-related traits have been related to invasiveness across multiple studies (van Kleunen et al. 2010; Kuester et al. 2014) and may be important in determining invasion along environmental or disturbance gradients.

Recent meta-analyses and trait-based assessments of large-scale data sets have shown that there are suites of functional traits that distinguish invasive species from naturalized species (van Kleunen et al. 2010; Kuester et al. 2014). In particular, invasive species often have higher rates of reproduction and vegetative spread, achieved by a combination of higher growth rates, and are more likely to have annual life-history strategies, greater dispersal abilities and overall fitness levels as well as increased tolerance to stressful soil conditions (van Kleunen et al. 2010; Kuester et al. 2014). Understanding differences in ecological traits between invasive and naturalized non-native species can be useful in achieving ecological restoration goals (Laughlin 2014).

We use a functional approach to better understand the abiotic drivers structuring the non-native plant community along elevation gradients and distance from roads. Specifically, we examine whether distribution patterns of non-native species are driven by random (spatial distance) or deterministic (habitat filtering) processes. If stochastic processes drive non-native species distribution patterns, we expect probability of occurrence to decline predictably with increasing distance from roadside and increasing elevation. If non-random processes drive non-native species distribution patterns, species turnover should be related to one or more environmental variables after controlling for differences in elevation. We address the following questions to evaluate the roles of abiotic variables and functional types in driving patterns of invasion in the Willowa Mountains: (1) do common invaders have predictable distribution patterns along roadside or elevation gradients; (2) does plant functional type or invasive status of non-native species influence spread into native vegetation or elevational range; and (3) does elevation alone explain changes in non-native community composition or can we identify environmental variables that are important in determining non-native species turnover? We use life-history strategy and life-form groupings as proxies for plant functional trait differences. Together, these questions will help managers identify whether function groups and environmental variables explain pathways of invasion of non-native plant species.

Methods

Site description and data collection

The study was conducted in the Willowa range of the Blue Mountains in northeast Oregon, USA (45°18' N, 117°48' W) as part of a global investigation documenting plant invasions in montane systems by the Mountain Invasions Research Network (MIREN) (McDougall et al. 2010; Alexander et al. 2011; Seipel et al. 2012). Elevation ranged from 900 to 2500 m a.s.l., mean annual temperature

ranged from 2.8 to 9.2 °C, and mean annual precipitation ranged from 608 to 1460 mm (Table 1). Natural vegetation of the area ranged from bunchgrass communities at low elevations to conifer-dominated sub-alpine forests (Parks et al. 2005). However, the lowland (<1000 m) habitat matrix was heavily used for cattle ranching, timber extraction and agriculture. Much of the area has been designated as public lands managed by the USDA Forest Service, particularly at mid- to high elevations.

Three roads separated by 10–60 km with similar environmental conditions and traffic loads were selected to maximize elevational range within an 80 km region of the Wallow Mountains (Table 1, Appendix S1). Non-native vegetation was sampled during Aug and Sept 2007, following standardized protocols (see Appendix S1 in Seipel et al. 2012). Each road was divided into 19 equally spaced elevational sections for a total of 20 sampling locations. At each location, 'T-transects' consisted of one 2 × 50 m transect set parallel to the road and a 2 × 100 m transect set perpendicular to the road, beginning at the mid-point of the roadside transect. Transects were divided into 2 × 10 m subplots ($n = 900$) to record all non-native species.

We supplemented field data with geospatial layers to examine plant invasion patterns with climate parameters and geographic position. Topographic variables were extracted from digital elevation models (DEM; Gesch et al. 2002). Latitude, longitude and elevation for each transect were used to estimate values for climate variables from the Parameter-elevation Regressions on Independent Slopes Model, with an 800-m resolution (PRISM; Daly et al. 2002). We used the 30-yr mean values from 1981–2010 and derived climate variables from the program ClimateWNA (Wang et al. 2012). Soils and geology data were extracted from Natural Resources Conservation Service Web Soil Survey at a 1:24:000 scale for Union and Baker counties and Willowa-Whitman National Forest (websoil-survey.nrcs.usda.gov).

We extracted species 'trait' data from plant databases, including life-history strategy (annual/perennial), growth form (forb, grass, shrub), invasion status ('invasive' and 'naturalized'; Whitson et al. 2012; GRIN www.ars-grin.gov; INVADERS invader.dbs.umt.edu; Oregon Department of Agriculture www.oregon.gov/ODA/PLANT/WEEDS/lists.shtml#Noxious_weed_policy_list). Non-native species were defined as any species introduced after AD 1500 and were verified using the PLANTS database (plants.usda.gov), Oregon Vascular Plant Checklist (www.oregonflora.org) and the Taxonomic Name Resolution Service (TNRS tnrs.iplantcollaborative.org; Boyle et al. 2013). Invasive status was determined from multiple sources (Appendix S2). The term 'invasive' encompassed those non-native species that are most likely to become problematic in our study region. These species had a high

Table 1. Site characteristics of the three roads sampled. Latitude and longitude are for the lowest elevation transect for each road, all other values represent the mean (±SE), minimum and maximum values recorded along the road. Location and elevation data were extracted from digital elevation models (Gesch et al. 2002) and climate variables were estimated based on transect location using the program ClimateWNA (Wang et al. 2012) and 1961–2010 climate data extracted from PRISM (Daly et al. 2002).

Road	Latitude	Longitude	Elevation (m a.s.l.)	MAT (°C)	MWMT (°C)	MCMT (°C)	MAP (mm)	Number of frost free days
Fish Lake (FL)	44°56'51" N	117°7'40" W	1652 ± 85.4	5.7 ± 0.4	17.4 ± 0.5	-5.5 ± 0.2	1094 ± 51.5	164 ± 5.2
		Min	1043	2.8	13.8	-7.0	691	126
Mount Harris (MH)	45°22'18" N	117°53'36" W	1471 ± 79.4	6.5 ± 0.3	17.5 ± 0.3	-3.3 ± 0.2	976 ± 59.4	196 ± 3.8
		Min	904	4.2	15.1	-4.9	608	163
Moss Springs (MS)	45°17'5" N	117°45'11" W	1656 ± 71.1	5.5 ± 0.3	16.1 ± 0.3	-4.4 ± 0.2	1214 ± 34.8	176 ± 5
		Min	1161	3.4	14.0	-6.0	881	141
		Max	2163	7.5	18.3	-2.8	1374	208

MAT, mean annual temperature; MWMT, mean temperature of the warmest month; MCMT, mean temperature of the coldest month; MAP, mean annual precipitation.

probability of spread and ability to maintain self-sustaining populations and were often of management concern where they occur. The term 'naturalized' described all other non-native species along the invasion process (Blackburn et al. 2011; Simberloff et al. 2013). Overall, 41 species were categorized as naturalized and 35 species were categorized as invasive under these specifications. We examined whether these invasion status designations were related to extent of spread up the elevation gradient and into the native vegetation matrix.

Statistical analyses

Predicted distributions patterns of globally common invaders

We modelled the probability of occurrence of eight frequently encountered species to examine the extent to which the Wallowa Mountains ecosystem has been invaded by locally and globally problematic non-native species (Appendix S2). We selected two species of each combination of annual/perennial and forb/grass functional groups to model the probability of occurrence with increasing elevation and distance from the main road using GLM with binomial errors and logit link function fit for each species and variable separately using the 'glm' function. Species presence/absence data were pooled by transect ($n = 60$) for elevation and by distance classes starting at the roadside to 100 m for each road ($n = 33$).

We used variance partitioning to gain a better understanding of how patterns of species abundances varied across the hierarchical spatial scales of the study. For each of the eight focal species, we fit a LMM to examine variance in species abundance across the nested random effects of road, transect and subplot using the function 'lme' in the R package nlme. We used the function 'varcomp' in the R package 'ape' to extract the variance components of each of the nested random effects in the model (Paradis et al. 2004). All statistical modelling was conducted in R (R Foundation for Statistical Computing, Vienna, AT).

Patterns of invasion in mountain systems

We extracted maximum distance from the road and minimum and maximum elevation of occurrence for all 76 species from the survey data. For distance from road, values were calculated based on 11 binned distance categories of the transect subplots for each road (0, 5, 15, 25, 35, 45, 55, 65, 75, 85, 95 m). Distance from road data were pooled across elevations because most spread into the vegetation matrix occurred at lower elevations (Seipel et al. 2012). ANOVA was used to test for differences in maximum distance from the road, minimum and maximum elevation of occurrence

based on species life-history strategy (annual or perennial), growth form (grass or forb) and invasion status (naturalized or invasive), as well as combinations of these groups. Model reduction was based on AIC values using a forward and backward step-wise procedure.

Community-wide shifts along environmental gradients

To examine the multivariate influence of climate, soil and topographic parameters on species turnover we performed partial constrained Canonical Correspondence Analysis (pCCA) ordination using species presence/absences in each transect as the dependent variable and elevation as a co-variable. The maximum fitted pCCA models included variables identified as significantly correlated with changes in the plant community in Mantel tests (Appendix S3). We conducted a permutation-based step-wise model building procedure for constrained ordinations to find the environmental variables most related to changes in the plant community. Model selection was based on metrics resembling a deviance measure and permutation tests (with 999 permutations) were used to determine the *P*-values of the final models. The pCCA allowed us to remove the effect of elevation on community structure and examine the variation in the community that can be explained by the climate and environmental variables. We extracted the site pCCA scores to examine correlations with environmental variables, and the species pCCA scores to compare the homogeneity of variance of the first two pCCA axes of naturalized and invasive species. We used Pearson correlation tests to examine among-transect relationships between species richness, site-based pCCA scores, topographic, soil and climate variables. All pCCA tests were conducted using functions in the R package 'vegan'.

Results

Predicted distributions patterns of globally common invaders

All eight species occupancy models showed that probability of occurrence declines with increasing elevation ($P < 0.05$), but not distance from the road (Fig. 1). The annual grasses dropped out of the community by 1500 m a.s.l., whereas the two annual forbs are predicted to maintain a low probability of occurrence at the highest elevations (Fig. 1a). Perennial species decreased in probability of occurrence with increasing elevation, but with lower intercept (non-significant for *Bromus inermis*) and slope values (Fig. 1b). *Cirsium arvense* maintained a probability of occurrence >0.1 through the highest elevations. In contrast, distance

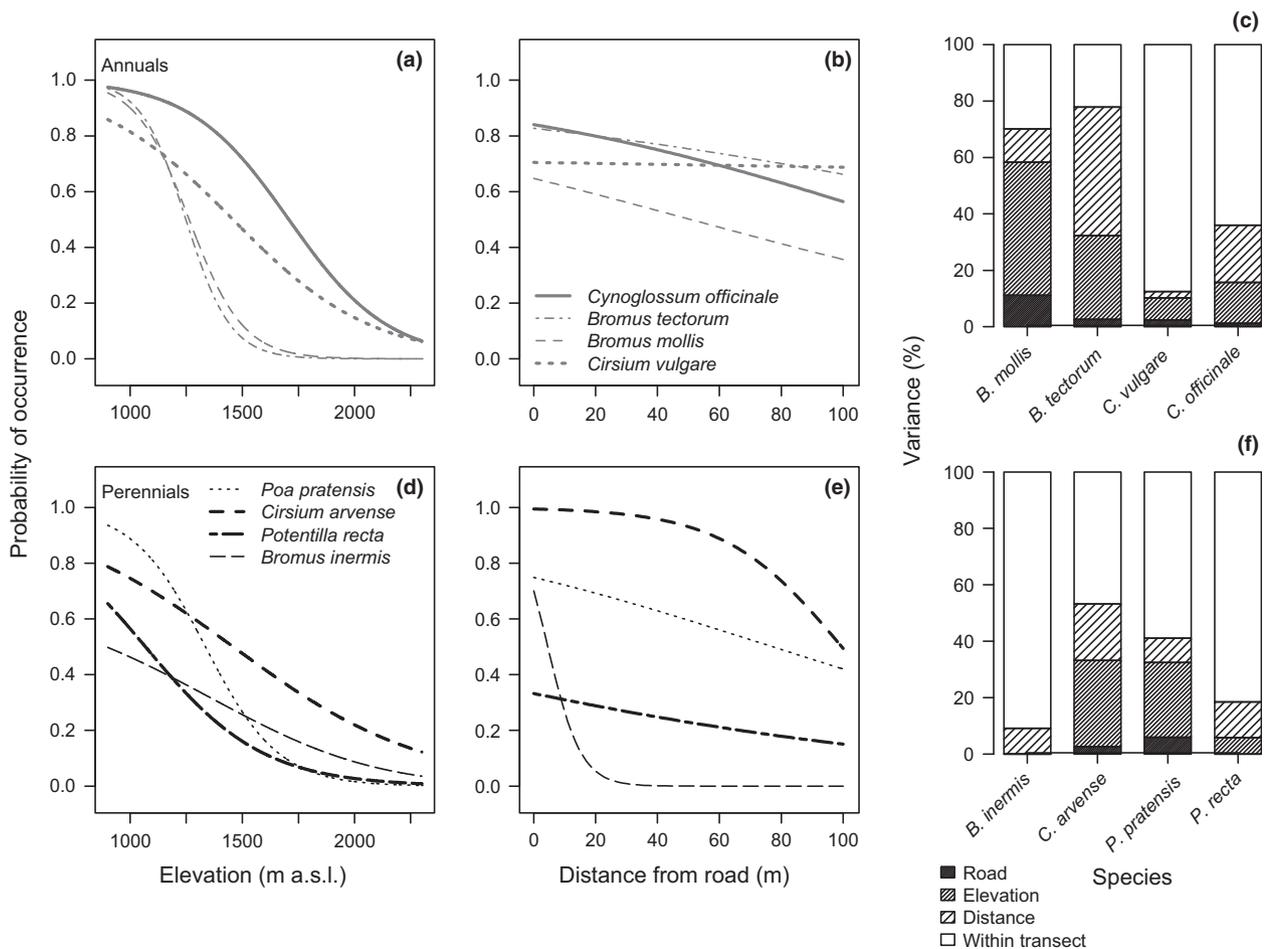


Fig. 1. Probability of occurrence of eight common invasive species. Probability of occurrence of annual and biennial species (a–c; grey) and perennial species (d–f; black) with increasing elevation based on presence/absence for each transect (a, d; $n = 60$) or with increasing distance from the road based on presence/absence in each distance class across all transects per road (b, e; $n = 33$). Percentage of the total variance in species abundance found at each level of the hierarchical sampling regime for (c) annual and (f) perennial species ($n = 900$).

from road was not a good predictor of occurrence for any species (Fig. 1c,d). Species showed little change in probability of occurrence with increasing distance from the road except for *B. inermis*, which declined rapidly over the first 20 m from the side of the road and *C. arvense*, which declined after 50 m from the road.

Variance in species abundances was not distributed evenly across the different spatial scales and shows the patchiness of species distribution patterns (Fig. 1e,f). The majority of the variation in species abundance was at the finest spatial scale, within-transect, which accounted for 22–90% of the variance. Distance from the road accounted for 2–20% of the variance in species abundances, except for *Bromus tectorum* for which it accounted for 46% of the variance. Elevation accounted for 6–47% of the variance in species abundance, except for *B. inermis* for which most of the variance is explained at smaller spatial scales. Road,

the largest spatial scale, accounted for just 11% of the variation in abundance for any of top eight invasive species.

Patterns of invasion in mountain systems

Spread into natural vegetation

The majority of the non-native species were recorded from the roadside to interior vegetation sites. Nonetheless, we found that 25% of the species recorded were restricted to the roadside (<20 m from the road), whereas only 7% of the species were restricted to interior sites. Invasive species spread significantly further into the native vegetation than naturalized species ($F = 6.50$, $P < 0.05$), regardless of life-history strategy. However, this pattern was only significant for perennial species, for which all but two species occur in all the subplots from the roadside to the furthest subplots from the road (Fig. 2a).

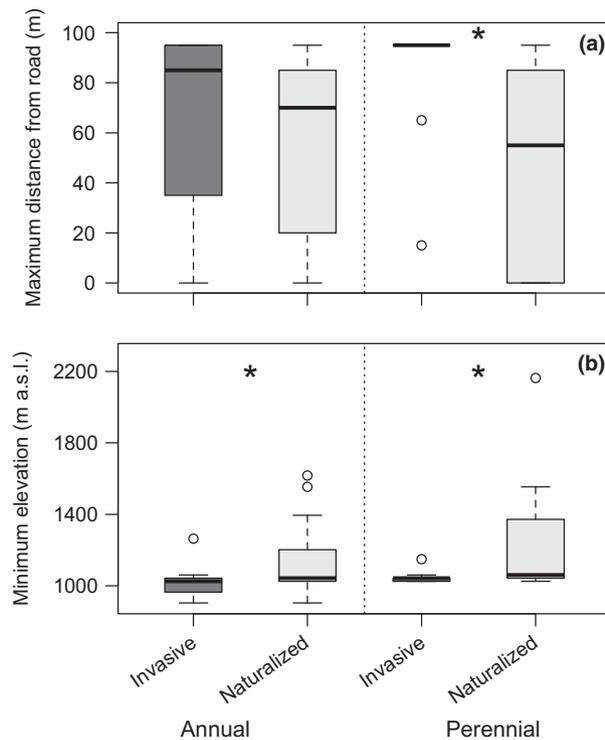


Fig. 2. Maximum distance from road and minimum elevation. **(a)** Invasive species (dark filled symbols) spread significantly further into interior vegetation than naturalized species (open symbols; $F = 6.5$, $P < 0.05$), especially for perennial species. Box plots with the median, 25 and 75% quantiles with whiskers extending to 2 SD of the minimum elevation where species occurred. **(b)** Invasive species had lower minimum elevation of occurrence than naturalized species for both life-history stages. Annual species had lower minimum elevation of occurrence than perennial species ($F = 4.96$, $P < 0.05$). Asterisks denote significant differences between the invasion status groups ($P < 0.05$).

Elevation

Life-history strategy, invasive status and growth form influenced the minimum and maximum elevation of non-native species. Perennial species had higher minimum elevation of occurrence compared to annual species (Fig. 2b; mean elevation difference = 96 m a.s.l.; $F = 4.96$, $P < 0.05$). Across both life-history strategies, species in the invasive category had a lower minimum elevation of occurrence compared to naturalized species (mean elevation difference = 141 m a.s.l.; $F = 11.24$, $P < 0.01$). Species with perennial life-history strategies also reached a higher maximum elevation compared to species with annual life-history strategies (Fig. 3; mean elevation difference = 382 m a.s.l.). The final model for maximum elevation of occurrence included life-history strategy ($F = 27.06$, $P < 0.0001$), growth form ($F = 0.89$, $P > 0.1$) and invasive status ($F = 2.18$, $P > 0.1$), but only life-history strategy groups differed significantly in maximum elevation.

Community-wide shifts along environmental gradients

Most environmental variables were correlated with elevation (Appendix S4). Transect (site) scores for CCA 1 were positively correlated with elevation, canopy openness and precipitation variables, and negatively correlated with soil pH and temperature variables (Appendix S4). Transect (site) scores for CCA 2 were positively correlated with slope and soil clay content, and negatively correlated with available water-holding capacity of soil, soil silt content and soil organic matter content. Floristic similarity was correlated with differences in elevation among transects, as well as with differences in most environmental variables (Appendix S3). The pCCA revealed that changes in temperature-related variables, mean annual precipitation (MAP), soil moisture (AWC), soil texture (clay) and canopy openness among the sites explained 35% of the variation in species composition, with elevation explaining an additional 13% (Fig. 4, Appendix S5). Invasive species CCA scores had a narrow distribution along CCA 2 whereas naturalized species CCA 2 scores had a higher variance ($F = 0.16$, $P < 0.0001$). Variances in CCA 1 scores and mean CCA scores were similar for invasive and naturalized species. Annual species shifted towards positive values along CCA 1, whereas perennial species were clustered along the centroid ($t = 2.02$, $P < 0.05$).

Discussion

Patterns of invasion in mountain systems

Environmental variables and functional groupings influenced community structure of non-native plant species and invasion patterns of globally common invaders. Previous analyses documented non-native species richness declines with increasing elevation and distance from the road and related to progressive filtering of the lowland species pool along the elevational gradient (McDougall et al. 2010; Alexander et al. 2011; Seipel et al. 2012). At regional scales (>100 km), there is a general pattern of environmental filtering along elevational gradients, whereas at small scales (<0.1 km) patterns of invasion appear to be governed by stochastic processes (Seipel et al. 2012). Here, we demonstrated that these patterns hold true for both community assembly as well as for focal species of concern in the Willowa Mountains, OR. However, functional groups, defined by life-history strategy and invasion status, differed in their invasion and spread along environmental gradients.

Spread into natural vegetation

Distance from road can influence the non-native plant community (Pollnac et al. 2012; Seipel et al. 2012). Roads

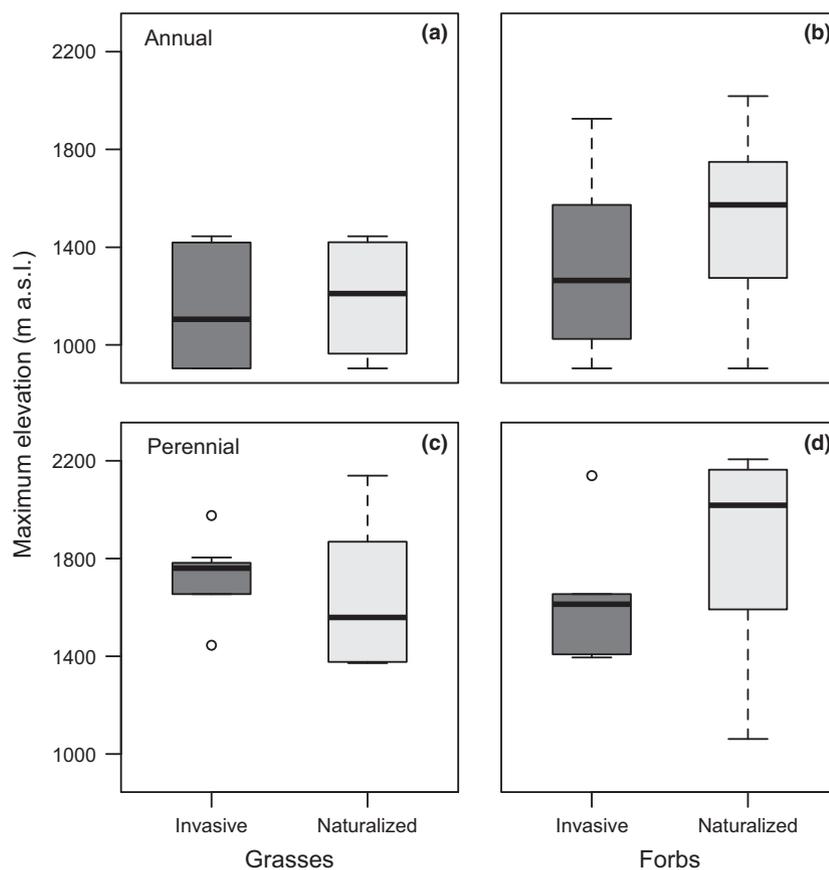


Fig. 3. Maximum elevation of occurrence of non-native species in the Willowa Mountains, OR. Box plots represent median, 25 and 75% quantiles with whiskers extending to 2 SD for annual or biennial (**a, b**) and perennial (**c, d**) life-history strategies for grass (**a, c**) and forb (**b, d**) species. Perennial species have a higher maximum elevation of occurrence than annual species ($F = 27.06$, $P < 0.0001$), but there are no differences based on life form or invasion status.

can act as conduits for invasion by providing high propagule loads, high light availability, disturbance and low competition from native vegetation (Watkins et al. 2003; Theoharides & Dukes 2007; Menuz & Kettenring 2013). Furthermore, roads can offer novel habitats compared to interior vegetation (Neher et al. 2013) that might enhance colonization by non-native species (Theoharides & Dukes 2007). This may be especially true at higher elevations or in more protected areas, where there is a sharper contrast between roadside and interior habitat conditions (Pollnac et al. 2012; Seipel et al. 2012). Most species enter the native vegetation matrix at the roadside, with invasive species, particularly perennial species, spreading into adjacent native vegetation. Many non-native species are ruderal species with preferences for disturbed habitats (Rejmánek & Richardson 1996; Parendes & Jones 2000). In our study, all but five species were found in roadside subplots and only 25% of the species were restricted to the roadside subplots. This suggests that few species are roadside specialists and the remaining species have already invaded at least

100 m into natural vegetation. Nonetheless, it is important to note that invasion into natural vegetation was primarily limited to low to mid-elevations and that at higher elevations non-native species were constrained to roadside habitats (Seipel et al. 2012).

Elevation

Understanding patterns of spread into natural vegetation is critical in managing invasive species (Pauchard et al. 2009; Bradley et al. 2010). Our findings corroborate global comparisons showing non-native species enter the plant community at lower elevations near the roadside and spread upslope and into the native vegetation matrix (McDougall et al. 2010; Alexander et al. 2011; Seipel et al. 2012). However, functional groups differ in their current distribution patterns along elevation and roadside gradients. Annual grasses are the first functional group to be filtered out of the non-native community along the elevational gradient, followed by annual forbs. Thus, there is a shift

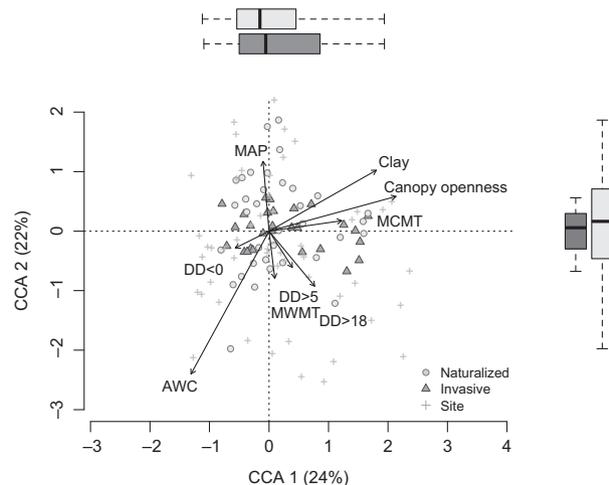


Fig. 4. Constrained partial canonical correspondence analysis (pCCA) ordination plot. Arrows represent environmental variables that significantly explain variation in community composition among transects after variation related to elevation has been taken into account. Direction of the arrow follows the most rapid change in that variable and length is proportional to the strength of correction with the species ordination. Symbols represent mean CCA scores for site (+), invasive (O) and naturalized (Δ) species, and are based on frequency of occurrence in 52 transects (sites). Box plots represent the median, 25 and 75% percentiles with whiskers extending to 2 SD of CCA scores for naturalized (light grey) and invasive (dark grey) non-native species. Median values do not differ for either axis, but the variation of CCA 2 scores is significantly higher for naturalized species than invasive species. This suggests that naturalized species are filtered along CCA2 whereas invasive species share similar habitat requirements near the centroid. Note: AWC, available water capacity; DD < 0, degree days below 0 °C; DD > 5, degree days above 5 °C; DD > 18, degree days above 18 °C; MAP, mean annual precipitation; MCMT, mean coldest month temperature; MWMT, mean warmest month temperature.

from fast-growing species at lower elevations to longer-lived, persistent species at higher elevations. This suggests that although the more ruderal and problematic invasive species are confined to lowlands, it is the more conservative and naturalized species that are able to invade the harsher climates of the high elevations.

Community-wide shifts along environmental gradients

Climatic and soil variables explained the majority of variation in species turnover, or β -diversity, whereas geographic distance had little explanatory power. This pattern was likely related to the overwhelming influence of elevation on climate and soil variables (Marini et al. 2012). Invasive non-native species had a narrow niche breadth for soil-related conditions, whereas naturalized non-native species had higher species turnover along soil-related gradients. Temperature and climate variables correlated with elevation had strong filtering effects on both naturalized and

invasive non-native species. Thus, climate shifts associated with global change may influence non-native species future distribution along the elevation gradients, particularly for species with a higher plasticity for soil regimes. Adding edaphic variables to models predicting future species distributions under global change scenarios may greatly improve the precision and ecological implications of such studies (Bertrand et al. 2012; Dubuis et al. 2013).

Barriers to invasion

Our analysis identified two barriers limiting the spread of non-native species across the Wallowa Mountain region: (1) soil conditions, primarily soil water availability and texture, and (2) life-history strategy, with annual species falling out of the non-native species pool at lower elevations than perennial species. Together, these abiotic and ecological barriers structure the non-native plant community in the Wallowa Mountains.

First, soil conditions represent an environmental barrier that can constrain species distributions and filter community membership at multiple spatial scales (Theoharides & Dukes 2007). Soil moisture and texture are key environmental conditions related to differences in naturalized and invasive species distribution patterns in this semi-arid system. Furthermore, these results indicate that different ecological processes may structure the non-native plant community based on functional strategies. Invasive community converges in habitat occupation with similar environmental conditions, whereas naturalized community shows rapid species turnover along the same environmental gradients. Using trait-based approaches and identifying key environmental barriers can be used in management strategies focusing on habitats of importance along the invasion continuum (Funk et al. 2008; Richardson & Pyšek 2012; Cleland et al. 2013).

Second, species traits are often related to invasion success. Traits conferring rapid reproduction and prolific seed production are associated with invasiveness (Richardson & Pyšek 2012). Annual and perennial species had differing distribution patterns along the elevation gradient, with annual species distributions skewed towards lower elevations and perennial species skewed upslope (McDougall et al. 2010). Functional differences in the ability to grow and reproduce in harsher environments with shorter growing seasons may influence upslope invasion (Haider et al. 2010, 2012; McDougall et al. 2010). Perennial bunchgrasses dominate the native ground vegetation in the Wallowa Mountain region (Parks et al. 2005). Thus, non-native perennial species may be pre-adapted to higher elevation climate regimes or they may have higher phenotypic plasticity that allows them to invade higher elevation sites compared to annual species (Alexander et al. 2009;

Richardson & Pyšek 2012). Conversely, the lower elevations of the Wallowa Mountain region are dominated by an agricultural landscape (Parks et al. 2005), providing more propagule sources of non-native species as well as habitats that may favour annual species (Pauchard et al. 2009; McDougall et al. 2010; Haider et al. 2012). In habitats of this agricultural matrix, annual species may benefit from higher soil nutrient and water resources as well as increased pulses of these resources (Besaw et al. 2011). This has implications for native vs non-native competition and management strategies along these gradients (Pauchard et al. 2009; McDougall et al. 2010, 2011).

Conclusions

By taking a multi-faceted approach that combines focal species distributions and community-wide patterns with those for key functional groups, our study adds to the understanding of patterns of invasion in the Wallowa Mountains and beyond. Annual species and invasive species occupy lower elevations, whereas perennials and naturalized species have spread to higher elevations. Furthermore, invasive perennial species have spread further into the natural habitat matrix than naturalized species. The community-wide analyses further suggest that different ecological processes may structure the non-native plant community based on functional strategies. Species in the invasive community occupy similar habitats, whereas species in the naturalized community partition habitats along the same environmental gradients. These functional groups explain some of the differences in non-native species distribution patterns and could facilitate management strategies tailored towards the different life-history strategies of these plant groups.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Map of road and transect locations.

Appendix S2. Full species list and corresponding information including reference lists.

Appendix S3. Methods and results of Mantel tests among environmental variables and community patterns.

Appendix S4. Pearson correlation table for environmental variables.

Appendix S5. Additional results from canonical correspondence analyses.