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RESEARCH PAPER

Processes at multiple scales affect richness and similarity of non-native plant species in mountains around the world

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ABSTRACT

Aim To investigate how species richness and similarity of non-native plants varies along gradients of elevation and human disturbance.

Location Eight mountain regions on four continents and two oceanic islands.

Methods We compared the distribution of non-native plant species along roads in eight mountainous regions. Within each region, abundance of plant species was recorded at 41–84 sites along elevational gradients using 100-m^2 plots located 0, 25 and 75 m from roadsides. We used mixed-effects models to examine how local variation in species richness and similarity were affected by processes at three scales: among regions (global), along elevational gradients (regional) and with distance from the road (local). We used model selection and information criteria to choose best-fit models of species richness along elevational gradients. We performed a hierarchical clustering of similarity to investigate human-related factors and environmental filtering as potential drivers at the global scale.

Results Species richness and similarity of non-native plant species along elevational gradients were strongly influenced by factors operating at scales ranging from 100 m to 1000s of km. Non-native species richness was highest in the New World regions, reflecting the effects of colonization from Europe. Similarity among regions was low and due mainly to certain Eurasian species, mostly native to temperate Europe, occurring in all New World regions. Elevation and distance from the road explained little of the variation in similarity. The elevational distribution of non-native species richness varied, but was always greatest in the lower third of the range. In all regions, non-native species richness declined away from roadsides. In three regions, this decline was steeper at higher elevations, and there was an interaction between distance and elevation.

Main conclusions Because non-native plant species are affected by processes operating at global, regional and local scales, a multi-scale perspective is needed to understand their patterns of distribution. The processes involved include global dispersal, filtering along elevational gradients and differential establishment with distance from roadsides.

Keywords
Alien, altitude, beta-diversity, elevational gradients, plant invasions.

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INTRODUCTION

Plant invasions are influenced by interacting abiotic and biotic processes spanning a wide range of spatial scales (Cassey *et al.*, 2006; Meyerson & Mooney, 2007; Ibáñez *et al.*, 2009). At the global scale, gradients of energy affect large-scale species distributions (Field *et al.*, 2009), and patterns of human trade and migration determine the identity and frequency of species introductions (Mack & Lonsdale, 2001; Simberloff, 2009; Wilson *et al.*, 2009). Within regions, abiotic gradients such as climate, resource availability and land use can also affect the richness and similarity of non-native plant assemblages (Lonsdale, 1999; Brown & Peet, 2003; Pauchard *et al.*, 2004; Davis, 2009), and at local scales, heterogeneity in abiotic and biotic factors – many of them influenced by human activities – can determine the degree of invasion at a site (Degasperis & Motzkin, 2007; Davis, 2009).

Ecologists increasingly recognize that a full understanding of biological invasions will only be possible if we take account of the scales over which particular processes operate (Lonsdale, 1999; Pauchard & Shea, 2006; Jiménez *et al.*, 2008; Kueffer & Hirsch Hadorn, 2008). For example, native and non-native species richness are often negatively correlated at the community scale but positively correlated at a landscape scale. This apparent contradiction arises because local competitive interactions determine whether a species can invade (Tilman, 1997), while habitat diversity is more important at a larger scale (e.g. Lonsdale, 1999; Fridley *et al.*, 2007). For practical reasons, however, most studies of plant invasions have been conducted at a local or regional scale, and the differing methods used make larger-scale comparisons difficult (Lonsdale, 1999).

Plant invasions into mountain regions provide an excellent opportunity to investigate how plant distributions are influenced by processes operating at a range of spatial scales (Dietz, 2005; Alexander *et al.*, 2009a; Pauchard *et al.*, 2009). Different mountains systems are similar in exhibiting strong environmental gradients, but differ in many other respects including biodiversity, climate and land-use history. Several studies have found a strong decrease in non-native plant species richness at the highest elevations, although patterns at lower and middle elevations vary among regions (Pauchard *et al.*, 2009). In some cases, species richness has been found to decline continuously across the entire gradient (Becker *et al.*, 2005; Daehler, 2005), while in others, hump-shaped patterns comparable to those for native species have been recorded (Arévalo *et al.*, 2005; Nogués-Bravo *et al.*, 2008). Several reasons for the decline in species richness at higher elevations have been proposed, including introduction pathways from low to high elevations (Becker *et al.*, 2005; Alexander *et al.*, 2011), decreasing anthropogenic land use and habitat disturbance with elevation (Parks *et al.*, 2005; Marini *et al.*, 2009), and harsh climate conditions at higher elevations (Pauchard *et al.*, 2009).

In this paper, we investigate the drivers of non-native plant species composition (richness and similarity) in eight mountainous regions around the world. For this purpose, we distinguish three spatial scales: (1) global, representing factors operating a large scale (1000s of km) and determining differences in species composition among mountain systems; (2) regional, representing factors changing at a regional scale (100s of km), and especially along elevational gradients; and (3) local, representing factors varying among neighbouring habitats (< 100 m). Based on this framework, we ask three main questions:

1. What is the relative contribution of each spatial scale to variation among sites in richness and similarity of non-native species?
2. Are patterns of non-native species richness along gradients of elevation and human disturbance consistent across biogeographic regions?
3. How do factors operating at different scales interact to affect the richness and similarity of species at the local level?

METHODS

Description of regions

The eight regions were Tenerife (Canary Islands, Spain), the Australian Alps, Swiss Alps (Canton Valais), Central Chile, South Chile, Montana-Yellowstone National Park (NP), Blue Mountains Oregon (both USA), and two of the Hawaiian islands (Hawaii and Maui) (Table 1). Four of these regions have a temperate climate, two a mediterranean climate and two are subtropical oceanic islands that are strongly affected by trade winds, resulting in dry, mediterranean-like leeward and humid windward climates (Table 1).

Survey design

In each region we selected three roads – or four in Hawaii and Switzerland – that extended over a broad elevational gradient and were open to vehicular traffic for at least part of the year. The elevational range of all regions exceeded 1000 m (Table 1, Appendix S1 in Supporting Information), and road surfaces included both gravel and pavement. The bottom of a road was defined as the point below which there was no substantial change in elevation, and the top was the highest point accessed by the road, though these were not necessarily the lowest or highest elevations in each region. Starting at the bottom, the elevational range of each road was divided into 19 equally spaced bands, giving 20 sample locations per road (Appendix S1). Locations were determined prior to going into the field, and were subsequently located using a global positioning system (GPS) or topographical map. Sample locations were ranked (numbered) by elevation along each road from lowest (1) to highest (20).

At each sampling location, three 2×50 m^2 plots were laid out in a T-shaped transect, so that one plot lay parallel to the road, centred on the sampling location. The other two plots extended perpendicularly from the road (centred at the sampling location) and midpoints of the plots were 25 m and 75 m from the roadside (Appendix S1). This design was applied in all regions except the Hawaiian islands, where the plots were confined to the roadside (Table 1). Each plot was divided into five 2×10 m^2

Table 1 Characteristics of the eight regions, including the location, the climate zone (Med, mediterranean; Temp, temperate; Island, subtropical oceanic island with strongly contrasting leeward and windward climates), the number of roads sampled, the number of sampled plots per region with the percentage of plots with no non-native species recorded in parentheses, the range from the minimum to the maximum elevation of the sampling plots, and the total number of non-native flowering plants recorded per region.

Region	Coordinates	Climate	Roads	Samples	Elevation range (m a.s.l.)	Species
Australian Alps[1]	36°06′ S 148°18′ E	Med	3	60 (0)	410–2125	102
South Chile[2]	36°58′ S 71°24′ W	Med	3	60 (0)	274–1668	84
Central Chile[2]	33°54′ S 70°18′ W	Temp	3	41 (0)	1895–3585	45
Swiss Alps[3]	46°12′ N 7°12′ E	Temp	4	84 (29.8)	411–1802	19
Tenerife, Canary Islands[4]	28°12′ N 16°36′ W	Island	3	60 (38.3)	5–2250	38
Hawaiian islands[5]	19°48′ N 155°30′ W	Island	4	73 (1.4)	507–4147	162
Montana-Yellowstone NP[6]	44°48′ N 110°24′ W	Temp	3	60 (6.7)	1803–3307	33
Oregon Blue Mountains[7]	45°18′ N 117°48′ W	Temp	3	60 (6.7)	902–2265	83

NP, national park.
[1]McDougall *et al.*, 2005; [2]Jiménez *et al.*, 2008; [3]Alexander *et al.*, 2009b; [4]Arévalo *et al.*, 2005; [5]Jakobs *et al.*, 2010; [6]Rew *et al.*, 2005; [7]Parks *et al.*, 2005.

subplots within which we recorded the abundance of all non-native species. For this purpose, we used a three-point scale to reflect the number of individuals or ramets (1–10, 10–100, 100+). In the subsequent analysis, the values for the subplots were summed to give a single presence–absence measure for the entire 100 m^2 plot.

Any species introduced after AD 1500 was considered to be non-native. A comprehensive list of all species recorded in the survey was compiled and consolidated to the species level using the GRIN database (http://www.ars-grin.gov/), eFloras (http://www.efloras.org/) and the PLANTS database (http://plants.usda.gov/). The origin of species was also determined from these databases.

Land-use intensity – including agriculture, forestry, mining, road infrastructure, etc. – was recorded using a three-point scale (0 = none, 1 = low, 2 = high), based upon a visual assessment in the vicinity of each sampling point. In the same way, human disturbance was recorded by noting the amount of recent digging, mowing or cutting of trees in each plot. These two variables were later summed to give a single measure of human impact that ranged from 0, where impact was minimal to 4 where human land use and disturbance were greatest.

To record habitat type, we used the same list of habitats in all regions – grass–herb, shrubland, open forest, closed forest and rock. Habitat diversity was then determined by counting the number of habitats recorded at each sample location. Tree canopy cover in each plot was estimated visually.

Data analysis

Variance components of different spatial scales

All analyses were performed in R (R Development Core Team, 2008). The contributions of each spatial scale – among regions (global), among roads within regions, along elevational gradients (regional) and along transects from roadsides (local) – to total variation in species richness and similarity were estimated by fitting all variables as random effects within generalized linear mixed-effects models (GLMMs, using the R package lme4; Bates & Sarkar, 2007). We fitted the GLMM of richness with a Poisson error distribution and log link. In these analyses, rank elevation rather than absolute elevation was used in order to maximize the independence of the elevational and regional variables and to account for differences in elevational range among regions.

Pairwise similarity among plots was measured using Jaccard index and the β-sim index (Koleff *et al.*, 2003), both calculated in the R package Vegan (Oksanen *et al.*, 2008). Because the β-sim index is not sensitive to differences in richness, this parameter allowed us to determine whether variation in similarity was due to the loss or turnover of species. The similarity measures were then used as dependent variables in a GLMM, with the hierarchical scales as random effects – pairwise binary comparison from the same region or not, a pairwise binary comparison from the same road or not, pairwise Euclidean distance between rank elevations, and pairwise Euclidean distance of plot distance from the roadside, assigned 1–3 (Legendre *et al.*, 2005).

Global scale analyses

At the global scale, we fitted a generalized linear model of regional richness ($n = 8$) dependent on latitude, longitude and climate type (Table 1), and selected the best-fit model using Akaike's information criterion (AIC) (Burnham & Anderson, 2002). We also examined the hierarchical clustering of regions based on similarity using the average and Ward methods of agglomeration (Legendre & Legendre, 1998).

Regional models of elevational species richness gradients

GLMMs were used to investigate variation in species richness along gradients of elevation and distance from the roadside. These analyses provided a clearer picture of how species richness varied with elevation in the various regions. These regional

Table 2 Akaike information criterion (AIC) scores from models of species richness, where *k* is the number of parameters, predicted by intercept only, elevation (elev), quadratic equations of elevation (quad elev), distance to road (dist road) and the interaction of elevation and distance to road.

Model variables	*k*	Australian Alps	Montana-Yellowstone NP	Oregon Blue Mountains	Swiss Alps	Tenerife, Canary Islands	South Chile	Central Chile	Hawaiian islands
Intercept only	2	1405	627	1426	220	377	702	385	432
Dist road	4	726	445	1156	195	368	654	371	n.a.
Elev	3	1340	458	748	195	273	500	166	212
Quad elev	4	1250	448	735	189	240	491	167	**196**
Elev + dist road	5	661	276	478	172	264	452	**152**	n.a.
Quad elev + dist road	6	571	266	465	**167**	**231**	**443**	153	n.a.
Elev × dist road	4	641	257	431	173	268	455	155	n.a.
Quad elev × dist road	10	**541**	**236**	**406**	171	238	447	158	n.a.

NP, national park.
Bold values indicate the best-fit models with the lowest AIC score.

models used a Poisson distribution and logit link, and roads were fitted as random effects to account for the nested spatial structure of the data. Elevation and distance to a road were treated as fixed effects. AIC was used to compare the eight competing richness models and determine the best-fit model (that with the lowest AIC; Burnham & Anderson, 2002). The models were: intercept only, elevation only, distance to road only, distance to road and elevation – separate models with elevation as both a single term quadratic equation – and finally the interaction of elevation and distance to road with elevation as both a single term and quadratic equation (Table 2).

A two-sample *t*-test was used to compare the influence of conservation status (i.e. comparing regions with and without a conservation designation such as national park or national forest) upon the decline in species richness with distance from the road. In three regions – Montana-Yellowstone NP, Blue Mountains Oregon National Forest, and Kosciuszko NP in the Australian Alps – most of the area surveyed was protected; in contrast, the study areas in South Chile, Central Chile and Tenerife were the property of many smaller landowners and had at most limited protection status. Because the Swiss Alps had so few non-native species and the Hawaiian islands had only roadside plots these regions were excluded from this comparison.

In mountainous regions, the most intensively used land is usually at lower elevations, and these areas also have the highest richness of non-native species. To investigate whether this was also the case in our study areas, we calculated Spearman rank correlations of species richness against land-use intensity, habitat diversity, elevation and canopy cover (Appendix S2).

RESULTS

Factors at multiple spatial scales explain variation in non-native plant species richness and similarity

A total of 375 non-native taxa were identified to species level. A majority of these (210 species) were of Eurasian or circumboreal origin, of which approximately 150 species (40% of total species pool) were native to temperate Europe. The other 165 species came from North America (28), South America (28), the Americas (25), Africa (16), tropical Asia (13), Australia (9), east temperate Asia (4) or the Pacific region (4). The remainder were pan-tropical (20), or of unknown origin (18).

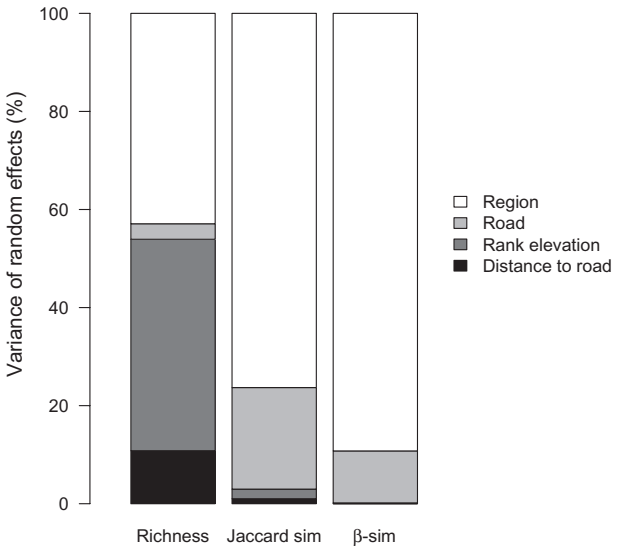

Figure 1 Variance components of generalized linear mixed-effects models of richness and similarity. The variables distance to road, rank elevation, road and region were all fitted as random effects.

Non-native species richness varied greatly among regions, along elevational gradients and with distance from roadsides. Region and elevation each accounted for 43% of the variation in richness explained by the model, while distance from the road accounted for 11%, and different roads only 3% (Fig. 1). In contrast, region dominated variation in similarity, accounting for 76% of variation using the Jaccard index, and 89% using the β-sim index, while roads accounted for 20% and

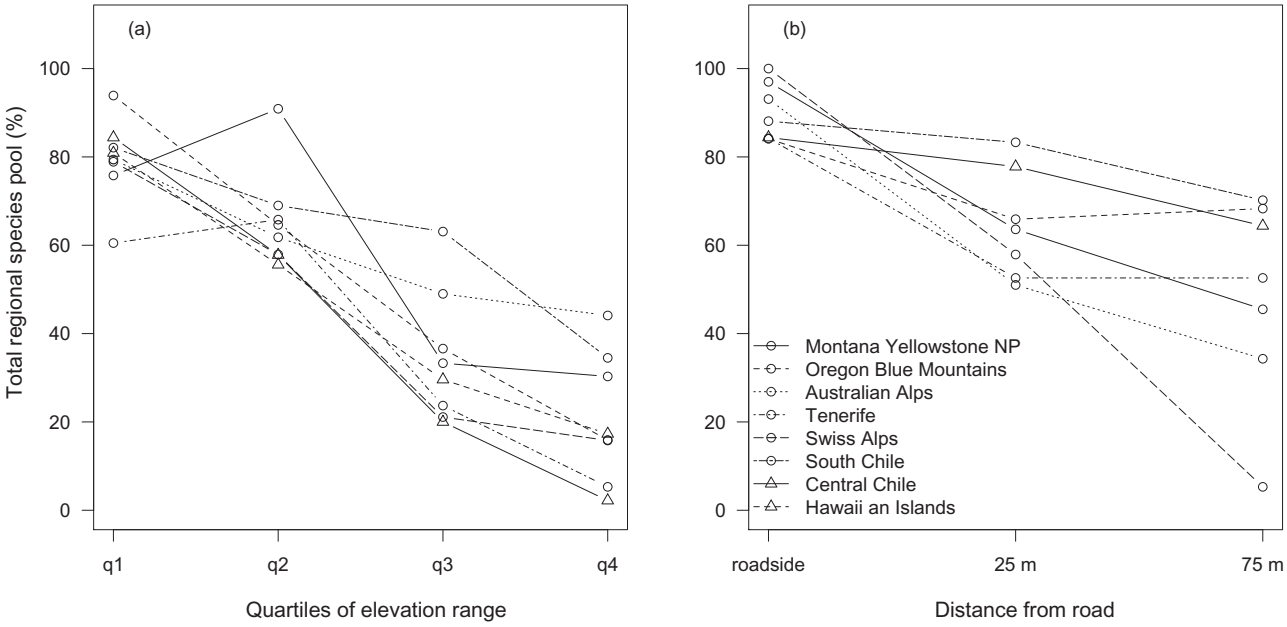

Figure 2 (a) Percentage of the total species pool found in each of the quartiles of the elevation range grouped by region. (b) Percentage of the total species pool found at each distance from road grouped by region.

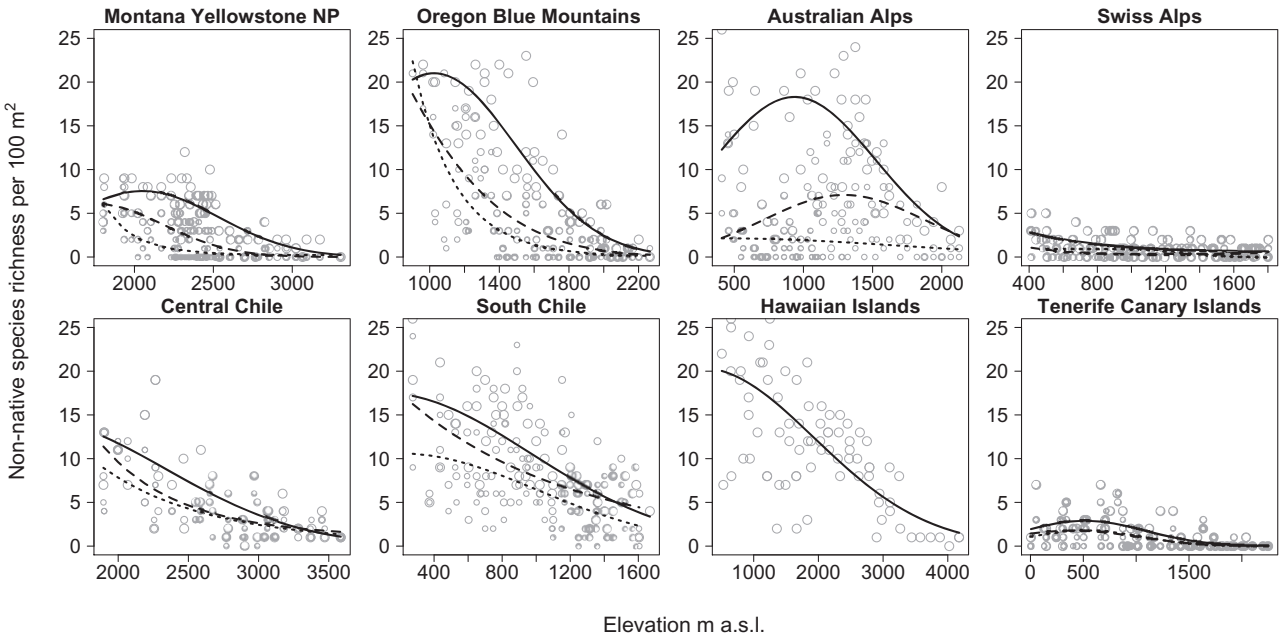

Figure 3 Fitted relationships between elevation and non-native species richness in plots at increased distance from roadsides [at the roadside (solid), and centred at 25 m (dashed) and 75 m (dotted) from the road]. The largest points are roadside plots; the smallest points are 75 m from the roadside.

10% of variation, respectively. In the same analysis, elevation accounted for only 2% of variation using the Jaccard index, and even less using the β-sim index. In all regions, distance from the road explained little of the variation in similarity, regardless of the measure used; this was because most species (mean = 80%, s.d. = 20%, Fig. 2) occurred both along roadsides and in adjacent natural habitats. Thus, although species richness declined with distance from roadsides (Figs 1 & 3), the effect of this decline upon similarity was much smaller than the effect of elevation (Fig. 2).

Variation between regions

Most non-native species (73%) were found in only one of the eight regions, and 97% were found in three or fewer. Of the non-Eurasian species, only two occurred in three regions

(*Cynodon dactylon* and *Sporobulus indicus*), and then only at low elevations, while six Eurasian species occurred in six regions (Fig. 4). Furthermore, 43 of the 50 most frequently recorded species were native to temperate Europe (Fig. 4). There were positive correlations between the number of regions where a species was found and the total frequency of the species (r = 0.77) (Fig. 4), as well as the number of regions and maximum elevation a species reached (r = 0.59).

The number of non-native species sampled varied from 162 on the Hawaiian islands to 19 in the Swiss Alps (Table 1). Differences in richness were best explained by longitude and climate type (AIC = 78; R^2 = 0.82), followed by longitude and latitude (AIC = 78, R^2 = 0.77), longitude (AIC = 82), and latitude (AIC = 86). The effect of longitude reflected the contrast between Old and New World regions.

The maximum similarity between regions, based upon all species, was approximately 30% (Fig. 5a). The first dichotomy in the cluster analysis separated the Old and New World regions. Because most of the non-native species in the Swiss Alps and on Tenerife (Old World) were of American and Asian origin, while the commonest species in the New World (including the Australian Alps) were of Eurasian origin, there was little similarity between Old and New World regions. The second dichotomy was weakly correlated with climate; thus, one cluster was formed by the three warm, dry regions (Hawaiian islands leeward low elevations, Australian Alps and South Chile; see Appendix S3 for the comparison of climates), which shared approximately 18% of species, and another by the adjacent temperate regions, Montana-Yellowstone NP and the Blue Mountains Oregon. Despite their proximity, the two Chilean regions were not the most similar to each other. Similar dichotomies among regions

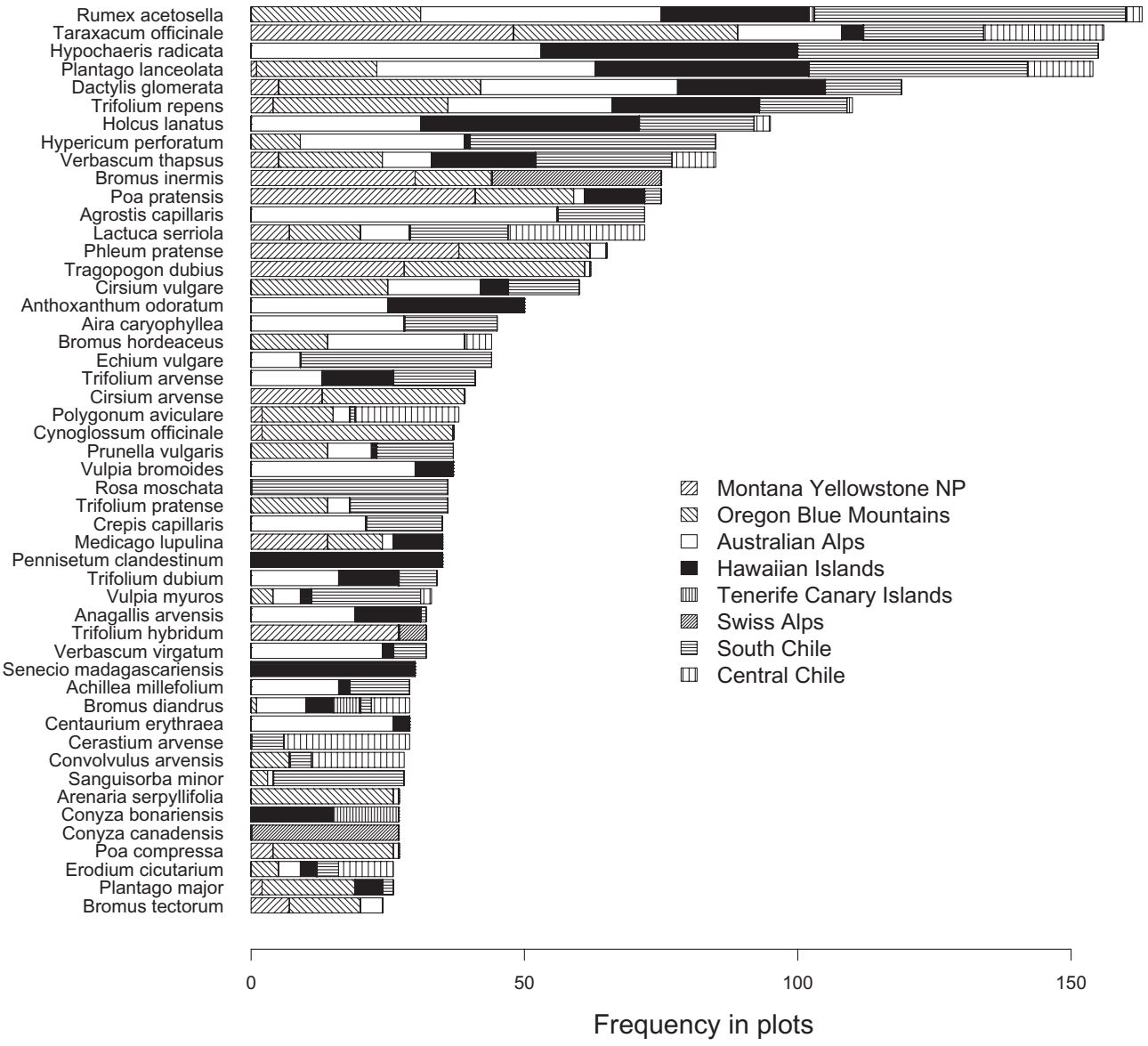

Figure 4 The 50 most frequent species of the survey and the corresponding frequency of occurrence within in each of the survey regions.

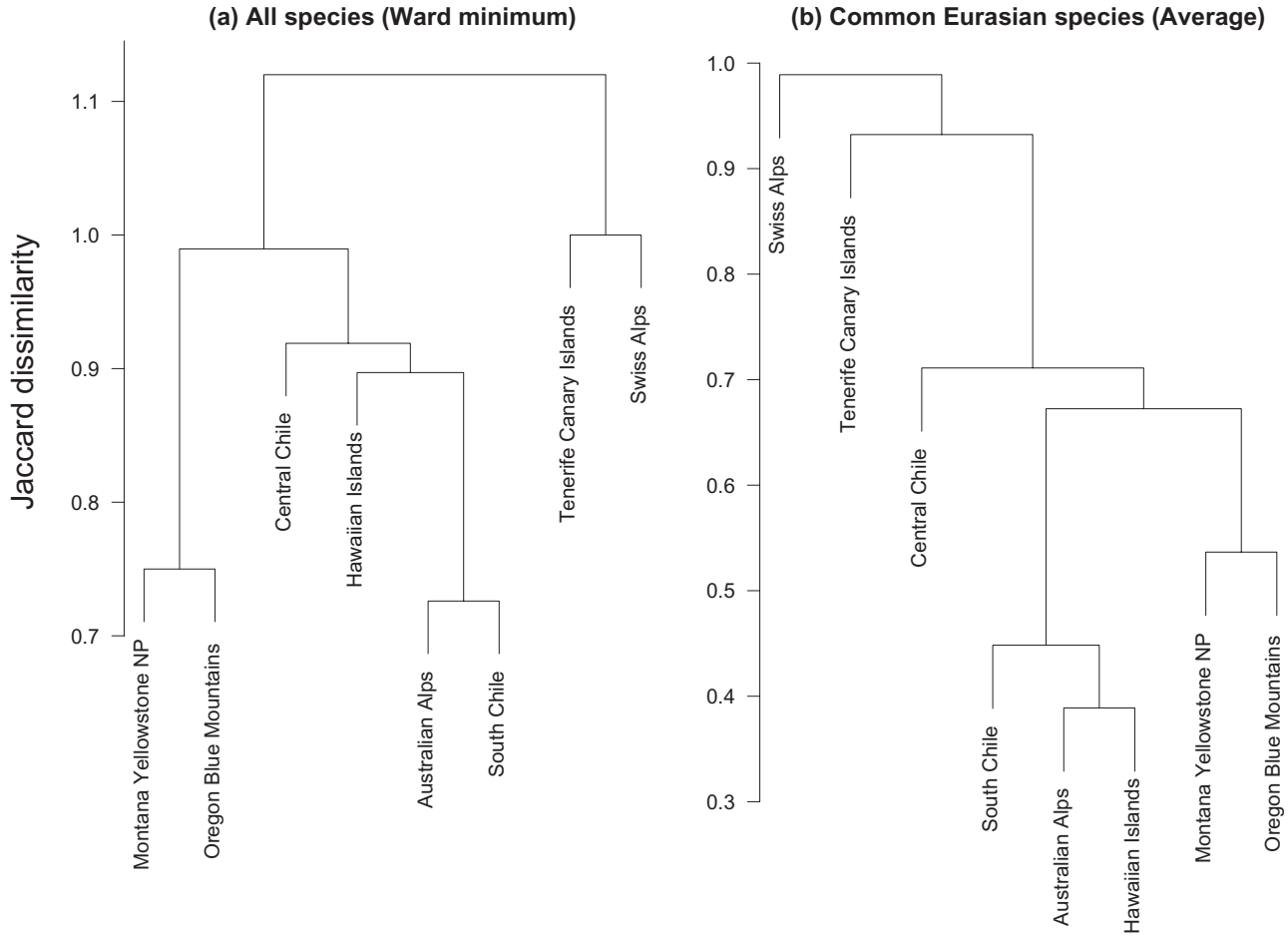

Figure 5 Hierarchical clustering of Jaccard dissimilarity measures of species composition among regions. All roads were most similar to those within the sampling region (not shown). Panel (a) is clustered by Ward linkage. Panel (b) shows the average regional dissimilarity based on Jaccard dissimilarity measured using temperate Eurasian species that occurred in at least two regions.

were obtained in analyses performed using only species recorded at least 20 times, and only species native to temperate Eurasia (Fig. 5b). This suggests that patterns of similarity among regions were determined largely by the widespread Eurasian species.

Regional species richness gradients in response to elevation and local disturbance

Species richness peaked in the lower third of the elevational gradient near roadsides, and declined with increasing elevation and distance from the road in all regions (Fig. 3). Human impact, based on a combined measure of land-use intensity and plot disturbance intensity, was also highest at low elevations, and was correlated with non-native species richness (Appendix S2). Only in the Australian Alps and on Tenerife was there a clear hump-shaped pattern in species richness with elevation. In the Hawaiian islands the decline in richness in response to elevation was best characterized by having a slight hump-shaped relationship or inflection, as in seven of the eight regions (Table 2). In Central Chile, in contrast, the best-fit model was a monotonic decline in richness in response to elevation and distance to the road. In three regions (Swiss Alps, Tenerife and South Chile), the best-fit model was a quadratic equation of elevation and distance from the road. In the three remaining regions (Montana-Yellowstone NP, Blue Mountains Oregon and the Australian Alps), species richness declined away from the road more steeply as elevation increased; hence the best-fit model contained an interaction term for distance to a road and quadratic elevational variable (Table 2, Fig. 3).

The three regions with important interactions were regions where habitat was protected for conservation (i.e. national park or national forest). In these areas, species richness also declined more steeply with distance from the road than it did in unprotected regions (significant difference in regression slopes; $t = -8.75$, d.f. = 3.98, $P \leq 0.001$). Indeed, in the two Chilean regions – neither of which was protected – the total pool of non-native species was greater away from the roadside.

DISCUSSION

Processes at multiple spatial scales shape patterns of plant invasions in mountains

Our results demonstrate that the distribution of non-native plants in mountainous regions is shaped by factors operating at a broad range of spatial scales. Thus, large-scale factors (in the order of 1000s of km) such as climate and historical patterns of trade and migration determine the pool of species that can occur in a particular region. Within this region, factors such as elevation (varying on the order of 100s of km) are important in explaining the assemblages of non-native species. And at a local level, factors associated with disturbance – which scale on the order of 0.1 km – interact with broader-scale factors to form idiosyncratic patterns of richness and similarity. That ecological patterns should be determined by processes varying over such vastly different spatial scales may be a particular characteristic of biota that have assembled only recently (i.e. the past 200–500 years) as a result of anthropogenic activities.

Introduction history and climate shape global patterns

The high dissimilarity of regional species pools indicates the importance of introduction histories for patterns of plant invasion. Thus, although a few species were recorded in several regions, most occurred in only one or two. Similar long-tailed distributions of relative abundance have been reported for non-native species in other studies, for example in US national parks (Allen *et al.*, 2009) and on oceanic islands (Kueffer *et al.*, 2010). Two factors were especially important in accounting for this dissimilarity. First, because many species were of Eurasian origin, they were not recorded as non-natives in the Swiss Alps and Tenerife, which explains the high dissimilarity between the Old and New World regions. Second, while approximately 90% of the non-Eurasian species were found in a single region, many species native to Eurasia occurred in at least two regions and therefore contributed to the similarity between regions. Importantly, Eurasian species were shared equally among all pairs of New World regions despite the large geographic distances separating them. The geographically isolated Australian Alps, for instance, shared 36 species with the Blue Mountains of Oregon, 38 with the Hawaiian islands and 42 with South Chile. Thus, while non-Eurasian species were restricted to particular regions, local Eurasian species pools represented subsamples of a globally dispersed species pool. No doubt this reflects the colonial history of the New World regions, with non-native species associated with the introduction of European agricultural practices (see below).

The inconsistent effect of geographic distance on similarity between regions probably reflects local climatic variation and the different histories of introduction. For example, although the non-native floras of nearby Montana-Yellowstone NP and Blue Mountains Oregon were closely similar, those of south and Central Chile were dissimilar. Normally a steep decline of richness in response to latitude is expected (Field *et al.*, 2009), but the importance of historic factors may override this, which would explain why richness was related only weakly to latitude. However, there was some tendency toward climatic structuring of similarity among the New World regions, for instance in the clustering of regions with a Mediterranean climate (South Chile, the Australian Alps and Hawaii Islands, which also has a mediterranean climate in leeward lowland locations). And the warmer and wetter sites of the New World (Appendix S2) had more species than the temperate dry sites, which may be due to higher available energy or more favourable conditions for plant growth (Field *et al.*, 2009).

Climatic filtering along regional elevational gradients

At a regional scale, patterns of species richness and similarity along elevational gradients were highly consistent. In all regions we found a decline in non-native species richness with elevation, confirming the trends previously reported from individual regions (Daehler, 2005; Marini *et al.*, 2009; Pauchard *et al.*, 2009). A hump-shaped distribution was found only in two regions, indicating that species richness patterns of non-native species tend to be different from those of native species, which usually peak at mid-elevations (Nogués-Bravo *et al.*, 2008). The fact that a similar decline was recorded in all regions allows us to rule out some potential causes for this pattern. Thus, the decline is unlikely to be related to available area, as this does not decline consistently with elevation in all regions; and it is unlikely to reflect time lags in dispersal to higher elevations, because dispersal along roadsides was probably effective in some if not all regions (Alexander *et al.*, 2009a). We conclude that the decline was due, at least partly, to human land use, which was usually most intensive at lower elevations. The decline in richness in temperate regions may also be related to low temperature (Marini *et al.*, 2009), while on subtropical oceanic islands it may reflect a combination of low temperature and increased evapotranspiration stress at high elevations (Haider *et al.*, 2010; Jakobs *et al.*, 2010); thus, the decline in species richness with increasing elevation reflects differing environmental gradients in different regions. We conclude therefore that species introduced into disturbed habitats at low elevations are progressively filtered out by the increasingly harsh climatic conditions along an elevational gradient, though the particular factor accounting for this harshness may vary (Alexander *et al.*, 2011).

Distance from roadside and stochastic processes at the local scale

Lower non-native richness away from roadsides has been reported in several studies (Gelbard & Belnap, 2003; Pauchard & Alaback, 2004; Arteaga *et al.*, 2009), and could have several causes. For example, it could reflect the intentional sowing of certain species along road verges, or differing environmental conditions at the roadside or greater habitat resistance away from the road. In our survey, invasion away from the road was lowest in the three regions with protected areas, and especially where dense forest occurred along much of the elevational gradient. Furthermore, invasion away from roadsides declined with

increasing elevation, indicating an interaction between processes operating at regional and local scales. This could be due to decreased human land-use intensity, lower colonization pressure or greater resistance to invasion of more natural communities at higher elevations, any of which would also explain why the interaction was strongest in the regions with protected areas. The effect upon species richness of distance from the road was only slightly less than the effect of elevation, highlighting how community resistance can be effective over short distances (< 100 m). Indeed, in some regions – especially the Australian Alps – species richness at 75 m from the roadside was very low and independent of roadside species richness, indicating that colonization pressure could not overcome habitat resistance. In general, patterns of similarity at the local scale were hard to predict and were probably contingent upon a series of interactive processes that changed along the elevational gradient.

Interactions among spatial scales: the global dominance of Eurasian species

Patterns of non-native plant richness and similarity in mountains can be best understood as the product of introduction history and climate at a global scale, climatic filtering along regional elevational gradients and habitat and stochastic factors at a local scale. This interaction is well illustrated in the striking preponderance of Eurasian species in the non-native flora of mountains world-wide. A comprehensive compilation of published non-native mountain floras world-wide has also confirmed the dominance of Eurasian species (McDougall *et al*., 2010). The migration of European settlers to the Americas and Australia since the 16th century led to the introduction of a wide range of European species, especially those associated with agriculture as either forage crops or weeds (e.g. Mack & Lonsdale, 2001; Crosby, 2004; Daehler, 2005; Gravuer *et al*., 2008). The dominance of European species can therefore be understood partly by their pre-adaptation to European pastoral agriculture (Di Castri, 1988; McDougall *et al*., 2010).

It is striking that many European species were not only present in several regions but also occurred along the entire elevational gradient within those regions. The dominance of European species might therefore also be related to their broad climatic plasticity. The native ranges of many of these species extend from the Mediterranean to the boreal zone, and from the Atlantic coast to continental climates in eastern Europe, Russia or temperate Asia. Many Eurasian species have also experienced recurrent climatic oscillations in the past related to glacial cycles, which may have further selected for broad climatic tolerances (Dynesius & Jansson, 2000).

CONCLUSIONS

Non-native species are influenced by processes operating over a wide range of spatial scales, and a multi-scale approach is therefore required to understand their distribution patterns. The processes involved include global dispersal through human agency, filtering along elevational gradients and differential establishment depending upon disturbance. The fact that variation in richness was equally accounted for by regional differences at the global scale and elevation at the regional scale highlights the importance of global dispersal in recent community assembly of non-native plant species. Ideally future research will concentrate on the assembly of native and non-native species along the elevational gradient, phylogenetic relatedness, homogenization and the implications of global change on floras in mountainous regions.

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SUPPORTING INFORMATION

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

Appendix S1 Figure detailing sample location and plot layout along roads.

Appendix S2 Correlations of land use, richness, habitat diversity and elevation.

Appendix S3 Boxplots detailing variation in mean annual temperature and total yearly precipitation for regions; data taken from WorldClim (http://www.worldclim.org/).

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