Running off the road: roadside non-native plants invading mountain vegetation

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Abstract

Prevention is regarded as a cost-effective management action to avoid unwanted impacts of non-native species. However, targeted prevention can be difficult if little is known about the traits of successfully invading non-native species or habitat characteristics that make native vegetation more resistant to invasion. Here, we surveyed mountain roads in seven regions worldwide, to investigate whether different species traits are beneficial during primary invasion (i.e. spread of non-native species along roadside dispersal corridors) and secondary invasion (i.e. percolation from roadsides into natural adjacent vegetation), and to determine if particular habitat characteristics increase biotic resistance to invasion. We found primary invasion up mountain roads tends to be by longer lived, non-ruderal species without seed dispersal traits. For secondary invasion, we demonstrate that both traits of the non-native species and attributes of the receiving natural vegetation contribute to the extent of invasion. Non-native species that invade natural adjacent vegetation tend to be shade and moisture tolerant. Furthermore, non-native species invasion was greater when the receiving vegetation was similarly rich in native species. Our results show how mountain roads define which non-native species are successful; first by favouring certain traits in mountain roadsides (the key dispersal pathway to the top), and secondly by requiring a different set of traits when species invade the natural adjacent vegetation. While patterns in species traits were observed at a global level, regional abiotic and biotic variables largely generated region-specific levels of response, suggesting that management should be regionally driven.

Keywords

Biotic resistance, elevation gradient, management, primary invasion, secondary invasion, traits

Introduction

Plant invasions in natural vegetation can cause impacts on biodiversity, ecosystem services and ecological processes, including nutrient cycling (Simberloff 2011), water production (LeMaitre et al. 1996), and fire regimes (Mack and D'Antonio 1998; Ehrenfeld 2010; Simberloff 2011). Prevention of new invasions is typically regarded as the most cost-effective management action to avoid these impacts (Leung et al. 2002). To pursue this strategy, land managers can make use of the fact that the spread of non-native species follows typical dispersal pathways, like roads and railways tracks, and from there they invade into natural vegetation (McDougall et al. 2011; Pollnac et al. 2012; Seipel et al. 2012). However, in reality it is impossible to monitor such pathways in a whole region and manage or eradicate all newly established populations of non-native species. Therefore, management may be more effective if it is targeted at 1) the species possessing traits that are likely to increase their invasiveness in natural vegetation and 2) the characteristics of natural vegetation that make it less resistant to invasion.

A long-standing goal of invasion research has been to identify species traits that increase the invasiveness of a species, starting with Baker's idea of the 'ideal weed' in the 1960s (Baker 1965). Since then, numerous studies have compared traits between native and non-native species (Daehler 2003; van Kleunen et al. 2010a), or between non-native and invasive species, and, several consistent patterns have been identified. For instance, van Kleunen et al. (2010b) reported in their meta-analysis of over 100 field or common-garden studies that invasive non-native species scored higher in performance-related traits than non-invasive species. But a limitation of these studies is that they do not distinguish between traits favouring establishment and spread in anthropogenically disturbed habitats such as dispersal corridors, and traits that enable a non-native species to percolate from there into natural vegetation. Indeed, favourable species traits are likely to differ between "primary" (anthropogenically disturbed habitat) and "secondary" (natural habitat) phases of the invasion process (Dietz and Edwards 2006). During primary invasion, usually in resource-rich and disturbed environments, species with a ruderal ecological strategy (sensu Grime 1977) possessing traits that promote establishment and spread along invasion corridors, such as short (i.e. annual) generation times, highly dispersive seeds and tolerances for open dry conditions, are hypothesised to have an advantage (Dietz and Edwards 2006). In contrast, species with traits conferring greater

competitive ability or higher stress-tolerance, such as clonality, perennial life history or shade tolerance, are expected to be more successful during secondary invasion (Dietz and Edwards 2006). That different selection pressures operate at different stages of invasion might help explain why research results sometimes seem to be contradictory and the process of invasion has been regarded as idiosyncratic (Lockwood et al. 2005; Dietz and Edwards 2006; Kueffer et al. 2013a).

Beside species traits, characteristics of the receiving site can play an important role in determining invasibility, with some vegetation types in a region typically being more resistant to invasion than others (e.g. Vilà et al. 2007; Milbau et al. 2013; Speziale and Ezcurra 2011). This may be explained by the frequency and magnitude of disturbances, which affect the availability of resources (e.g. Davis et al. 2000; Lake and Leishman 2004; Lembrechts et al. 2017), and facilitation (e.g. Cavieres et al. 2007) or competition (Cavieres et al. 2018) by resident native plants. At a local scale, vegetation structure may be important with, for instance, natural gaps in forest being entry points for invasive species (e.g. Knapp and Canham 2000; Knight et al. 2008). Vegetation that is species diverse tends to be more resistant to invasion (Elton 1958; McCann 2000), although there are inconsistencies across spatial extents and habitats (Fridley et al. 2007).

Even though these and other drivers of invasibility and invasiveness have been extensively explored, little is known about how the relative importance of different drivers varies between regions with differing environmental contexts. For example, the meta-analysis of van Kleunen et al. (2010b) showed that in tropical climates the difference in growth rates between invasive and non-invasive species is much greater than in temperate climates. Similarly, drivers of invasibility and invasiveness might be expected to change across environmental gradients within regions (Pauchard et al. 2009). For example, traits associated with stress tolerance might become increasingly important for non-native species establishment as environmental harshness increases (Zefferman et al. 2015), even in anthropogenically disturbed habitats. Furthermore, factors promoting the invasibility of natural habitats might increase or decrease in importance depending on environmental severity. For example, if disturbance acts to reduce competitive pressure from native species, then disturbance might be an especially important driver of non-native species establishment under benign environmental conditions (Pauchard et al. 2009; Lembrechts et al.

2014). To address these questions, and so achieve a more complete picture of the determinants of invasion success, the challenge is to obtain data on non-native species establishment in both anthropogenically disturbed and natural vegetation, across environmental gradients and in multiple regions.

Mountains offer ideal conditions for investigating the spread of non-native species from dispersal corridors into adjacent vegetation along environmental gradients. Non-native species are typically introduced at low elevation and spread towards higher elevation along roads (Alexander et al. 2011; Haider et al. 2018). Once established along the disturbed road edges, non-native species may then move into the adjacent vegetation that is typically less affected by humans and dominated by native plant species. A strong decline in non-native species richness away from mountain roads has been observed (Seipel et al. 2012), indicating that invasion does occur beyond roads but that there are substantial barriers that limit it (Pollnac et al. 2012). An advantage of this study system is that the geographical distance between pathway and natural vegetation is short. This excludes the possibility that propagule availability and climate are the limiting factors and potential barriers, because non-native species have already established along the roadsides. Furthermore, the decline in non-native species richness away from roads is increasingly steep at higher elevations (Seipel et al. 2012), suggesting that climate interacts with other community or species characteristics to affect invasion into natural vegetation. Finally, these patterns have been observed in multiple mountain regions around the world, providing the opportunity to assess the extent to which particular correlates of habitat invasibility and species' invasiveness are region-specific.

In this paper, using data from widely separated global regions, we investigate which species traits promote invasion along roadsides (i.e. primary invasion) and from there into natural vegetation (i.e. during secondary invasion), and which characteristics of the habitat away from the roads influence resistance to invasion. In addition, we analyse for the first time whether factors influencing non-native species secondary invasion change along steep elevation gradients. We predict that (1) particular traits and ecological attributes will be associated with higher levels of invasion, specifically that long-lived species, with good competitive abilities, and the ability to tolerate shadier, cooler and moister conditions are more likely to invade natural vegetation. In addition, we expect that seed traits related to dispersal adaptation are not relevant to spread from roadsides into adjacent vegetation, due to the environmental and species trait

filters associated with primary invasion and the availability of propagules over the short distances involved. Further we predict that (2) natural vegetation has a higher invasion resistance if it has a high native species-richness, with a high proportion of tree species that compete for light and resources with the invader, and a low level of disturbance.

With the use of our systematic sampling approach along elevation gradients we explore the importance of factors influencing non-native species richness in natural vegetation not only along environmental gradients within regions, but also the variation of these patterns between regions, asking what generalizations emerge across regions.

Methods

Study areas and survey design

We sampled roads and their adjacent vegetation in seven mountain regions: Nahuel Huapi National Park in Argentina; Kosciuszko National Park in Australia; south-central Andes in Chile; northern Scandes in Norway; Canton Valais in Switzerland; two regions in the United States – the Greater Yellowstone Ecosystem in Montana and Wyoming, and the Wallowa Mountains in north-eastern Oregon (Table 1).

In these seven regions, we selected three roads that extended over broad elevational gradients (Table 1) and were open to vehicular traffic for at least part of the year. The roads sampled ranged from low use, gravel roads to asphalt highways. The road edges typically had shallow soils, reduced tree canopy cover (compared to adjacent vegetation) and much bare ground. In many cases the surface soils of the road edge were heavily altered, or not native to the area having been imported for road-making. The adjacent vegetation was less or un-disturbed, had native soils, and plants native to the region dominated. All sampling was conducted between 2011 and 2015.

Twenty locations were selected on each road at approximately equal elevational intervals (see also Seipel et al. (2012) and Haider et al. (2018)). The highest sample was generally at the highest point that could be reached by road and the bottom was the point below which there was no substantial change in elevation or further sampling became impractical (e.g. because of land tenure). At each location, three 2 m x 50 m (100 m^2) plots were sampled; one in road habitat at the edge of the road surface and with the long

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side parallel to it, one perpendicular to it in adjacent vegetation, from 50 m to 100 m away from the road and a third (not used in this paper because it represents an ecotone between disturbed roadsides and more natural vegetation), 0 m to 50 m from the road. Topographic constraints (e.g. cliffs) and cultivated farmland prevented the sampling of some plot pairs in two regions (Table 1). The covers of all vascular plant species and bare ground were recorded in each plot using the following ordinal scale: 1 = <1%, 2 = 1 to <5%, 3 = 5 to <25%, 4 = 25 to <50%, 5 = 50 to <75%, 6 = 75 to <95%, 7 = 95 to 100%. Taxonomy was standardised between regions using the Taxonomic Name Resolution Service v4.0 (Boyle et al. 2013; http://tnrs.iplantcollaborative.org/TNRSapp.html, accessed April 2015) and local published floras. Species were classified as either native or non-native according to local and regional floras (for details see Haider et al. 2018).

Species traits

Intra-specific trait variation can be remarkably high along elevation gradients for some traits (e.g. specific leaf area, see Rosbakh et al. 2015), and in such cases species' average trait values would not be appropriate for our study design. Therefore, we chose to use species traits that are or are more likely to be spatially invariant: 1) life history (obtained from local floras and personal knowledge); 2) ecological traits: Grime strategy (Grime 1977) obtained from the BiolFlor database (Klotz et al. 2002) and Ellenberg indicator values for moisture, light and temperature (Ellenberg and Leuschner 2010); and 3) seed characters relating to dispersal, obtained from the D^3 database (Hintze et al. 2013) (Table 2). These traits are indirectly related to plant performance (e.g. perenniality or competitive behaviour, differential dispersal capacity, and habitat preference). For some species, trait data were not available; availability ranged from 45 to 100% of species (Table 2).

Data analysis

Do trait patterns of non-native species differ along elevation gradients and between roadside and adjacent vegetation?

We modelled the proportion of non-native species in a plot possessing particular traits as a function of the elevation of the plot, and whether it was located in roadside or natural adjacent vegetation. We calculated the proportion of species with a certain trait at the plot level by dividing the number of non-native species with that trait in each plot by the total number of non-native species in that plot. Then, we fitted models across all regions for the proportion of each trait, using generalized linear mixed models with a binomial distribution (GLMMs, function glmer, package lme4; Bates et al. 2011), with elevation (regionally scaled with mean = 0 and standard deviation = 1), plot type (roadside vs. adjacent) and their interaction as fixed effects, and including 'road' nested in 'region' as random effects. We also fitted models including random effects of transect (nested in road), but these were not supported based on a comparison of Akaike Information Criterion values (AICc, corrected for small sample sizes; Zuur et al. 2009), and so were dropped from the models. For each trait, we then made a set of models with all possible combinations of the abovementioned fixed factors as explanatory variables. Next, we used model averaging of the estimates of all models in which the AICc differed less than 2 from the best model (function model.avg, package MuMIn; (Bartoń 2015)), and weighted the estimates based on the support for each model, with more weight given to models with a lower AICc (Burnham and Anderson 2002). Such an approach has been advocated to result in more robust model fitting than single-model methods and stepwise model selection, as it provides a quantitative measure of relative support for competing hypotheses and the uncertainty surrounding each predictor (Burnham and Anderson 2002).

Which biotic and abiotic plot-level factors increase non-native species richness in adjacent vegetation?

We investigated the effect of five environmental factors collected at the plot level on non-native species richness in the adjacent vegetation plots using GLMMs. In preliminary analyses with region and road (nested) as random effects, models were uninformative because of large regional differences and so, unlike the trait analysis, models were fitted for each region separately. The following factors were assessed for each adjacent vegetation plot:

a) Non-native species richness in the corresponding roadside plot, as a proxy for propagule availability at the roadside;

b) Native species richness in the adjacent vegetation plot;

c) Disturbance: the cover of bare ground in adjacent plots (on the ordinal classes outlined above);

d) Elevation recorded in the adjacent plot. Elevation in all regions was strongly inversely correlated with mean annual temperature and mean temperature of the warmest quarter and so this variable is reflective of climate at the plot scale (Table S1). Elevation was also positively correlated with annual precipitation and precipitation in the warmest quarter in all regions except in Argentina and Chile where it was negatively correlated (though weakly so in Chile);

e) Tree cover rank in adjacent plots: the rank in tree cover from lowest (1) to highest (equal to the number of plots in a region). To calculate tree rank for a plot, the median covers of the ordinal values for tree species in each plot were summed and the total was then ranked from lowest to highest.

Our approach to fitting the GLMMs here involved two steps. Firstly, we fitted models containing only main effects of the five explanatory variables listed above to estimate their overall effect sizes within each region. An exception was Switzerland, where due to lower sample size we only included three variables (native species richness, bare ground, elevation) in the models to avoid overfitting. Secondly, we fitted models including elevation and variables associated with properties of the adjacent vegetation (i.e. native species richness, bare ground and tree cover rank, but excluding roadside non-native species richness) and their two-way interactions with elevation (but only with bare ground in the case of Switzerland). In all cases we fitted the GLMMs for each region separately, with non-native species richness in adjacent plots as the response variable and "road" included as a random factor. Models were fitted assuming a Poisson distribution and log link function. All explanatory variables were standardised by region prior to analysis (with mean = 0 and standard deviation = 1) so that model estimates could be interpreted as relative effect sizes. Estimates and 95% confidence intervals were calculated for each explanatory variable. Variables for which the confidence intervals did not include zero were regarded as significant. The mixed model analyses were performed using the lme4 package (Bates et al. 2011), and all analyses were performed using in R version 3.4.3 (R Development Core Team 2014).

Results

Most non-native species on roadsides were recorded in Australia (114) and fewest in Norway and Switzerland (14; Table 3). Despite this, Australia had the second lowest percentage of non-native species reaching adjacent vegetation at a regional scale (37%); Oregon had the highest (92%). There were large regional differences at the plot scale. In Norway for instance, on average only 7% of non-native species in roadside plots were found in the adjacent plots while in Chile on average more than half of the species in roadside plots (55%) were present in the adjacent plots. Most non-native species recorded on roads (63%) were only recorded in one region, making it difficult to generalise at the species level.

Do trait patterns of non-native species differ between roadside and adjacent vegetation, along elevation gradients?

Both along roadsides and in the adjacent vegetation, the proportion of all perennial non-native species significantly increased with increasing elevation, while the proportion of all annuals decreased (Fig. 1). The proportion of ruderal non-natives increased significantly with increasing elevation in adjacent vegetation but remained relatively constant along the roadsides (Fig. 1, Supplementary Material Table S2). Contrarily, the proportion of non-ruderals decreased with elevation in adjacent vegetation, but slightly increased along the roadsides. Overall, we found a higher proportion of non-ruderal species in adjacent vegetation compared to roadside plots (Table S2). Across the whole elevation gradient, we found higher proportions of non-native species preferring moister (Ellenberg values for moisture M5-10) and shadier conditions (values L4-7) in the adjacent vegetation (Fig. 1). The proportion of species invading adjacent vegetation preferring cooler sites (values T3–5) increased with elevation, while the proportion of non-native species preferring warmer sites (values T6–8) decreased in proportion with increasing elevation, with some support for a relative increase in cold-adapted species in the adjacent vegetation across the whole elevation gradient (Fig. 1). The proportion of non-native species with seeds adapted for dispersal (Fig. 1, see Table 2 for adaptations included) decreased with elevation, while the proportion of non-native species without dispersal-adapted seeds increased with elevation (Fig. 1).

Which biotic and abiotic plot-level factors influence non-native species richness away from roadsides?

Non-native richness on roadsides had an effect on non-native richness in adjacent vegetation in only two regions: Argentina (negative) and Australia (positive) (Fig. 2a). Native species richness in adjacent vegetation was significantly positively related to non-native richness in adjacent vegetation in all regions except Switzerland (Fig. 2a). In Argentina and Australia, these positive effects of native species richness became stronger with increasing elevation (Fig. 2b). Bare ground had a positive influence on non-native species richness in adjacent vegetation in three regions (Argentina, Australia and Oregon) but a negative effect in Chile (Fig. 2a). However, these effects depended on elevation, decreasing in Chile and Argentina and increasing in Australia and Oregon with increasing elevation (Fig. 2b). Elevation had a negative effect on non-native species richness in adjacent vegetation in five regions (Argentina, Chile, Montana, Oregon and Switzerland). Tree cover had a negative effect on non-native richness in adjacent vegetation in three out of six regions (Australia, Chile and Montana).

Discussion

While it is by now well established that non-native species richness declines with elevation in mountains around the world (Alexander et al. 2016), less is known about the ability of these species to spread away from disturbed roadside corridors into natural adjacent vegetation. Here we show that both traits of the non-native species and attributes of the receiving natural vegetation contribute to the extent of invasion. Interestingly, we had consistent results regarding the species traits which support secondary invasion away from the roads, however, biotic and abiotic plot-level characteristics varied strongly across regions.

<u>Do trait patterns of non-native species differ between roadside and adjacent vegetation, along elevation gradients?</u>

We identified several species traits that varied in proportion either along elevation gradients within regions, or between roadside and natural adjacent habitat. This suggests the presence of two filters operating on non-native species in mountain environments (Dietz and Edwards 2006): one acting on the species pool as species spread upwards along the elevation gradient (Alexander et al. 2011), and a second related to the subsequent invasion into natural vegetation away from roads (Lembrechts et al. 2014). The

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increase in the proportion of perennial species with increasing elevation – and corresponding reduction in the proportion of annuals – is consistent with global trends and explained by the difficultly of completing the life-cycle within a single growing season at high elevation (Körner 2003). However, the proportion of perennial species was not higher in adjacent vegetation compared to roadsides as we expected. Thus, we assume that short-lived species are not only filtered out through biotic, competition-related mechanisms during secondary invasion, but that environmental filtering during primary invasion limits the spread of non-perennial species. We did not find an increase of cold-adapted species at higher elevations, strengthening the assumption that species need to establish first under lowland conditions and from there spread to high-elevations. Interestingly, the proportion of species with dispersal abilities decreased with increasing elevation. This suggests that the overall low invasion rate in most mountain regions is not due to dispersal limitation, but that other species traits (e.g. climatic pre-adaptation) might be more important.

Other species traits were disproportionately associated with non-native species that established away from roadsides. In particular, these species tended to show a preference for moister and shadier habitats, in contrast to the open and well-drained conditions typical of many roadside habitats (Forman and Alexander 1998). While the traits that appear to be disproportionately affected by elevation and habitat filters make intuitive sense, our analyses also suggested that these filters only rarely interact. The only exception was the proportion of species with a ruderal strategy, which strongly increased with elevation in adjacent vegetation, while it was rather constant along roadsides. Likely, this refers to a decrease of competition levels in natural adjacent vegetation with increasing elevation, which allows ruderal species to establish. However, it is counter-intuitive that the proportion of ruderal species at high-elevations is lower in roadside compared to adjacent plots. In this case, we might expect that the few species that do spread away from roadsides are ecological opportunists. Contrarily, the species attributes that were associated with successful establishment away from roadsides rarely changed with elevation (i.e. proportion of moist- and shade-adapted species). While the limited amount of interactions between elevation and habitat filters suggests that, for example, an ability to tolerate higher elevation environments does not necessarily trade-off with attributes (such as shade-tolerance) that would promote invasion of higher elevation habitats away from roadsides, it is likely that the number of species with traits necessary

for both primary and secondary stages of spread is limited. The additive effect of these filters thus helps explain why the number of non-native species decreases with both elevation and distance from roads (Seipel et al. 2012).

That elevation and climate gradients serve as a directional filter for non-native species with certain traits was already known (Alexander et al. 2011). However, our results reveal how mountain roads also define which non-native species are successful; first by favouring certain traits in mountain roadsides (the key dispersal pathway to the top), and secondly by providing a secondary filter – requiring a different set of traits - when species invade the natural adjacent vegetation.

Which biotic and abiotic plot-level factors influence non-native species richness away from roadsides?

Invasion success into adjacent vegetation was also influenced by the characteristics of the receiving vegetation, though not always in ways we expected. We expected invasion resistance in natural vegetation to occur where there was high native species-richness, a high cover of tree species that compete for light and resources with the invader, and a low level of disturbance. However, only the last two of these were supported by our analyses and then not in all regions and not in consistent ways. In all but one region, there was greater invasion where native species richness was higher in the adjacent vegetation. Greater invasibility of species-rich habitat has been observed at coarser spatial scales (Fridley et al. 2007). Native species-rich habitat might indicate good resource availability so that many species can co-exist. Such communities will tend to have greater capacity to accept additional, non-native species than resource-poor habitat. Our study plots of 100 m², might indicate that the positive effect of microhabitat variability on species richness operate at this relatively fine scale. Light is an important resource for invading species, and native tree cover had a negative impact on invasion in three of the six regions. Knight et al. (2008) found a negative relationship between tree cover and invasibility but a positive relationship between native species richness and non-native cover, concluding that native species and non-native species respond similarly to resource availability (in this case light) where the resource is limited. The positive relationship we observed between non-native and native species richness may thus simply reflect natural processes associated with

tree death, with opportunistic native and non-native species colonising canopy gaps, at least in plots below the tree line.

Bare ground is typically associated with disturbance and had a significant positive effect on invasion in three regions but in Chile the effect was negative. There is little doubt that disturbance can aid invasion of natural vegetation by non-native plant species (e.g. Petryna et al. 2002; Lake and Leishman 2004; Hansen and Clevenger 2005; Lembrechts et al. 2016). Disturbances such as fire (e.g. Keeley et al. 2003) and animal digging (e.g. Larson 2003) typically create room for establishment of non-native species by seed. The lack of an effect of bare ground in some regions is perhaps temporal. Many disturbances causing bare ground are ephemeral (e.g. fire, landslides, flood, road maintenance). If the time since disturbance was long, bare ground might already have been covered by regenerating and establishing plants. The negative effect of bare ground on the richness of non-native species in Chile is likely explained by the dry Mediterranean-type climate generating a patchy vegetation, as bare ground was typically highest in areas with a high cover of rock. It is possible that the shallow and dry soils of these sites, although exposed, were not conducive to plant establishment in general.

While climatic conditions (as represented by elevation) and habitat characteristics were important drivers of non-native species richness away from roadsides in most regions; the effect of non-native species richness on the roadside was only significant in Argentina and Australia. If non-native richness at roadsides can be taken as a proxy for propagule availability, this suggests that plant invasion away from the roadside in mountains is not just a stochastic process driven by the roadside non-native species pool, but that it depends on a match between species traits and habitat characteristics (Pollnac and Rew 2014; Lembrechts et al. 2018).

Management implications

We found that there are large differences within and between regions in the degree of invasion away from roadsides. Some of this variation might be attributable to differences in management between regions, with considerable control of non-native species occurring in some regions (e.g. Australia and the US) but

barely in others (e.g. Chile). Yet although herbicides are used to reduce non-native species abundance in Australia and the US, the level of invasion was low in Australia and high in Oregon.

Our results can help identify good practices for management. At the most general level, the study makes a strong case for the importance of multiple filters in mountain invasions: only species that are both successful in primary invasions at disturbed sites and along broad elevational gradients, and in secondary invasions into natural vegetation, will eventually become invasive. This supports the idea that direct human introduction of mountain-adapted species to high elevations, which surpasses the primary invasion filters, can greatly increase invasion risks in mountains through non-native species that are filtered out at present in the primary invasion phase (McDougall et al. 2011; Kueffer et al. 2013b). As a result, many novel invasive species not yet present in mountains might emerge in coming years (McDougall et al. 2011).

The region-specificity of many of the observed patterns suggests that it will be difficult to globally target individual species, a group of species or general habitat types for management of non-native species based on the combined data. Indeed, while the non-native species pool in high elevation adjacent vegetation showed some specific traits that could be targeted (for example cold-, moist- and shade-adapted), the degree to which these species escape into the natural vegetation was largely habitat-specific, and the large overlap in species in roadsides and natural adjacent vegetation suggests invasion into the adjacent vegetation might be largely idiosyncratic though ultimately inevitable. Targeted management may still be possible region by region, however, and some of our study regions have already identified priority species for control (e.g. Kueffer et al. 2013a). The regional patterns observed in this study might help in that regard, as we do report several region-specific habitat characteristics that were related with higher non-native species richness. In Australia at least, the positive relationship between non-native species richness on roads and non-native species richness in adjacent habitat suggests that a simple approach to non-native species management will be to reduce non-native species richness on roads. This might be achieved with regular application of herbicide or mechanical removal, and vehicle and visitor hygiene where practicable (Rew et al. 2018). Where herbicides are frequently applied, managers should be mindful of secondary invasion; i.e. removing one non-native species may simply create space for another (Kuebbing and Nuñez 2016; Pearson et al. 2016). Habitat restoration using native species or sterile non-native species,

in combination with herbicide application, is likely to be a better long-term solution in most cases. Whatever the approach to management of non-native species on roads, adaptive management (e.g. vigilance, rapid response and monitoring) is required to deal with future, possibly unpredictable, threats from non-native species.

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Table 1. Characteristics of the seven regions: location, the number of sampled plots, the range from the minimum to the maximum elevation of the sampling plots, and the range of mean annual temperature and rainfall (extracted from downscaled 30 arc second Worldclim data (Hijmans *et al.* 2005)).

Region	Coordinates (approx.)	Sample pairs	Elevation range (m a.s.l.)	Mean annual temperature range (°C)	Annual rainfall range (mm)
Argentina	41°S, 72°W	60	857 – 1678	3.6 – 7.5	883 – 1240
Australia	36°S, 148°E	60	410 – 2125	3.9 – 13.2	856 – 1842
Chile	37°S, 71°W	51	378 – 1666	6.5 – 11.6	1150 – 2285
Norway	68°N, 18°E	60	13 – 696	-4.3 – 1.9	700 – 862
Switzerland	46°N, 7°E	29	411 – 1800	0.3 – 8.8	780 – 1770
USA: Montana	45°N, 110°W	60	1803 – 3315	-3.1 – 4.7	487 – 777
USA: Oregon	45°N 118°W	60	902 – 2264	0.5 – 8.6	462 – 715

Table 2. Species trait data analysed, the categories (attributes) within each trait, and the percentage of species for which trait data were available. The Grime strategy category was compressed from the original data to the three key components (C, R and S; i.e. a species regarded as CR was included in both categories). The Ellenberg indicator values were grouped so that there was an approximately equal number of species in each category. The last column indicates for how many species (in %) trait data were available.

Species traits	Categories	Species (%)
Life history	Annual / perennial	100
Grime strategy	Competitive (C species) / not competitive (Ruderal (R species) and Stress tolerant (S species))	70
Ellenberg moisture	Indicator values: M2–4 (drier) / M5–9 (moister)	52
Ellenberg temperature	Indicator values: T3–5 (cooler) / T6–8 (warmer)	45
Ellenberg light	Indicator values: L4–7 (shadier) / L8–9 (brighter)	56
Seed dispersal characters	Present (seeds are nutritious, flat, elongated, hooked or mucilaginous) / absent (no dispersal adaptations)	84

Table 3. The minimum - median - maximum numbers of non-native species per plot in roadside and

adjacent vegetation, and the total number of species recorded (in parentheses) in the seven regions.

| Region	Roadside	Adjacent vegetation	Non-native species reaching adjacent vegetation (total % for region)	Non-native species reaching adjacent vegetation (mean % by plot)
Argentina	0 – 7 – 15 (45)	0 – 0 – 9 (23)	51	28
Australia	2 – 18 – 38 (114)	0 – 2 – 13 (42)	37	17
Chile	2 – 7 – 19 (62)	0 – 4 – 14 (37)	60	55
Norway	0 – 3 – 6 (14)	0 – 0 – 1 (3)	21	7
Switzerland	0 – 1 – 8 (14)	0 – 0 – 4 (7)	50	24
USA: Montana	0 – 6 – 12 (37)	0 – 0 – 11 (23)	60	24
USA: Oregon	0 – 11 – 27 (63)	0 – 2 – 31 (58)	92	42
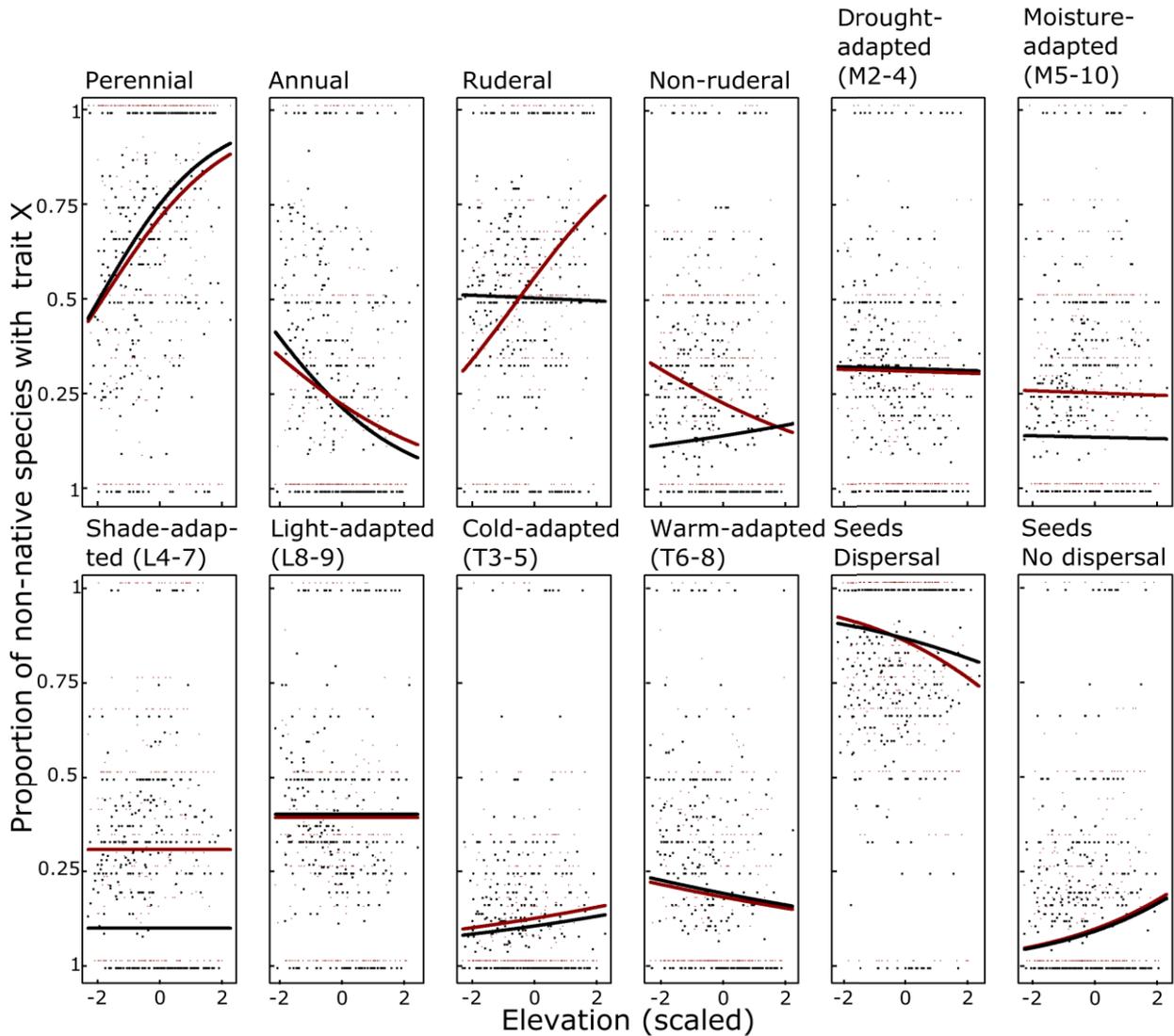
Fig. 1. Model predictions (weighted averages of all models with ΔAICc < 2, see Supplementary Material

Table S2 for model support) for the proportion of non-native species with a certain trait (panel header) as a

function of elevation (x-axis, scaled with mean = 0 and sd = 1), plot type (roadside = black line, adjacent

vegetation = red line). Ruderal: Grime-strategy = R; Non-ruderal: Grime-strategy = C or S; Drought-adapted:

Ellenberg moisture values of 2 to 4; Moist-adapted: Ellenberg moisture values of 5 to 10; Shade-adapted:

Ellenberg light values of 4 to 7: Light-adapted: Ellenberg light values of 8-9; Cold-adapted: Ellenberg

temperature values of 3 to 5; Warm-adapted: Ellenberg temperature values of 6 to 8; Seeds dispersal:

seeds with traits adapted for dispersal (see Table 2 for adaptations included); Seeds no dispersal: seeds
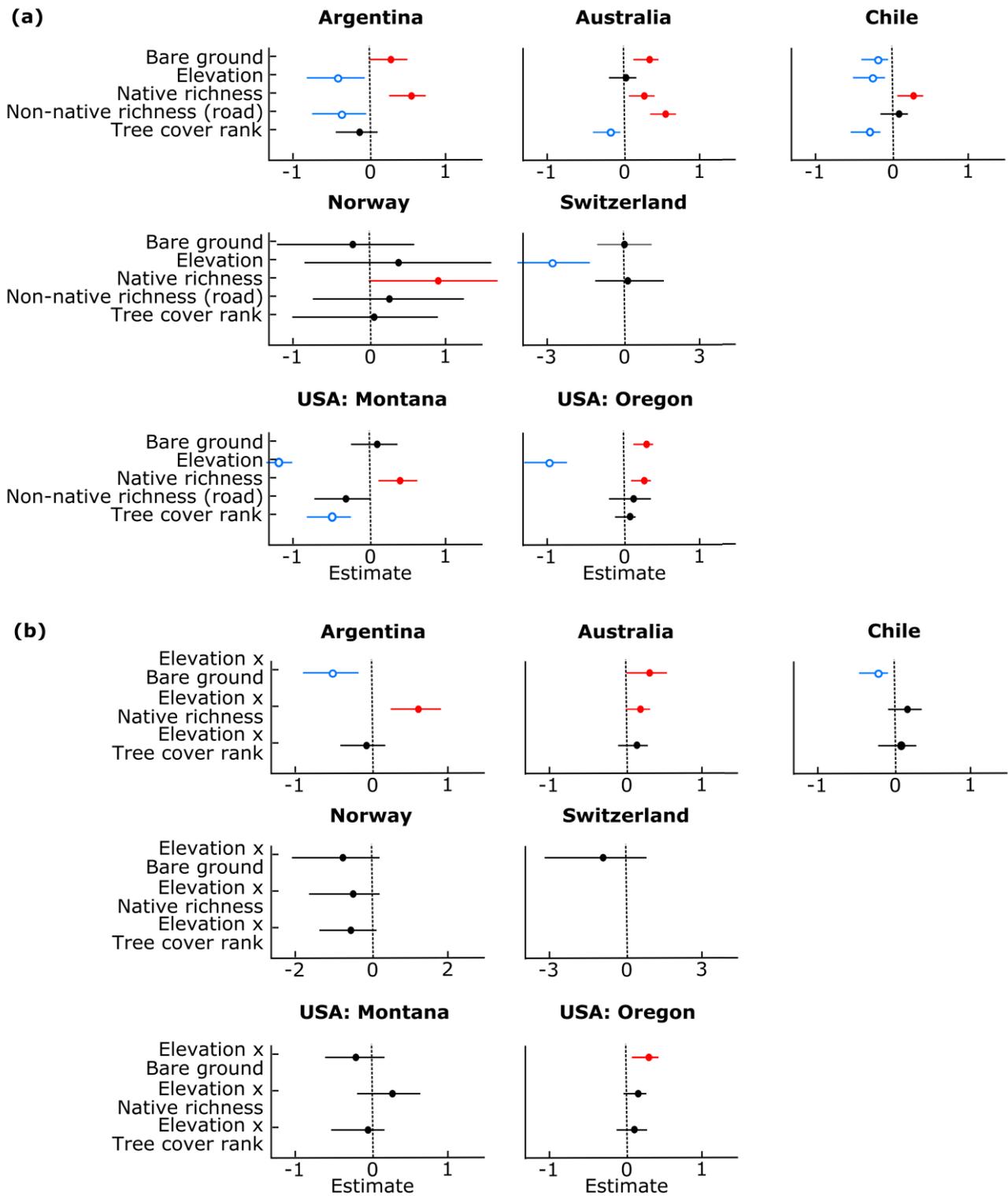
without dispersal-adaptations.

Fig. 2. Effect size (estimate) and 95% confidence intervals for a) variables in generalised linear mixed effects models of non-native species richness in adjacent vegetation and b) interactions between elevation and selected variables. Significantly positive estimates are indicated in red (with full dots), negative in blue (open dots).