RESEARCH PAPER

Mountain roads and non-native species modify elevational patterns of plant diversity

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Abstract

Aim: We investigated patterns of species richness and community dissimilarity along elevation gradients using globally replicated, standardized surveys of vascular plants. We asked how these patterns of diversity are influenced by anthropogenic pressures (road construction and non-native species).

Location: Global.

Time period: 2008–2015.

Major taxa studied: Vascular plants.

Methods: Native and non-native vascular plant species were recorded in 943 plots along 25 elevation gradients, in nine mountain regions, on four continents. Sampling took place in plots along and away from roads. We analysed the effects of elevation and distance from road on species richness patterns and community dissimilarity (beta-diversity), and assessed how non-native species modified such elevational diversity patterns.

Results: Globally, native and total species richness showed a unimodal relationship with elevation that peaked at lower-mid elevations, but these patterns were altered along roads and due to non-native species. Differences in elevational species richness patterns between regions

disappeared along roadsides, and non-native species changed the patterns' character in all study regions. Community dissimilarity was reduced along roadsides and through non-native species. We also found a significant elevational decay of beta-diversity, which however was not affected by roads or non-native species.

Main conclusions: Idiosyncratic native species richness patterns in plots away from roads implicate region-specific mechanisms underlying these patterns. However, along roadsides a clearer elevational signal emerged and species richness mostly peaked at mid-elevations. We conclude that both roads and non-native species lead to a homogenization of species richness patterns and plant communities in mountains.

1 | INTRODUCTION

In the last two decades, research into elevational species richness patterns has gained renewed attention, and in a large number of regional studies (e.g. Grytnes, Beaman, Romdal, & Rahbek, 2008; Siefert, Lesser, & Fridley, 2015) and several global meta-analyses (e.g. Guo et al., 2013; Steinbauer et al., 2016) a variety of different patterns have been observed. The different patterns could result from a range of different drivers (see e.g. Romdal & Grytnes, 2007 and references therein; McCain & Grytnes, 2010), but also from differences in survey protocols.

Unimodal patterns of species richness along elevation gradients have often been detected around the world (Rahbek, 2005). Mid-elevational peaks in species richness could result from geometrical constraints on the random placement of species' ranges within a bounded elevational domain, causing greatest overlap of species' ranges at the centre of the gradient (known as the mid-domain effect; Colwell & Lees, 2000; Grytnes et al., 2008). But such a pattern could also have biotic explanations, for example if fewer environmental specialists occur towards the extremes of the gradient (Kammer & Möhl, 2002).

Beta-diversity, that is community dissimilarity, is expected to increase with elevational distance between sampling units because increasing environmental (e.g. climatic) differences select for different suites of species, and because geographic distance imposes dispersal constraints to species exchange (distance decay; Nekola & White, 1999). Few studies based on empirical data have simultaneously addressed the response of species richness and community dissimilarity to environmental variation across large geographic extents (e.g. Valdés et al., 2015). Moreover, neither have elevation gradients been considered.

Historically, biodiversity patterns have been predominantly shaped by natural factors such as climatic gradients, but natural environments are now intensely modified by human activities (Sanderson et al., 2002). Increasing evidence indicates that mountain biodiversity is affected by climate change (Gottfried et al., 2012; Lenoir & Svenning, 2013), human land use (Dainese & Poldini, 2012) and non-native species invasion (Marini et al., 2012; Pauchard et al., 2009, 2016; Pyšek,

Jarošík, Pergl, & Wild, 2011; van Kleunen et al., 2015). A feature of many mountains is that they have roads that connect lowlands with high elevation sites. Compared to semi-natural habitats more distant to roads, the habitat directly next to the road is often characterized by high rates of disturbance and reduced competition (Forman & Alexander, 1998; Spellerberg, 1998), plus increased propagule pressure and potential for long-distance dispersal by vehicles (Rew et al., 2018; Taylor, Brummer, Taper, Wing, & Rew, 2012; von der Lippe & Kowarik, 2007). Such habitats also have more homogenous abiotic conditions as a result of similar construction techniques and management practices (e.g. mowing). As a result, species have been shown to have larger elevational ranges along roadsides compared to adjacent semi-natural habitats (Lembrechts et al., 2017; Pollnac, Seipel, Repath, & Rew, 2012).

Contrary to native species, non-native plant richness has been shown to consistently decrease with elevation, at least from the lowest third of the gradient upwards (Haider et al., 2010; Seipel et al., 2012; Tanaka & Sato, 2016; Zhang et al., 2015). This pattern is likely caused by range expansion from low to high elevations, coupled with ecological filtering on a pool of predominantly low-elevation non-native species (Alexander et al., 2011). Thus, non-native species at high elevations are a subset of the low-elevation non-native species pool (Haider et al., 2010; Alexander et al., 2011; Averett et al., 2016). We expect non-native species to increase similarity between the communities they invade across elevation gradients, because they tend to be environmental generalists (Alexander et al., 2011) and typically have good dispersal abilities (Vicente et al., 2014).

We conducted, to our knowledge, the first multi-region survey of native and non-native plants along elevation gradients that is based on a systematic design in a multi-scale hierarchical framework (Kueffer et al., 2014). Our standardized approach allows us to directly compare elevational species richness patterns of vascular plants across regions, and to test how elevation affects differences in the species composition of plant communities. We simultaneously addressed the effects of roads, non-native plant species and their interaction on diversity patterns across nine mountain regions and tested the following hypotheses:

1. Native species richness peaks at mid-elevations. More specifically, we expect the unimodal pattern to be clearer along roadsides compared to plots away from roads, because roadsides enable higher migration rates (stronger range overlap) and have more homogenous environmental conditions.

2. Non-native species shift the peak of species richness to lower elevations because they predominantly spread from low to high elevation: we expect the effect to be stronger along roadsides.

3. Community dissimilarity is reduced by non-native species, especially along roadsides.

4. The decline in community dissimilarity in response to elevational distance is more gradual along roadsides and when non-native species are included in the analysis.

2 | METHODS

2.1 | Study regions

Standardized vegetation surveys were conducted in nine regions: Norway (northern Scandes), Switzerland (European Alps; Canton Valais), Canary Islands (Mount Teide; Tenerife), Montana (Beartooth Mountains and Yellowstone National Park), and Oregon (Blue Mountains) in the northern hemisphere, and Australia (Australian Alps; New South Wales), central Chile and southern Chile (both Andes), and southern Argentina (southern Andes) in the southern hemisphere. The study regions comprise a range of climatic zones, stretching from a subarctic to Mediterranean climate (Table 1, Supporting Information Figure S1). In all regions three roads were selected (except for central Chile with only one road) along which the vegetation sampling took place, giving a total of 25 roads. Most of the roads started in lowland agricultural settings, followed by an extensive forested montane zone. In five regions, the elevation gradient reached beyond the tree line and thus into alpine vegetation (Table 1). Roads were both paved and unpaved, but all were open to vehicular traffic at least part of the year.

2.2 | Sampling design

The elevation gradient of each road was divided into 19 equally spaced elevation bands, giving 20 sample locations ('transects'; see also Seipel et al., 2012). Exceptions were Switzerland where roads were divided into 20 bands, and central Chile with only 12 bands. (As the elevation gradients differed in length, a standardized elevational distance between transects would have resulted in large differences in the number of sample locations per road and region, and was thus not applied.) At each elevation, 50 m × 2 m plots were sampled. One plot was parallel and next to the road (hereafter 'roadside'). Another 50 m × 2 m plot was placed perpendicular to the roadside plot in semi-natural habitat, and started 50 m, and ended 100 m, away from the road (hereafter 'interior'). Due to natural obstacles (like canyons or very steep slopes) not all plots could be established. Particularly in Switzerland, rough topography and private property adjacent to the roads often prevented sampling in the interior plots. Overall, 943 plots were sampled (Table 1).

In each plot we recorded the presence of all vascular plant species. Species names across regions were standardized with the Taxonomic Name Resolution Service (Boyle et al., 2013). We assigned the status of native or non-native at a regional scale for all species, based on regional databases and literature (Supporting Information Table S1).

2.3 | Diversity measures

Species richness represents the number of species recorded in a plot and was calculated for native, non-native, and native and non-native species combined (hereafter 'all'). To assess the change in community dissimilarity between plots (beta-diversity), we applied the framework of Carvalho, Cardoso, and Gomes (2012), which divides total beta-diversity into two additive components (species richness differences and species replacement) and thus allows insights into ecological processes shaping a change of total beta-diversity (Carvalho et al., 2012; Marini et al., 2013; Podani & Schmera, 2011).

For all pairwise comparisons of species composition among plots that were located within the same plot type (interior or roadside) within

TABLE 1 Location and climatic conditions of the nine study regions (Abbr. = abbreviation, Lat. = latitude, Long. = longitude), vertical range of the sampled elevation gradient, elevation of the tree line, and number of recorded interior and roadside plots

Region	Abbr.	Mountain(s)	Lat.	Long.	Climatic zone	Elevation gradient (m a.s.l.)	Gradient length (m)	Tree line (m a.s.l.)	Recorded plots interior/roadside
Northern hemisphere:									
Norway	NOR	Northern Scandes	68.247	17.654	Subarctic	13–696	683	600	60/60
Switzerland	CH	European Alps (Canton Valais)	46.263	7.509	Temperate	415–1800	1385	2200	28/63
Canary Islands	IC	Mount Teide (Tenerife)	28.250	−16.603	Mediterranean	5–2250	2245	1900	53/55
Montana	MT	Beartooth Mountains, Yellowstone National Park	44.777	−110.196	Temperate	1803–3315	1512	3000	60/60
Oregon	OR	Blue Mountains	45.237	−117.531	Temperate	902–2264	1362	2750	60/60
Southern hemisphere:									
Australia	AUS	Australian Alps (New South Wales)	−36.038	148.359	Temperate	410–2125	1715	1900	60/60
Central Chile	CLC	Andes	−33.338	−70.292	Mediterranean	1900–3585	1685	2200	13/13
Southern Chile	CLS	Southern Andes	−37.568	−71.565	Temperate	274–1686	1412	1800	58/60
Argentina	ARG	Southern Andes	−41.011	−71.530	Temperate	857–1678	821	1700	60/60

a region, total beta-diversity was calculated using the Jaccard dissimilarity index, where values range from 0 (identical species composition) to 1 (no shared species) (Colwell & Coddington, 1994). Total beta-diversity $= (b+c)/(a+b+c)$, where a indicates the number of species shared between plots, and b and c are the number of species that occur in just one of the two plots, respectively. The species richness component of beta-diversity was calculated as the absolute difference in species richness between two plots, beta-diversity (richness differences) $= |b-c|/(a+b+c)$. The species replacement component of beta-diversity is given by the substitution of n species in the first plot from n species in the second plot (Cardoso, Borges, & Veech, 2009). Beta-diversity (replacement) $= 2 \times \min(b,c)/(a+b+c)$, with $\min(b,c)$ being the lower number of species per plot between the two plots.

Total beta-diversity and its two components of species richness differences and species replacement were computed with the 'beta' function in the package 'BAT' (Cardoso, Rigal, Carvalho, & Kembel, 2015) in the R statistical environment (R Core Team, 2016).

2.4 | Data analysis

2.4.1 | Global analysis of species richness patterns

To describe patterns of species richness along the elevation gradient we fitted a global model using data from all regions. The model was fitted using a linear mixed-effects model ('lmer' in the R package 'lmerTest'; Kuznetsova, Brockhoff, & Bojesen Christensen, 2016) with species richness as the response. The predictor variables included a second-order polynomial of elevation, species status that indicated whether the species richness value was for all species combined (native and non-native species) or just the native species, plot type (interior or roadside), and all interactions as fixed effects. For the second-order polynomial, we summarized the linear and the quadratic term of elevation making use of the 'poly' function in R, which uses QR factorization to generate monic orthogonal polynomials. Using polynomials made sure that the linear and quadratic terms were uncorrelated (i.e. orthogonal) and allowed us to show their combined effects in the result tables. A quadratic term was included to account for unimodal patterns of species richness along the elevation gradient. Elevation and species richness were scaled between 0 and 1 in every region to allow comparison among regions with different elevational extents and different ranges of species richness. Species richness was scaled separately for native species and all species combined. For scaling we used the 'decostand' function with the method 'range' in the R package 'vegan' (Oksanen et al., 2016). We added the nested terms region, road, transect and plot as random effects to account for the nested structure of the sampling design and for the fact that richness of native species and all species combined were not independent because records were made in the same plot. p-values were calculated from F-statistics of type III sum of squares with Satterthwaite approximation to estimate the denominator degrees of freedom (R package 'lmerTest').

2.4.2 | Regional species richness patterns

We also compared elevational patterns of species richness within each region separately. Within each region two mixed-effects models with

species richness as the response were fitted that included a second-order polynomial of elevation (see explanations above), species status, plot type, and all interactions as predictor variables (fixed effects). The two regional models differed in the species status to be compared: the first model compared species richness of native species and all species combined, while the second model compared native and non-native species richness. Elevation was scaled and centred by using the 'scale' function. Random effects were the nested terms road (except for central Chile with only one road), transect and plot. As before, p-values were calculated from F-statistics of type III sum of squares with Satterthwaite approximation.

All models (global and regional) were simplified by consecutively deleting non-significant terms, beginning with the three-way interaction. By using likelihood ratio tests based on Chi-squared, we further tested if species richness was better explained by a linear or a parabolic relationship with elevation for the resulting most parsimonious models. For model comparisons we used maximum likelihood (ML), while the final best models were re-fitted with restricted maximum likelihood (REML).

To assess the peak species richness individually for each plot type (interior or roadside) and species status (all species combined, native species or non-native species), we fitted for each region six generalized linear mixed-effects models ('glmer' in R package 'lme4'; Bates, Maechler, Bolker, & Walker, 2013). Species richness was the response (for one of the six combinations of plot type and species status) and elevation was the only explanatory variable. Road identity was added as a random effect. For central Chile generalized linear models ('glm') were used without the random effect because there was only one road. Models were fitted with a Poisson family and log link, or in the case of overdispersion (residual deviance/residual degrees of freedom >1.2) with a negative binomial distribution (quasi-Poisson and log link for the glms for central Chile). Each model was initially fitted with the linear and the quadratic term of elevation ('poly' function in R), and then compared to a simpler model containing only the linear term of elevation by using a likelihood ratio test based on Chi-squared. When there was no significant difference between these two models, the simpler model was also compared to a model containing only the intercept and random effects. We extracted the peak of species richness and its elevation from the model predictions for models with a significant quadratic elevation effect. With a binomial test we sought statistical evidence that the richness peak of all species combined was lower than that of native species.

2.4.3 | Analyses of beta-diversity

We tested with global and regional linear mixed-effects models (R package 'lmerTest') whether beta-diversity depended on species status (native or all species combined), plot type (interior or roadside) or their interactions. To avoid pseudoreplication, as all plots are included in numerous plot pairs, we calculated for each plot the mean beta-diversity from all respective plot pairs that contained that plot. This was done separately for native species and all species combined. In the models, random effects included plot nested in region for the global model, and only plot for the regional models. We fitted models

separately for the response of total beta-diversity and its components of species richness differences and species replacement.

To analyse the effect of elevational distance between plots on beta-diversity, matrix regression models (MRMs) were fitted using the R package 'ecodist' (Goslee & Urban, 2007). The explanatory variable was Euclidean distance of plot elevation. Response matrices were total beta-diversity and its components of species richness differences and species replacement. Statistical significance of elevational distance was achieved by using permutation tests with 10,000 runs. Matrix regression models were fitted separately for interior and roadside plots and for native species and all species combined. From these 108 models (nine regions × two plot types × two species status × three beta-diversity response matrices) we extracted the slope between the response and elevational distance. To test if the steepness of the slope depended on plot type and species status, we fitted linear mixed-effects models with these variables and their interaction as fixed effects and region as a random effect (R package 'lmerTest'). However, as the interaction was not significant for any of the response matrices, we fitted the models again without the interaction. For all mixed-effects models, model statistics were taken from type III sum of squares with Satterthwaite approximation to estimate the denominator degrees of freedom.

3 | RESULTS

Overall, we recorded 2,410 vascular plant species, with regional total species richness ranging from 159 to 604. In all regions, we recorded a greater total number of native than non-native species, and across plot types native species were on average also more numerous at the plot level (Supporting Information Table S2). The total number of native species was larger for interior plots than roadside plots (except for Norway, Switzerland and Argentina), while the mean number of native species per plot was greater along roadsides in five of the nine regions (Supporting Information Table S2). The total number of non-native species as well as mean non-native species richness per plot were larger for roadside plots compared to interior plots in all regions (Supporting Information Table S2). Norway and Switzerland had the highest ratios of native to non-native species, while the four regions in the southern hemisphere had the lowest ratios (Supporting Information Table S2).

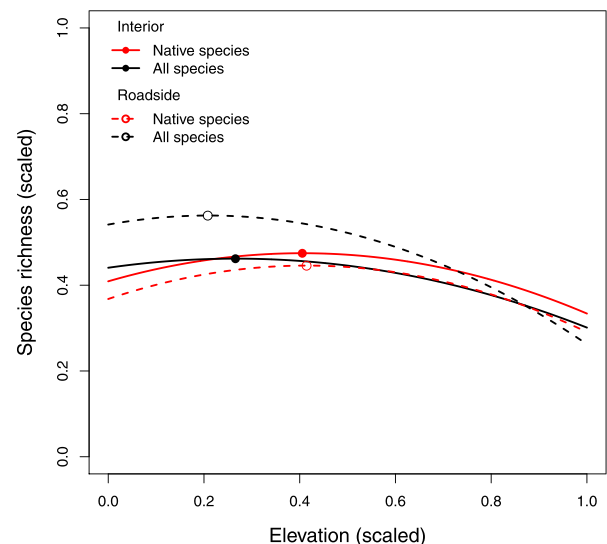### 3.1 | Elevational species richness patterns

At the global scale, there was a unimodal relationship between species richness and elevation, with maximum species richness occurring in the lower-mid section of the elevation gradient for native and all species and for interior and roadside plots (Table 2, Figure 1). At the regional scale, this pattern was found for all species combined in interior plots in three regions and for roadside plots in six regions (Figure 2, Supporting Information Table S3 and Figure S2). Also for native species, the most common shape of the elevational species richness pattern was a unimodal distribution, which we found in four and six regions for interior and roadside plots, respectively (Figure 2, Supporting Information

TABLE 2 Results from the global linear mixed-effects model for species richness as response of elevation, plot type (interior or roadside) and species status (native species or all species combined)

	d.f.	F-value	p-value
Elevation	473.19	20.064	**<.001**
Plot type	466.24	1.998	.1581
Species status	936.99	102.935	**<.001**
Elevation : plot type	470.95	1.549	.2136
Elevation : species status	936.99	64.465	**<.001**
Plot type : species status	936.99	236.416	**<.001**
Elevation : plot type : species status	936.99	17.536	**<.001**

Note. For elevation, we summarized the linear and quadratic term of elevation using orthogonal polynomials. As random effects we added the nested terms region, road, transect and plot. p-values were taken from type III sum of squares with Satterthwaite approximation to estimate the denominator degrees of freedom (d.f.). Significant p-values ($p < .05$) are indicated in bold.

Table S3 and Figure S2). Non-native species richness declined with elevation starting in the lowest fifth of the gradient in all regions, except for interior plots in Norway and Argentina. Roadsides had a strong effect on the shape of the species richness patterns, and the curve's shape differed between interior and roadside plots for native species in

FIGURE 1 Global pattern of species richness along elevation gradients. Curves and peaks of species richness are based on model predictions (see Methods and Table 2). Note that elevation and species richness were scaled prior to modelling, with species richness scaled separately for native species and all species combined. Native species are indicated in red, all species combined (native and non-native species) are indicated in black. Symbols represent the peak of species richness. Filled symbols and solid lines represent interior plots, unfilled symbols and dashed lines represent roadsides. The peak of native species richness is close to mid-elevations, while, for all species combined, the peak is in the lowest third of the elevation gradient. The shift of the species richness peak towards lower elevations through non-native species is stronger along roadsides compared to interior plots
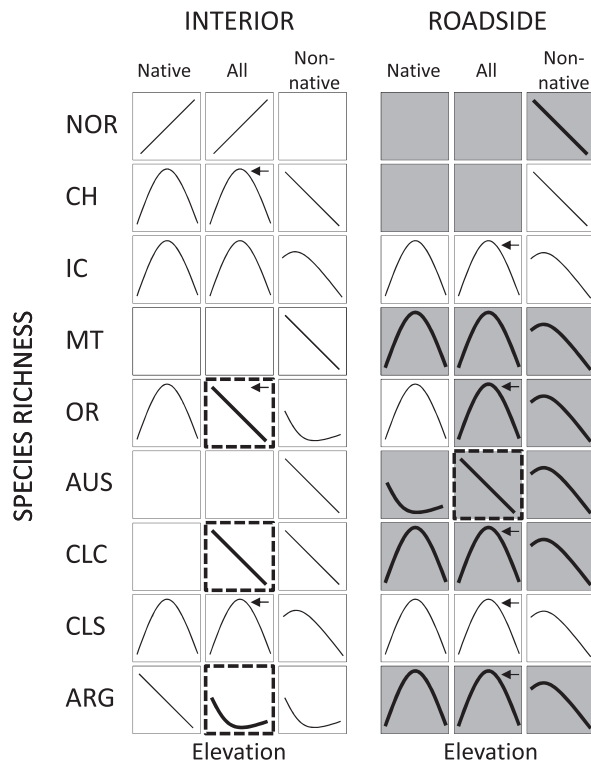
FIGURE 2 Schematic representation of species richness patterns along elevation gradients in the nine study regions (NOR = Norway, CH = Switzerland, IC = Canary Islands, MT = Montana, OR = Oregon, AUS = Australia, CLC = central Chile, CLS = southern Chile, ARG = Argentina). The three columns on the left refer to plots away from the road, while the three columns on the right represent roadside plots. In each plot type, patterns for native species, all species combined and non-native species are displayed. Empty boxes indicate that there was no significant relationship between species richness and elevation. Bold curves within dashed boxes show that non-native species have changed the shape of the pattern of native species, so that curves of native and all species combined are different. Grey boxes with bold curves for roadside plots indicate that the relationship between species richness and elevation differs from interior plots for the respective species status. Small arrows pointing to the left show that the peak of species richness is at lower elevations for all species combined compared to native species. See Supporting Information Figure S2 for modelled species richness curves

six regions, for all species combined in seven regions and for non-native species in six regions (Figure 2).

Including non-native species resulted at the global scale in a displacement of the peak of species richness to lower elevations compared to the peak of species richness of native species. This shift was stronger along roadsides (Figure 1). At the regional scale, the species richness peak of all species combined was at lower elevation than that of native species in three regions in interior plots and in six regions in roadside plots (Supporting Information Table S4). However, these differences did not result in significant p-values in the binomial tests ($p = 1$ and $p = .289$, respectively).

Elevational species richness patterns differed in character for native and non-native species in seven regions, and non-native species changed the character of the native species' pattern in all nine study regions and also at the global scale. This was evident in a significant elevation-by-status interaction (Table 2, Supporting Information Table S5), which is brought about by a different slope of the richness curve, a shift of the elevation at which species richness is maximal or a combination of both. In addition, including non-native species resulted in a fundamentally different shape of the richness curves compared to the shape of native species richness in Oregon, central Chile and Argentina in interior plots and in Australia in roadside plots (Figure 2, Supporting Information Figure S2).

3.2 | Effects of roadsides and non-native species on beta-diversity

At the global scale, community dissimilarity (total beta-diversity, measured as Jaccard dissimilarity) was significantly greater in interior plots compared to roadside plots (Table 3; Figure 3a). Regionally, greater beta-diversity in interior plots was found in Switzerland, Montana, Australia, central and southern Chile (Supporting Information Table S6 and Figure S3a). At the global scale, this difference between plot types was mainly driven by a stronger decline in dissimilarity for roadsides when non-native species were included (significant species status-by-plot type interaction; Table 3). This was found also in Australia, Montana, Oregon and southern Chile (Supporting Information Table S6 and Figure S3a). In these regions, except Oregon, total beta-diversity of native species was significantly higher than that of all species combined, which also corresponded to the results at the global scale.

The beta-diversity component of species richness differences was greater for native species compared to all species combined at the global scale (Table 3, Figure 3b) and in five of the nine regions (Switzerland, Montana, Oregon, southern Chile, Argentina; Supporting Information Table S6 and Figure S3b). At the global scale, species richness differences for native species were greater along roadsides, but for all species combined they were larger in interior plots (significant species status-by-plot type interaction; Table 3, Figure 3b). However, the same pattern was not detected at the regional scale (Supporting Information Figure S3b). In Norway, Switzerland, Montana and southern Chile, differences in beta-diversity based on species richness differences were larger in interior plots, while it was the contrary in Australia, central Chile and Argentina (Supporting Information Table S6 and Figure S3b). In consequence, at the global scale there was no significant effect of plot type on species richness differences (Table 3).

Including non-native species increased species replacement between plots at the global scale (Table 3, Figure 3c) and in six out of nine regions (Norway, Switzerland, Montana, Oregon, Australia, southern Chile; Supporting Information Table S6 and Figure S3c). At the global scale, species replacement was significantly lower along roadsides (Table 3, Supporting Information Figure S3c), which we found also at the regional scale for Montana, Australia, Argentina and central Chile (Supporting Information Table S6 and Figure S3c).

The contribution of species richness differences to total beta-diversity was on average smaller than that of species replacement at the global and regional scales (Figure 3, Supporting Information Figure S3). At the global scale, this difference was particularly strong when

TABLE 3 Results from the global linear mixed-effects models for the response of beta-diversity [total beta-diversity (Jaccard dissimilarity index), species richness differences and species replacement] to species status (native species or all species combined) and plot type (interior or roadside)

	Beta-diversity								
	Total beta-diversity (Jaccard dissimilarity)			Species richness differences			Species replacement		
	d.f.	F-value	p-value	d.f.	F-value	p-value	d.f.	F-value	p-value
Species status	940.99	72.71	**<.001**	941.01	88.53	**<.001**	941.01	53.52	**<.001**
Plot type	933.08	39.84	**<.001**	933.66	0.19	.664	933.68	5.28	**.022**
Species status : plot type	940.99	130.16	**<.001**	941.01	26.69	**<.001**	941.01	0.60	.440

d.f. = denominator's degrees of freedom.

Note. D.f., *F*- and *p*-values are from type III sum of squares and Satterthwaite approximation. Significant *p*-values (*p* < .05) are indicated in bold.

non-native species were included. This trend was also observed in five regions (Switzerland, Montana, Oregon, Australia, southern Chile; Supporting Information Figure S3).

3.3 | Elevational decay of beta-diversity

Total beta-diversity (Jaccard dissimilarity) increased significantly with increasing elevational distance between plots in all regions and for interior and roadside plots as well as for native species and all species combined (Figure 4a, Supporting Information Table S7 and Figure S4a).

The response of species richness differences to increasing elevational distance was less consistent across regions (Figure 4b, Supporting Information Table S7 and Figure S4b). We found a statistically significant positive relationship for interior plots in three regions [Canary Islands, Oregon, southern Chile (only for native species)] and for roadside plots in seven regions [Canary Islands, Montana, Oregon, Australia, central Chile (only for all species combined), southern Chile, Argentina (only for all species combined)]. Norway was the only region where we found a significant negative relationship between species richness differences and elevational distance (Supporting Information Table S7).

Species replacement increased with increasing elevational distance in seven regions [Norway, Switzerland (only along roadsides), Montana (in interior plots only for all species combined), Oregon, Australia (only for interior plots), central Chile (in roadside plots only for native species), Argentina (in roadside plots only for native species)], but decreased in the Canary Islands and southern Chile (only for native species) (Figure 4c, Supporting Information Table S7 and Figure S4c).

The slope of these regional relationships did not differ significantly between interior and roadside plots or between native species and all species combined (Table 4).

4 | DISCUSSION

4.1 | Global and regional species richness patterns

Globally, in interior and roadside plots, species richness of native species as well as of all species combined showed a unimodal pattern that peaked at lower-mid elevations. At the regional scale, a unimodal relationship was also the most frequent shape, but we also observed linear or no relationship between species richness and elevation.
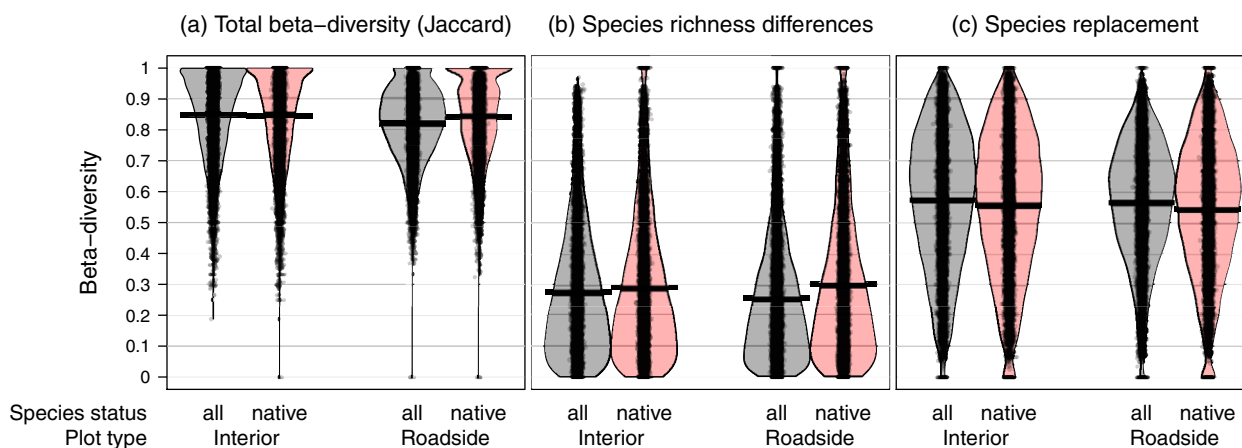
FIGURE 3 Total beta-diversity (Jaccard dissimilarity index) and its components of species richness differences and species replacement for the two different plot types (interior or roadside) and species status (native species or all species combined). Statistical results are given in Table 3. (a) Total beta-diversity was lower along roadsides, particularly when non-native species were included. (b) Species richness differences were reduced by non-native species. For native species, richness differences were higher along roadsides, while non-native species led to higher species richness differences in interior plots. (c) Species replacement was higher in interior plots and for all species combined
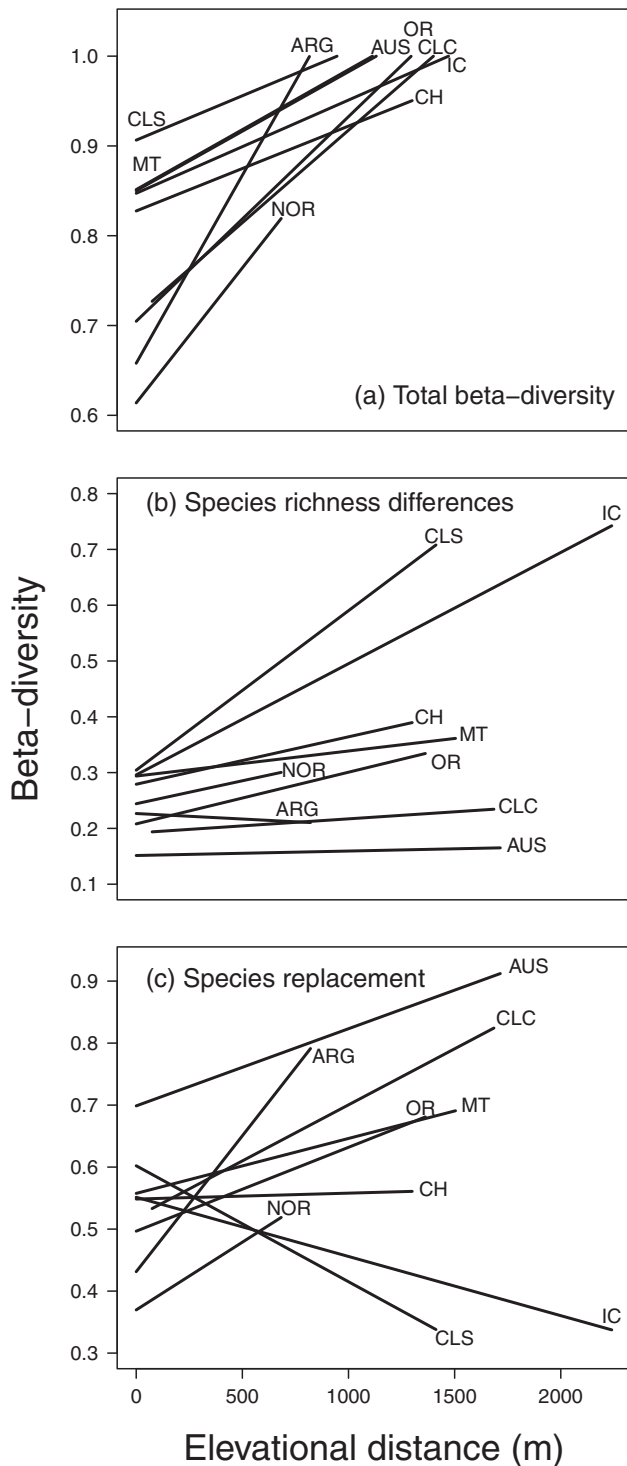
FIGURE 4 (a) Total beta-diversity (Jaccard dissimilarity index) and its two components of (b) species richness differences and (c) species replacement as response to elevational distance between plots. Each line represents one region (for abbreviations see Table 1). Only beta-diversity for native species in interior plots is displayed, because there was no statistically significant difference compared to all species combined and roadside plots, respectively (see Table 4; for regional details see Supporting Information Table S7 and Figure S4). We found a significant elevational decay of total beta-diversity in all regions (a), but there was no consistent pattern for species richness differences (b) and species replacement (c)

The mid-domain effect (Cardelús, Colwell, & Watkins, 2006; Colwell & Lees, 2000; Grytnes et al., 2008) might be an underlying mechanism in our study regions. In addition, biological, non-random processes might be acting: the unimodal species richness curve was more frequent along roadsides where dispersal is usually increased due to vehicle movement (Rew et al., 2018; Taylor et al., 2012; von der Lippe & Kowarik, 2007), and where competition is likely to be reduced due to disturbance. Both factors might allow the species to establish under less favourable abiotic conditions at higher (or lower) elevations, which might lead to larger species elevational ranges along roadsides (Lembrechts et al., 2017) and stronger range overlap at mid-elevations (Brehm, Colwell, & Kluge, 2007; Dunn, McCain, & Sanders, 2006; Wu et al., 2013). However, our regional analysis suggests that the specific shape of the unimodal curve is likely also related to other factors, including climate, vegetation type and human activity.

Argentina (interior) and Australia (roadside) showed a negative relationship between elevation and native species richness. This is the second most commonly observed pattern of plant species richness globally (Rahbek, 2005), and in our study regions might be explained by increasingly harsh abiotic conditions at high elevations (McCain & Grytnes, 2010). In contrast, native species richness in Norway increased with elevation, which might be the result of reduced competition from shrubs at high elevations (Lembrechts, Milbau, & Nijs, 2014). Also, increasingly positive net interactions in harsher climates might facilitate species co-existence (Choler, Michalet, & Callaway, 2001).

4.2 | Human-induced disturbance and dispersal modify region-specific patterns

We found different shapes of the species richness patterns of native, non-native and all species combined for interior and roadside plots for all but two regions. Across regions, patterns were more consistent along roadsides compared to those in interior plots. This suggests that disturbance and dispersal caused by road development, maintenance and use result in a weakening of region-specific effects. Mechanisms such as environmental filtering by temperature or precipitation, and increasingly positive biotic interactions that have been shown to be important drivers in interior plots, might be less important along roadsides or shifted to higher elevations (Alexander et al., 2011; Seipel et al., 2012).

4.3 | Consistent effect of non-native species

Non-native species displaced the peak of species richness to lower elevations, particularly along roadsides. Contrary to native species, non-native species richness decreased consistently with elevation, in some regions after a small peak in the lowest fifth of the elevation gradient. The decreasing richness pattern applied to both plot types (interior and roadside) and has been described also in other studies (Bhattarai, Måren, & Subedi, 2014; Seipel et al., 2012; Tanaka & Sato, 2016; Zhang et al., 2015). Thus, while we found region-specific

TABLE 4 Results from the global linear mixed-effects models to test if the steepness of the slope between beta-diversity and elevational distance between plots depends on species status (native species or all species combined) and plot type (interior or roadside)

	Slope between beta-diversity and elevational distance (elevational decay)								
	Total beta-diversity			Species richness differences			Species replacement		
	d.f.	F-value	p-value	d.f.	F-value	p-value	d.f.	F-value	p-value
Species status	25	0.16	.697	25	0.38	.543	25	0.46	.506
Plot type	25	0.78	.387	25	0.01	.932	25	0.04	.839

d.f. = denominator's degrees of freedom.
Note. Models were fitted separately for total beta-diversity (Jaccard dissimilarity index), species richness differences and species replacement. d.f., *F*- and *p*-values are from type III sum of squares and Satterthwaite approximation. The interaction of species status and plot type was removed from all models because it was insignificant in all three models.

patterns for native species richness, non-native species richness responded consistently across regions.

In all regions, the number of non-native species was higher along roadsides. This might be explained by greater disturbance, which is known to be a major promoter of plant invasions (Jauni, Gripenberg, & Ramula, 2015), and by greater seed and vegetative propagule load from traffic and road maintenance along roadsides. Either way, roadsides appear to act as conduits and sources of non-native species for percolation into semi-natural habitats (Bhattarai et al., 2014; Pollnac et al., 2012; Seipel et al., 2012; Zhang et al., 2015).

Non-native species changed the character of the elevational native species richness patterns in all regions by altering the rate of species richness change with elevation, shifting the location of the species richness peak, or both. However, a change of the pattern's general shape (e.g. from unimodal to decreasing) could only be observed in four regions (interior plots in Oregon, central Chile and Argentina, and roadsides in Australia). These regions were among those with the lowest ratio of native to non-native species. Thus, with continuing invasions, other regions might be expected to undergo changes in the shape of the species richness pattern in the future. The spatial shift of the native species richness peak to lower elevations through invasion of non-native species – already observed in two-thirds of our regions – might be considered as a first sign of changing species richness patterns.

4.4 | Roads and non-native species reduced community dissimilarity

Globally, roads reduced total beta-diversity and species replacement, which suggests roads homogenize mountain flora. The higher levels of disturbance along roadsides and associated resource release might reduce small-scale habitat differences. In combination with higher dispersal of plant propagules along roads, this might lead to larger species ranges (Lembrechts et al., 2017), and thus to reduced differences in local community composition. In interior plots, greater species replacement between plots points to greater environmental heterogeneity compared to roadsides. In Norway and Switzerland, higher species replacement along roadsides might result from the larger pools of native species found along roadsides, and overall much lower richness of non-native species.

Non-native species richness has been shown to be highest at low elevations, and only few or no non-natives were found at high elevations (Haider, Alexander, & Kueffer, 2011; Seipel et al., 2012; Tanaka & Sato, 2016; Zhang et al., 2015). Therefore, we expected that the inclusion of non-native species increases differences in species richness. In line with this assumption, Marini et al. (2013) observed that beta-diversity of non-native species in Italy was mainly related to differences in species richness. However, in our study, at the global scale, non-native species reduced plot dissimilarity by reducing differences in species richness, an effect that was particularly strong along roadsides. A possible explanation is that non-native species increased species richness in the lower part of the elevation gradient, but not considerably at mid-elevations (i.e. where native species richness peaks), so that specifically the differences in species richness between low and mid-elevations were reduced.

Furthermore, species replacement increased through non-native species at the global scale and in two-thirds of the study regions. This result, too, was contrary to our expectations. Elevational nestedness of non-native species (Alexander et al., 2011; Marini et al., 2013) and smaller elevational niches of native species (more specialists) should result in lower species replacement for all species combined compared to native species. The increase of species replacement through inclusion of non-native species might have been caused by a patchy distribution of non-native species, despite their elevational nestedness.

In summary, the negative effect of non-native species on species richness differences was stronger than the positive effect on species replacement, so that non-native species overall led to a homogenization of plant communities (Arévalo et al., 2010; McKinney, 2004).

4.5 | Elevational decay of community dissimilarity

We found a decline in community dissimilarity in response to elevational distance in all study regions, both along roadsides and in interior plots and with or without non-native species. Such elevational decay has been observed for plants (Chapman & McEwan, 2013), and other taxonomic groups, for instance aquatic microorganisms (Wang et al., 2012). The elevational decay was found for species richness differences as well as for species replacement, but the regional responses for these two components were less consistent compared to the response

of total beta-diversity. This suggests that idiosyncratic regional factors determine species richness differences and replacement.

We did not detect statistically significant differences in the rate of elevational decay for interior compared to roadside plots, or for native species compared to all species combined. This suggests that biological invasions in mountains are not yet such a strong homogenizing factor as they can be in lowland ecosystems (McKinney, 2004). However, geographic distance was the most important factor explaining dissimilarity in non-native species composition in Portugal (Vicente et al., 2014), and so the impact of non-native species on beta-diversity may increase in the future.

5 | CONCLUSIONS

Our study showed that human-induced disturbance and non-native species have a strong impact on native species richness patterns and community dissimilarity in mountains, partly overruling the global mechanisms that bring about these patterns. We suggest that three mechanisms – increased human-assisted dispersal, higher habitat homogeneity, and presence of generalist non-native species – drive biotic homogenization along elevation gradients at a regional scale. Biotic homogenization not only leads to a reduced differentiation of plant communities among elevational zones in a particular mountain system, but also to a reduction in the diversity of species richness patterns in semi-natural habitats. Our study is the first global comparison of the effects of roads and non-native species on diversity patterns in mountains, and suggests that more attention should be paid to the influence of anthropogenic factors on broad-scale macroecological patterns.

DATA ACCESSIBILITY

Data were collected by members of MIREN. Species occurrence data with sampling date and geographic coordinates will be available on GBIF (https://www.gbif.org/).

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REFERENCES

Alexander, J. M., Kueffer, C., Daehler, C. C., Edwards, P. J., Pauchard, A., Seipel, T., & MIREN Consortium (2011). Assembly of nonnative floras along elevational gradients explained by directional ecological filtering. *Proceedings of the National Academy of Sciences USA*, *108*, 656–661.

Arévalo, J. R., Otto, R., Escudero, C., Fernández Lugo, S., Arteaga, M. A., Delgado, J. D., & Fernández Palacios, J. M. (2010). Do anthropogenic corridors homogenize plant communities at a local scale? A case studied in Tenerife (Canary Islands). *Plant Ecology*, *209*, 23–35.

Averett, J. P., McCune, B., Parks, C. G., Naylor, B. J., DelCurto, T., & Mata-Gonzalez, R. (2016). Non-native plant invasion along elevation and canopy closure gradients in a middle Rocky Mountain ecosystem. *PLoS One*, *11*, e0147826.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2013). lme4: Linear mixed-effects models using Eigen and S4 (R package version 1.0–5).

Bhattarai, K. R., Måren, I. E., & Subedi, S. C. (2014). Biodiversity and invasibility: distribution patterns of invasive plant species in the Himalayas, Nepal. *Journal of Mountain Science*, *11*, 688–696.

Brehm, G., Colwell, R. K., & Kluge, J. (2007). The role of environment and mid-domain effect on moth species richness along a tropical elevational gradient. *Global Ecology and Biogeography*, *16*, 205–219.

Boyle, B., Hopkins, N., Lu, Z., Raygoza Garay, J. A., Mozzherin, D., Rees, T., … Enquist, B. J. (2013). The taxonomic name resolution service: an online tool for automated standardization of plant names. *BMC Bioinformatics*, *14*, 16.

Cardelús, C. L., Colwell, R. K., & Watkins, J. E. (2006). Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak. *Journal of Ecology*, *94*, 144–156.

Cardoso, P., Borges, P. A. V., & Veech, J. A. (2009). Testing the performance of beta diversity measures based on incidence data: the robustness to undersampling. *Diversity and Distributions*, *15*, 1081–1090.

Cardoso, P., Rigal, F., Carvalho, J. C., & Kembel, S. (2015). BAT - Biodiversity Assessment Tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. *Methods in Ecology and Evolution*, *6*, 232–236.

Carvalho, J. C., Cardoso, P., & Gomes, P. (2012). Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. *Global Ecology and Biogeography*, *21*, 760–771.

Chapman, J. I., & McEwan, R. W. (2013). Spatiotemporal dynamics of alpha- and beta-diversity across topographic gradients in the herbaceous layer of an old-growth deciduous forest. *Oikos*, *122*, 1679–1686.

Choler, P., Michalet, R., & Callaway, R. M. (2001). Facilitation and competition on gradients in alpine plant communities. *Ecology*, *82*, 3295–3308.

Colwell, R. K., & Coddington, J. A. (1994). Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *345*, 101–118.

Colwell, R. K., & Lees, D. C. (2000). The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology & Evolution*, *15*, 70–76.

Dainese, M., & Poldini, L. (2012). Plant and animal diversity in a region of the Southern Alps: the role of environmental and spatial processes. *Landscape Ecology*, *27*, 417–431.

Dunn, R. R., McCain, C. M., & Sanders, N. J. (2006). When does diversity fit null model predictions? Scale and range size mediate the mid-domain effect. *Global Ecology and Biogeography*, *16*, 305–312.

Forman, R. T. T., & Alexander, L. E. (1998). Roads and their major ecological effects. *Annual Review of Ecology and Systematics*, *29*, 207–231.

Goslee, S. C., & Urban, D. L. (2007). The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software*, 22, 1–19.

Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Benito Alonso, J. L., ... Grabherr, G. (2012). Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, 2, 111–115.

Grytnes, J.-A., Beaman, J. H., Romdal, T. S., & Rahbek, C. (2008). The mid-domain effect matters: simulation analyses of range-size distribution data from Mount Kinabalu, Borneo. *Journal of Biogeography*, 35, 2138–2147.

Guo, Q., Kelt, D. A., Sun, Z., Liu, H., Hu, L., Ren, H., & Wen, J. (2013). Global variation in elevational diversity patterns. *Scientific Reports*, 3, 3007.

Haider, S., Alexander, J., Dietz, H., Trepl, L., Edwards, P. J., & Kueffer, C. (2010). The role of bioclimatic origin, residence time and habitat context in shaping non-native plant distributions along an altitudinal gradient. *Biological Invasions*, 12, 4003–4018.

Haider, S., Alexander, J. M., & Kueffer, C. (2011). Elevational distribution limits of non-native species: combining observational and experimental evidence. *Plant Ecology & Diversity*, 4, 363–371.

Jauni, M., Gripenberg, S., & Ramula, S. (2015). Non-native plant species benefit from disturbance: a meta-analysis. *Oikos*, 124, 122–129.

Kammer, P. M., & Möhl, A. (2002). Factors controlling species richness in alpine plant communities: an assessment of the importance of stress and disturbance. *Arctic, Antarctic, and Alpine Research*, 34, 398–407.

Kueffer, C., Daehler, C., Dietz, H., McDougall, K., Parks, C., Pauchard, A., ... MIREN Consortium (2014). The Mountain Invasion Research Network (MIREN). Linking local and global scales for addressing an ecological consequence of global change. *Gaia-Ecological Perspectives for Science and Society*, 23, 263–265.

Kuznetsova, A., Brockhoff, P. B., & Bojesen Christensen, R. H. (2016). lmerTest: Tests in linear mixed effects models (R package version 2.0–32).

Lembrechts, J. J., Alexander, J. M., Cavieres, L. A., Haider, S., Lenoir, J., Kueffer, C., ... Milbau, A. (2017). Mountain roads shift native and non-native plant species' ranges. *Ecography*, 40, 353–364.

Lembrechts, J. J., Milbau, A., & Nijs, I. (2014). Alien roadside species more easily invade alpine than lowland plant communities in a subarctic mountain ecosystem. *PLoS One*, 9, e89664.

Lenoir, J., & Svenning, J.-C. (2013). Latitudinal and elevational range shifts under contemporary climate change. In S. A. Levin (Ed.), *Encyclopedia of Biodiversity* (pp. 599–611). Waltham, MA: Academic Press.

Marini, L., Battisti, A., Bona, E., Federici, G., Martini, F., Pautasso, M., & Hulme, P. E. (2012). Alien and native plant life-forms respond differently to human and climate pressures. *Global Ecology and Biogeography*, 21, 534–544.

Marini, L., Bertolli, A., Bona, E., Federici, G., Martini, F., Prosser, F., & Bommarco, R. (2013). Beta-diversity patterns elucidate mechanisms of alien plant invasion in mountains. *Global Ecology and Biogeography*, 22, 450–460.

McCain, C. M., & Grytnes, J.-A. (2010). Elevational gradients in species richness. In *Encyclopedia of life sciences* (pp. 1–10). Chichester, UK: Wiley.

McKinney, M. L. (2004). Measuring floristic homogenization by non-native plants in North America. *Global Ecology and Biogeography*, 13, 47–53.

Nekola, J. C., & White, P. S. (1999). The distance decay of similarity in biogeography and ecology. *Journal of Biogeography*, 26, 867–878.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., ... Wagner, H. (2016). vegan: community ecology package (R package version 2.4-1).

Pauchard, A., Kueffer, C., Dietz, H., Daehler, C. C., Alexander, J., Edwards, P. J., ... Seipel, T. (2009). Ain't no mountain high enough: plant invasions reaching new elevations. *Frontiers in Ecology and the Environment*, 7, 479–486.

Pauchard, A., Milbau, A., Albihn, A., Alexander, J., Burgess, T., Daehler, C., ... Kueffer, C. (2016). Non-native and native organisms moving into high elevation and high latitude ecosystems in an era of climate change: new challenges for ecology and conservation. *Biological Invasions*, 18, 345–353.

Podani, J., & Schmera, D. (2011). A new conceptual and methodological framework for exploring and explaining pattern in presence-absence data. *Oikos*, 120, 1625–1638.

Pollnac, F., Seipel, T., Repath, C., & Rew, L. J. (2012). Plant invasion at landscape and local scales along roadways in the mountainous region of the Greater Yellowstone Ecosystem. *Biological Invasions*, 14, 1753–1763.

Pyšek, P., Jarošík, V., Pergl, J., & Wild, J. (2011). Colonization of high altitudes by alien plants over the last two centuries. *Proceedings of the National Academy of Sciences USA*, 108, 439–440.

R Core Team (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rahbek, C. (2005). The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, 8, 224–239.

Rew, L. J., Brummer, T. J., Pollnac, F. W., Larson, C. D., Taylor, K. T., Taper, M. L., ... Balbach, H. E. (2018). Hitching a ride: seed accrual rates on different types of vehicles. *Journal of Environmental Management*, 206, 547–555.

Romdal, T., & Grytnes, J. A. (2007). An indirect area effect on elevational species richness patterns. *Ecography*, 30, 440–448.

Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. H., Wannebo, A. V., & Woolmer, G. (2002). The human footprint and the last of the wild. *BioScience*, 52, 891–904.

Seipel, T., Kueffer, C., Rew, L. J., Daehler, C. C., Pauchard, A., Naylor, B. J., ... Walsh, N. (2012). Processes at multiple scales affect richness and similarity of non-native plant species in mountains around the world. *Global Ecology and Biogeography*, 21, 236–246.

Siefert, A., Lesser, M. R., & Fridley, J. D. (2015). How do climate and dispersal traits limit ranges of tree species along latitudinal and elevational gradients? *Global Ecology and Biogeography*, 24, 581–593.

Spellerberg, I. F. (1998). Ecological effects of roads and traffic: a literature review. *Global Ecology and Biogeography Letters*, 7, 317–333.

Steinbauer, M. J., Field, R., Grytnes, J.-A., Trigas, P., Ah-Peng, C., Attorre, F., ... Beierkuhnlein, C. (2016). Topography-driven isolation, speciation and a global increase of endemism with elevation. *Global Ecology and Biogeography*, 25, 1097–1107.

Tanaka, T., & Sato, T. (2016). Contemporary patterns and temporal changes in alien plant species richness along an elevational gradient in central Japan. *Plant Ecology and Evolution*, 149, 177–188.

Taylor, K., Brummer, T., Taper, M. L., Wing, A., & Rew, L. J. (2012). Human-mediated long-distance dispersal: an empirical evaluation of seed dispersal by vehicles. *Diversity and Distributions*, 18, 942–951.

Valdés, A., Lenoir, J., Gallet-Moron, E., Andrieu, E., Brunet, J., Chabrerie, O., ... Decocq, G. (2015). The contribution of patch-scale conditions is greater than that of macroclimate in explaining local plant diversity

in fragmented forests across Europe. *Global Ecology and Biogeography*, *24*, 1094–1105.

van Kleunen, M., Dawson, W., Essl, F., Pergl, J., Winter, M., Weber, E., ... Pyšek, P. (2015). Global exchange and accumulation of non-native plants. *Nature*, *525*, 100–103.

Vicente, J. R., Pereira, H. M., Randin, C. F., Gonçalves, J., Lomba, A., Alves, P., ... Honrado, J. (2014). Environment and dispersal paths override life strategies and residence time in determining regional patterns of invasion by alien plants. *Perspectives in Plant Ecology, Evolution and Systematics*, *16*, 1–10.

von der Lippe, M., & Kowarik, I. (2007). Long-distance dispersal of plants by vehicles as a driver of plant invasions. *Conservation Biology*, *21*, 986–996.

Wang, J., Soininen, J., Zhang, Y., Wang, B., Yang, X., & Shen, J. (2012). Patterns of elevational beta diversity in micro- and macroorganisms. *Global Ecology and Biogeography*, *21*, 743–750.

Wu, Y., Yang, Q., Wen, Z., Xia, L., Zhang, Q., & Zhou, H. (2013). What drives the species richness patterns of non-volant small mammals along a subtropical elevational gradient? *Ecography*, *36*, 185–196.

Zhang, W., Yin, D., Huang, D., Du, N., Liu, J., Guo, W., & Wang, R. (2015). Altitudinal patterns illustrate the invasion mechanisms of alien plants in temperate mountain forests of northern China. *Forest Ecology and Management*, *351*, 1–8.

BIOSKETCH

This paper is part of the research carried out by the Mountain Invasion Research Network (MIREN; www.mountaininvasions.org). The aim of MIREN is to understand the effects of global change on species' distributions and biodiversity in mountainous areas. We perform observational and experimental studies along elevation gradients to evaluate and quantify the processes and mechanisms that are shaping mountain plant communities at regional and global scales.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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