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# No Signal of Biotic Resistance to Non-Native Species Establishment in High-Elevation Communities

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## ABSTRACT

**Questions:** There is growing evidence of plant invasions in high-elevation mountain ecosystems, but how these invasion patterns relate to native species diversity remains understudied. While the biotic resistance hypothesis states that highly diverse communities

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are less likely to be invaded than less diverse ones, the opposite pattern might arise from facilitative interactions in harsh environments, if these prevail at high elevations, especially in the alpine zone. Here, we investigate whether the relationship between native and non-native plant species diversity changes with elevation, and whether it is modified by disturbance resulting from mountain roads.

**Location:** Global.

**Methods:** By using standardized vegetation surveys and plant trait measurements, we modeled the relationship between non-native species richness and native species richness and functional diversity across elevation gradients, and whether they differ between (semi-)natural habitats and adjacent disturbed roadside habitats.

**Results:** At high elevations, we recorded more non-native species in functionally diverse natural habitats and in species-rich roadside habitats. At lower elevations, non-native and native species richness were positively associated, but fewer non-native species established in functionally diverse natural habitats. Lateral spread of non-native species from disturbed roadsides into natural habitats occurred with the same frequency at high and low elevations.

**Conclusions:** Our results suggest that once non-native species reach high elevations along dispersal corridors such as roads, native plant diversity may help promote, rather than inhibit, their spread into natural plant communities, contradicting the biotic resistance hypothesis. While the positive correlation between non-native and native species richness likely relies on beneficial environmental heterogeneity promoting both species groups, the seemingly inhibiting effect of native functional diversity at low elevations and its assumed supporting role at high elevations might reflect biotic processes such as limiting similarity and facilitation. This suggests that a complex interplay between native diversity and human disturbances shapes the invasibility of mountain ecosystems.

## 1 | Introduction

Mountains are areas of extraordinary biodiversity (Körner 2004; Körner and Spehn 2002; Rahbek et al. 2019) and harbor twice the number of flowering plants expected based on the area that they cover (Körner et al. 2011). These biodiverse ecosystems provide a multitude of services and are crucial for the sustainable development of human populations living in mountains (Payne et al. 2020). Today, mountain biodiversity is increasingly threatened by global climate change. In the European Alps, for example, temperatures have already increased by 1.8°C since 1880 (Kotlarski et al. 2023). This change in climate has caused an upward movement of plant species, leading to alterations in plant community composition, distribution, and interactions and therefore threatens well-adapted, highly sensitive mountain ecosystems (Intergovernmental Panel on Climate Change (IPCC) 2023; Körner and Spehn 2002). As species and treelines shift upwards, alpine environments are projected to be disproportionately affected, dramatically reducing habitat space for high-altitude endemics (Dirnböck et al. 2011). Additionally, urbanization, human population growth, and increased recreation and tourism pose threats to mountain biodiversity (IPBES 2018; Schickhoff et al. 2022; Yang et al. 2025).

Human activities and climate change are known to promote the spread of non-native species to new areas, including mountains and high-elevation habitats (Hulme et al. 2023). Negative impacts of some non-native species, specifically of those arriving after 1500 CE, include, for example, a higher risk of native species extinctions due to competitive exclusion, modification of trophic networks, and changes in nutrient cycling, hydrology, and habitat structure, which result in changes in ecosystem functioning and the delivery of ecosystem services (Bacher et al. 2023; McDougall et al. 2011; Pyšek et al. 2020). Thus far, mountain areas, particularly high-elevation alpine habitats, are not as heavily invaded as other ecosystems (Kueffer et al. 2013; Seebens et al. 2023). Typically, the number of non-native species is highest at the lowest part of the elevation gradient where they are predominantly introduced, while lower propagule pressure and environmental filtering prevent many non-natives from spreading to higher elevations (Alexander et al. 2011, 2016).

At the local scale, community composition and the establishment of non-native species are expected to be driven by both local environmental conditions and biotic interactions (Mitchell et al. 2006; Pauchard and Shea 2006; von Holle et al. 2020). The biotic resistance hypothesis states that diverse communities are more resistant to non-native species establishment than those with low diversity (Elton 1958; Enders et al. 2020). This resistance is thought to arise from more complete occupation of available niche space and, consequently, more efficient use of resources by a diverse assemblage of resident species (MacDougall et al. 2009; Rossignaud et al. 2022). This diversity refers not only to the species richness of resident communities, but also to their functional diversity, or the variation of traits present within a community (Guo et al. 2024; Li et al. 2022). This hypothesis assumes that biotic interactions are dominated by competition, which can limit the establishment of newly arriving non-native species. However, there is evidence that the importance of competition decreases and the relative role of facilitation (i.e., positive interactions) increases under more stressful environmental conditions (Bertness and Callaway 1994; Choler et al. 2001; He et al. 2013; Olsen et al. 2016). Therefore, within areas of less favorable environmental conditions such as those encountered at high elevations and in alpine areas where temperatures are low, growing seasons are often short, and radiation and wind are typically strong (Körner 2007), more diverse native communities potentially allow more opportunities for facilitation, which might not hinder, but rather promote the establishment of non-native species. For example, studies from the alpine zone of the Chilean Andes reported a higher abundance of non-native species compared to outside native cushion plant patches, concluding that native plants can serve as so-called "nurse plants" and favor non-native species' establishment in harsh environments by buffering extreme temperatures and

increasing soil moisture and nutrient availability (Badano et al. 2007; Cavieres et al. 2005). Such harsh conditions are, of course, not limited to high elevations, but can occur at both ends of an elevation gradient. For example, in an experimental study from Spain, facilitation was observed to be stronger in low-elevation environments with dry slopes compared to more wet slopes at high elevations (Gómez-Aparicio et al. 2004).

Additionally, shifts from negative to positive associations with increasing environmental heterogeneity have been found to promote the richness of both native and non-native species (Fridley et al. 2007; Shea and Chesson 2002). This, in combination with potential facilitative interactions at high elevations, suggests that local environmental conditions might determine the direction of native diversity effects on non-native species establishment.

Another important local factor influencing the establishment of non-native species is disturbance (Catford et al. 2012), often caused by humans but also as a result of natural events such as storms, heatwaves, and flooding. Such disturbances disrupt biotic interactions, reduce both competition and facilitation, and release additional abiotic resources such as space, water, and nutrients (Compagnoni and Adler 2014; Davis et al. 2000; Lear et al. 2020). Depending on its type and extent, disturbance can also locally increase environmental heterogeneity (Arévalo et al. 2005; Berli et al. 2003; Lee and Power 2013; Spooner 2015). In extreme cases, disturbance completely removes the existing plant community, requiring both native and non-native species to (re)establish or colonize from seed while nullifying any (positive or negative) biotic interactions (Davis et al. 2000). Therefore, the processes underlying the biotic resistance hypothesis, that is, competition and facilitation, are likely less prominent in disturbed roadside habitats.

In mountains, an important source of human-induced disturbance is the construction of infrastructure such as roads (Espinoza-Guzmán et al. 2023; Forman et al. 2003; Müllerová et al. 2011), which reach even to alpine areas. At low elevations, reduced competition due to biomass removal by disturbance in roadside communities weakens biotic resistance and may increase establishment success of non-native species (Jauni et al. 2015; Pauchard and Alaback 2004; Tyser and Worley 1992). At high elevations, in contrast, the partial or complete removal of vegetation following disturbance is likely to decrease facilitation and therefore reduce non-native species' establishment success. Despite this, roads have also been shown to be the most important dispersal corridor for vertical spread of non-native species into mountains (Fuentes-Lillo et al. 2021; Kalwij et al. 2015; Lembrechts et al. 2017; Pauchard and Alaback 2004). Thus, a lack of facilitative interactions along roads at high elevations might be compensated through increased propagule pressure. The upward dispersal of non-native species is additionally supported by the removal of climatic filters as a result of global warming, which further reduces the need for positive interactions. Non-native species that have established along roadsides are likely to spread horizontally into more natural vegetation (Falster et al. 2021; McDougall et al. 2018). This percolation from roadsides into natural communities can be hindered by biotic resistance. However, if facilitative interactions prevail, once a non-native species has reached high elevations through dispersal along roads, the onward colonization of natural habitats can be expected to be relatively fast compared to at low elevations.

Alpine habitats are at high risk of endemic species loss due to climatic factors such as rising temperatures and altered precipitation patterns (Wershow and DeChaine 2018), as well as human disturbance and competition from non-native species. Therefore, risk assessment and early detection of non-native species is crucial for the long-term protection of alpine species. In this study, we aimed to explore whether the assumption that diverse native communities maintain a higher biotic resistance against the establishment of non-native species is weakened, or even reversed, for high-elevation ecosystems. Specifically, we hypothesized that (1) at low elevations, high levels of competition from diverse native communities reduce the establishment of non-native species, whereas (2) at high elevations, including alpine zones, native diversity supports the establishment of non-native species due to the assumed increasing importance of facilitative interactions. Additionally, we assessed how disturbance modifies biotic resistance by comparing communities of disturbed roadsides to adjacent natural areas across elevation gradients. We hypothesized that (3) the relationship between the number of non-native species and native diversity is weakened in disturbed roadside habitats, and that, as a result of the expected shift from competition to facilitation along the elevation gradient, (4) the ratio of non-native species in natural vegetation to non-native species at the road will be greater at high elevations than at low elevations (Figure 1).

## 2 | Methods

### 2.1 | Vegetation Surveys

To calculate non-native and native species richness, we used road survey data from the Mountain Invasion Research Network (MIREN), which conducts research on spatiotemporal patterns of non-native and native plant diversity in response to climate and human disturbance in mountain regions. Data were collected on vascular plant species occurrence from 2012 to 2023. The surveys followed MIREN's standardized protocol for monitoring plant species distributions along roads that span broad elevation gradients (Haider et al. 2022) and covered 15 mountain regions across six continents, including diverse climatic zones and both continental and island systems. The regions included in this study were the Argentinian Andes (South and Central), the Chilean Andes (South and Central), the Austrian Alps, the Swiss Alps, the Northern Scandes (Norway), the Krkonoše Mountains (Czech Republic), the Changbai Mountains (China), the Himalayas (Kashmir, India), the Hawaiian Islands (Hawaii, USA), the Rocky Mountains (Montana, USA), the Blue Mountains (Oregon, USA), Teide (Canary Islands, Spain), and the Australian Alps (Table S1).

Sampling was conducted along one to four (predominantly three) mountain roads per region to record plant species from low to high elevations, including the alpine zone. With few exceptions, the roads started in the colline or montane zone and reached the subalpine or alpine area (Table S1). The roads had to be accessible to public traffic for at least parts of the year. Twenty sample sites along each road were selected so as to be evenly distributed between the lowest and highest

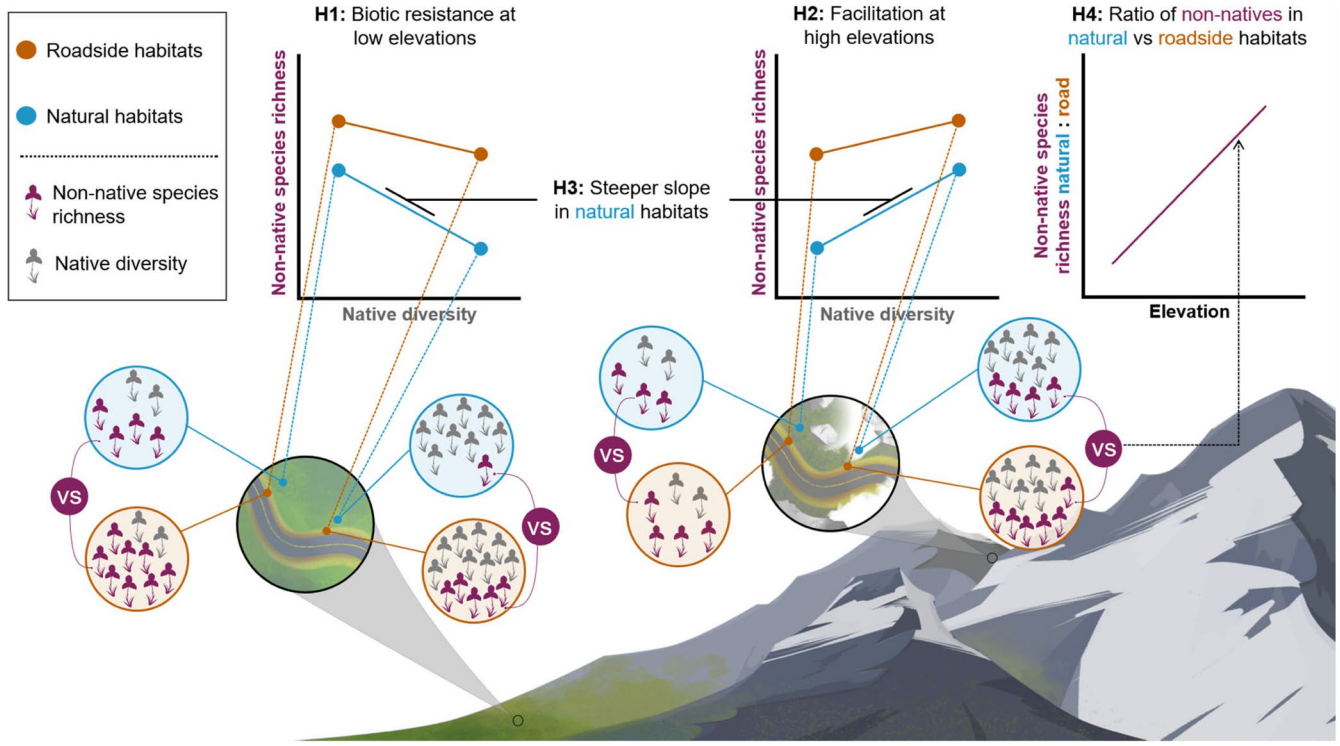


**FIGURE 1** | Conceptual figure of Hypotheses 1–4. At both low and high elevations, non-native species richness hypotheses are described for natural (blue) and disturbed roadside (orange) habitats at low and high native richness conditions. In Hypothesis 1 (H1), we expected that at low elevations, fewer non-native species would be found in communities with high native diversity due to competition. We hypothesized the opposite at high elevations (H2), with diverse native communities facilitating the establishment of non-native species. In Hypothesis 3 (H3), we anticipated a steeper slope of the relationship between non-native species richness and native diversity in natural habitats. Additionally, in Hypothesis 4 (H4), we hypothesized that the ratio of non-native species in natural versus disturbed roadside habitats would be higher in high-elevation environments than at low.

elevation of each road, with some roads overlapping sections of the elevation gradient. Each sample site comprised a roadside plot laid parallel and adjacent to the road, and an interior plot laid perpendicular to the roadside plot starting at 50 m from the road and leading into semi-natural or natural vegetation (Haider et al. 2022). We refer to these plots as roadside and—for simplicity—natural habitats which we assume to be less influenced by humans compared to the roadside habitats. Plots were rectangular—50 m long and 2 m wide. The dataset consists of the visually estimated cover of each species in each plot. In the Swiss Alps, Teide (Tenerife, Canary Islands, Spain), the Himalayas (Kashmir, India), the Rocky Mountains (Montana, USA), the Argentinian Andes (Central), the Krkonoše Mountains (Czech Republic), and the Northern Scandes (Norway), cover classes were classified as $1 \leq 0.1\%$, $2 = 0.1\%–1\%$, $3 = 2\%–5\%$, $4 = 6\%–10\%$, $5 = 11\%–25\%$, $6 = 26\%–50\%$, $7 = 51\%–75\%$, $8 = 76\%–100\%$. In the Austrian Alps, the Argentinian Andes (South), the Chilean Andes (Central and South), the Changbai Mountains (China), the Hawaiian Islands (Hawaii, USA), the Blue Mountains (Oregon, USA), and the Australian Alps, cover classes were classified as $1 = 0.1\%–1\%$, $2 = 1\%–5\%$, $3 = 6\%–25\%$, $4 = 26\%–50\%$, $5 = 51\%–75\%$, $6 = 76\%–95\%$, $7 = 96\%–100\%$. The mean cover for the class recorded was used as the cover value for each species and plot in subsequent calculations. Species were assigned as native or non-native based on regional species lists and local knowledge. Only species that arrived after 1500 CE were considered non-native (neophytes; Pyšek et al. 2004). Species names were harmonized across regions using World Flora Online (Kindt 2020).

## 2.2 | Trait Data Compilation

To calculate the functional diversity of each plot, we used a trait dataset that combined in situ trait values, predicted via near-infrared spectroscopy (NIRS), with trait values from TRY (Kattge et al. 2020) and other regional databases (see below). Trait collection and measurement details are described in Ratier Backes et al. (2023) and were applied in that way by all participating regions. Briefly, leaf samples were collected from one to three roads in the mountain regions included in this study, except for the Changbai Mountains (China), the Austrian Alps, the Blue Mountains (Oregon) and the Hawaiian Islands. In each region, we aimed to collect samples from the 50 most frequent native species and the 30 most frequent non-native species occurring in the region's plots. The actual number of sampled species depended on a region's total native and non-native species richness, species' distributions, and the region's capacity for sample collection. Sampling included all life forms (grasses, forbs, shrubs and trees). Leaves were collected at up to three locations per species, aiming for low, mid, and high-elevation locations, as long as their elevational distribution permitted. Sampling consisted of 10–50 leaves collected from 3 to 10 individuals per species within a location; this large range of leaves was to ensure sufficient leaf mass availability from species with very small leaves. When species did not occur throughout the entire elevation range of a region, we still sampled and included the species to prioritize in situ trait values over database information. Leaves from the same location were pooled into one sample per species. In each region, a subset of approximately 30 samples (i.e., 30 species) was

chosen that included native and non-native species, different life forms, and different elevations. For these samples, fresh weight, leaf area and dry weight were measured to calculate specific leaf area (SLA) and leaf dry matter content (LDMC). We refer to these samples as "reference" samples, as these were used later to develop trait prediction models to derive trait values for all samples, that is, all species (see below). Reference samples as well as all other samples were milled to fine leaf powder after drying. In the laboratory of the Geobotany group at Martin Luther University Halle-Wittenberg, the leaf powder of all samples was scanned with a near-infrared spectrometer (MPA, Bruker Optik, Ettlingen, Germany). For the reference samples, we used the leaf powder to measure leaf carbon (leaf C) and leaf nitrogen concentration (leaf N) gas-chromatographically with the Dumas method, from which we further calculated the leaf carbon to nitrogen ratio (leaf C:N). Leaf phosphorus concentration (leaf P) was determined with a photometric assay using ammonium heptamolybdate ($(NH_4)_6Mo_7O_{24}$) and ascorbic acid ($C_6H_8O_6$) (see Ratier Backes et al. 2023).

All analyses were conducted in R (version 4.4.1) (R Core Team 2024). Using the measured trait values from the reference samples together with their spectral data from the scans with the near-infrared spectrometer, we developed models in the *R* statistical environment to predict trait values for all collected leaf samples (Table S2; Ratier Backes et al. 2023). We built the prediction models following the framework described in Proß (2023), which incorporates a modified version of the "plantspec" package (Griffith et al. 2019). This approach significantly shortened the sample processing time, and allowed the simultaneous measurement of leaf C, N, and P across all samples, including those with low leaf mass that would otherwise be impossible to analyze chemically. For the following analyses, we aggregated the trait values into one value per species per region. For each plot where a species occurred, we assigned the trait value for that species in the respective region. In total, we amassed 1421 in situ samples accounting for 1078 species.

Additionally, we used trait databases to complement our own trait data: (1) For species for which we had no in situ samples, we used available database values for SLA, LDMC, leaf C, N, C:N and P. (2) For all species, we extracted database values for plant height, leaf area, seed mass and rooting depth.

To collect traits from databases, we first matched the complete list of species surveyed in all study regions with gap-filled data from TRY (version 5.0) (Kattge et al. 2020; Schrodt et al. 2015). We included both the harmonized and the unharmonized (original) species names to maximize the number of matches in TRY. We matched species based on both species name and continent, so that if a species was surveyed on multiple continents, the TRY observations were assigned to the corresponding species-continent combination. In cases where a species occurred in TRY only on a continent different from our study region, we used the TRY global average for that species. As a second step, we searched for any remaining missing trait values using BIEN Botanical Information and Ecology Network; (Enquist et al. 2016), AUSTraits (Falster et al. 2021), the Seed Information Database (SID; Society for Ecological Restoration et al. 2023), datasets from Díaz et al. Díaz et al. (2022), Barajas Barbosa et al. (2023), as well as local floras (www.floraargentina.edu.ar; http://www.chileflora.com/index.html).

In total, we had 11 traits that represent fundamental dimensions of plant form and function, and are commonly used to describe plant trait variation (Table S3) (Bruelheide et al. 2018; Díaz et al. 2016). To calculate the functional diversity of a plot, we only used species with all traits available. In total, this amounted to 2216 species.

## 2.3 | Diversity Measures Calculated

To better understand changes in biotic resistance to invasion across elevation and disturbance regimes, we used multiple measures of diversity. Native species richness was calculated as the number of native species within a plot. Additionally, we calculated native Shannon's diversity based on cover using the function "diversity" in the package "vegan" (Oksanen et al. 2025). The Shannon–Wiener diversity index is a commonly used measure of diversity that accounts for the relative abundance of species and is calculated as:

$$H' = -\sum_i P_i \log_b P_i$$

where $P_i$ is the proportional abundance (cover) of species $i$, and $b$ is the base of the logarithm. We used the default, natural logarithm, which is the most commonly used.

Traditional measures of diversity, such as species richness and Shannon's diversity, are limited to information on the number and relative abundance of species, without accounting for the degree of functional differences between them (Mouchet et al. 2010). Here, we additionally calculated Rao's quadratic entropy (Rao's Q) for native species, which accounts for both relative abundance and pairwise species differences in relation to their functional traits (Botta-Dukát 2005). It can therefore provide additional information about the biotic resistance of a native community. Rao's Q is a distance matrix-based diversity index that sums the distances between species, which are relative abundance-weighted (Botta-Dukát 2005; Mouchet et al. 2010). The equation of Rao's Q is defined as

$$FD_Q = \sum_{i=1}^{S-1} \sum_{j=i+1}^{S} d_{ij} P_i P_j$$

whereby $S$ is total species richness, $i$ and $j$ represent different species, $d_{ij}$ is the dissimilarity between species $i$ and $j$. $P_i$ and $P_j$ are the relative abundance of species $i$ and $j$, respectively (Rao 1982). Using the mean cover values for the recorded cover class of each species in each plot, we calculated Rao's Q using Gower's distance in the function "dbFD" in the "FD" package (Laliberté et al. 2025; Laliberté and Legendre 2010). All native species that had complete trait information in our database were used in this calculation. These species were weighted according to their relative cover within their respective community when calculating native functional diversity. Plots for which we did not have any species with trait values (i.e., no in situ sample and no database information) were excluded from the following analyses. Mean relative trait coverage per plot was 71%.

## 2.4 | Statistical Analyses

Native species richness, non-native species richness, native Shannon's diversity, and native Rao's Q were tested against elevation and habitat type to assess general patterns at the global scale. For native and non-native species richness, we fit generalized linear mixed-effects models using a Poisson distribution with the function "glmer" in the package "lme4" (Bates et al. 2015). Fixed effects included elevation and habitat type as well as their interaction. Random effects included sample site nested in road, then nested in region. To use elevation as a proxy for environmental gradients across multiple regions, we scaled elevation between 0 and 1 in each region. Although absolute elevations vary among regions, we assumed that the general pattern of biotic interaction, with competition being more prevalent at low elevations compared to the increased importance of facilitation at high elevations, may be broadly applicable across mountain regions, albeit with potential regional variation. Therefore, scaled elevation between regions is comparable as the processes involved in community interactions are the same. Both the linear and quadratic terms for elevation were included in separate models, then assessed against each other using a likelihood ratio test. For native Shannon's diversity and native Rao's Q, we fit linear mixed-effects models using the function "lmer" in the package "lmerTest" (Kuznetsova et al. 2017). The same fixed and random effects were used as the models described above, as well as the same testing of linear and quadratic elevation.

Non-native species richness was assessed against native species richness, native species Shannon's diversity, and native species functional diversity (Rao's Q). To test Hypotheses 1–3, we fit three generalized linear mixed-effects models with a Poisson distribution using the package "lme4" including a measure of native diversity (native species richness, native Shannon's diversity, and native functional diversity, respectively), scaled elevation, and habitat type (roadside or natural) as a three-way interaction, as well as sample site nested in road, in turn nested in region, as random effects (Bates et al. 2015). We assessed assumptions of normality and homoscedasticity using the "DHARMa" package (Hartig 2024), and no data transformations were necessary to fulfill the model requirements. Since we predicted significant changes in non-native species richness across the elevation gradient, we expected the relationship between non-native species richness and native diversity to change across elevation as well. Therefore, to test for this, we fit the same models using the quadratic form (second-order polynomial) of scaled elevation. The linear and quadratic elevation models were evaluated against each other using a chi-squared likelihood ratio test. We calculated *p* values using the function "mixed" in the package "afex" using the likelihood ratio test method (Singmann et al. 2024).

To visualize the relationship between non-native species richness and the three types of native plant diversity across the elevation gradient (species richness, Shannon's diversity, functional diversity), we calculated the slopes of the respective models using the function "slopes" in the package "marginaleffects" (Arel-Bundock et al. 2024).

To test the spread of non-native species from roadside into natural habitats (H4), we modeled the relationship between the proportion of non-native species in the natural versus disturbed habitats at each sample site by elevation using a linear mixed-effects model (Kuznetsova et al. 2017) with scaled elevation as the fixed effect and road nested in region as a random effect. This was also tested with linear and quadratic elevation, and *p* values for the best-fit model were calculated from *F*-statistics of Type III sum of squares with Satterthwaite approximation to estimate the denominator degrees of freedom.

# 3 | Results

## 3.1 | Elevational and Disturbance-Driven Trends in Species Richness and Diversity

Non-native species richness declined with elevation at roadsides and, to a lesser extent, in natural habitats. Non-native species richness was higher along roadsides (Figure 2A, Table S4). Native species richness peaked at mid elevations in natural and roadside habitats (Figure 2B, Table S4); however, roadside habitats harbored more natives at high elevations. Native Shannon's diversity followed a similar elevational pattern as native species richness with a peak at mid elevations. It was lower in natural habitats than at roadsides (Figure 2C, Table S5). Native functional diversity (Rao's Q) decreased with elevation and was lower in roadside habitats (Figure 2D, Table S5).

## 3.2 | Non-Native Species Establishment Versus Native Diversity

The relationship between non-native species richness and native diversity varied along the elevation gradient and between habitat types (for detailed statistical results, see Tables S6–S8). Due to similarity of patterns for native species richness and native Shannon's diversity, we focus on native species richness here, while Shannon's diversity results are presented in the Supporting Information (Figure S1, Tables S6 and S9).

At low to mid elevations, non-native species richness was greater with increasing native species richness in both natural and roadside habitats (Figure 3A). However, this relationship became less positive with increasing elevation and disappeared in natural habitats at high elevations. This indicates that in most cases, more non-native species were found in species-rich native communities, and this was strongest at the lowest elevations and stronger for roadside compared to natural habitats. At the regional level, more non-native species were found in communities with high native species richness in both roadside and natural habitats for many regions; however, there was remarkable variability between regions (Figure S2, Table S7).

In natural habitats at low to mid elevations, non-native species richness was lower with greater native functional diversity. However, this relationship weakened with increasing elevation and flipped to a positive relationship between non-native species richness and native functional diversity at highest elevations (Figure 3B). This indicates that at high elevations, functionally diverse native communities harbored more non-native species than functionally simple communities. In roadside habitats, we did not find a significant effect of native functional diversity on non-native species richness. At the regional scale (not considering

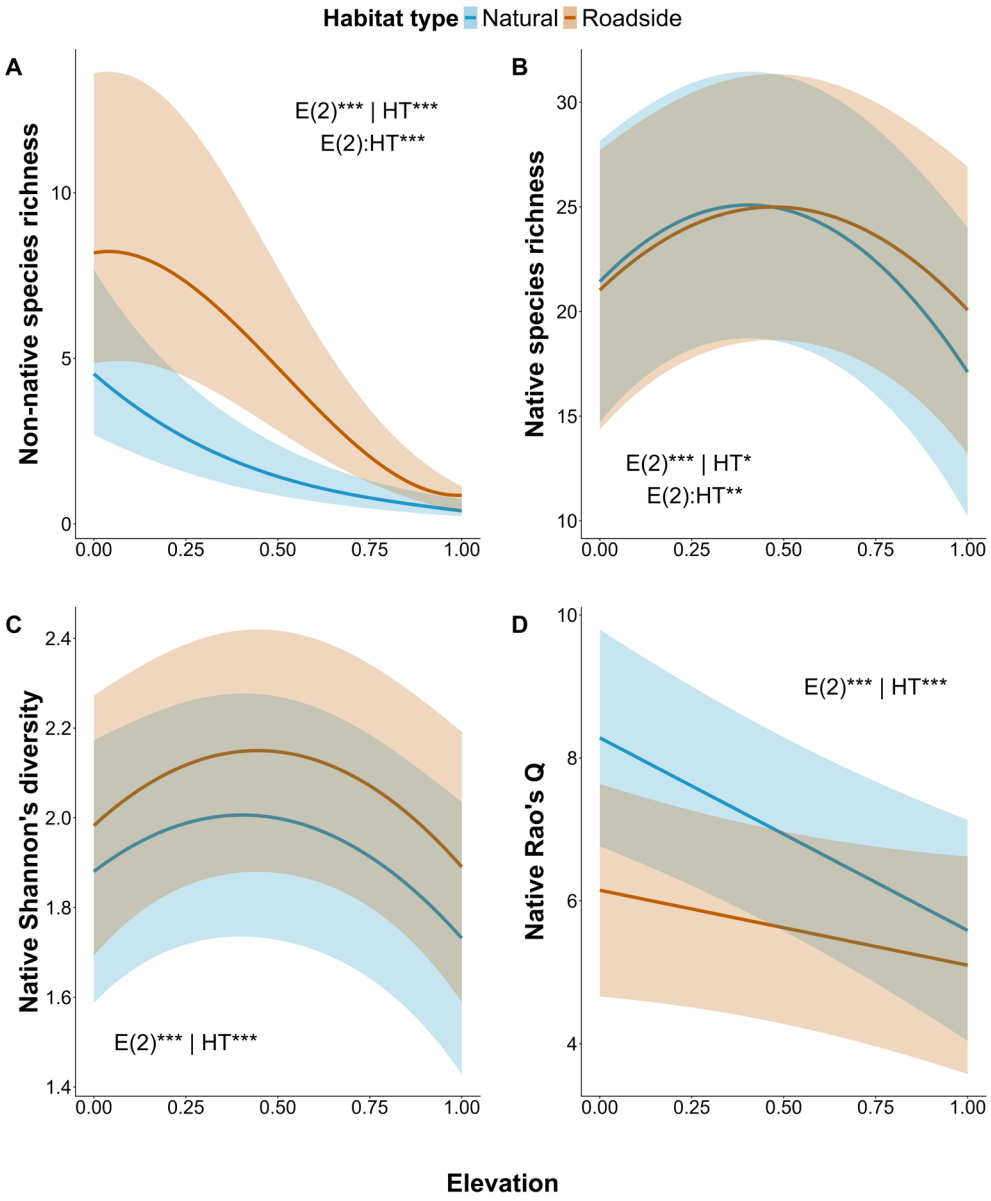


**FIGURE 2** | Non-native species richness (A), native species richness (B), native Shannon's diversity (C), and native Rao's Q (D) by elevation and habitat type at the global scale. For native (B) and non-native species richness (A), generalized linear mixed-effects models with a Poisson distribution were fit. Fixed effects included scaled elevation and habitat type and random effects included sample site nested in road, then nested in region. For both models, quadratic elevation provided a better fit over linear based on likelihood ratio tests (native richness: $\chi^2 = 20.10$, $p < 0.001$; non-native richness: $\chi^2 = 66.37$, $p < 0.001$). See Table S4 for complete statistical results. For native Rao's Q (D) and native Shannon's diversity (C), linear mixed-effects models were fit with elevation and habitat type as fixed effects and sample site nested in road then nested in region as random effects. For native Rao's Q, linear elevation provided a better fit than quadratic using a likelihood ratio test ($\chi^2 = 3.26$, $p > 0.05$) while, for native Shannon's diversity, quadratic elevation fit best ($\chi^2 = 13.668$, $p < 0.01$). See Table S5 for complete statistical results.

elevation), there was predominantly no effect of native functional diversity on non-native species richness (Figure S3, Table S8).

### 3.3 | Non-Native Species Across Habitats

The ratio of non-native species found in natural habitats compared to in the adjacent roadside habitat is highest at low and high elevations, and decreases at mid elevations ($p < 0.001$) (Figure 4). At low and high elevations, the ratio of non-natives in natural to roadside habitats was approximately 0.6.

## 4 | Discussion

### 4.1 | Lack of Biotic Resistance in High-Elevation Communities

With increasing variability in climatic factors as well as human disturbances, early monitoring of non-native species in alpine communities is vital to their long-term stability. In this global-scale study, we found that native diversity does not per se prevent the establishment of non-native species in high-elevation habitats, including in the alpine zone. Rather, we present evidence

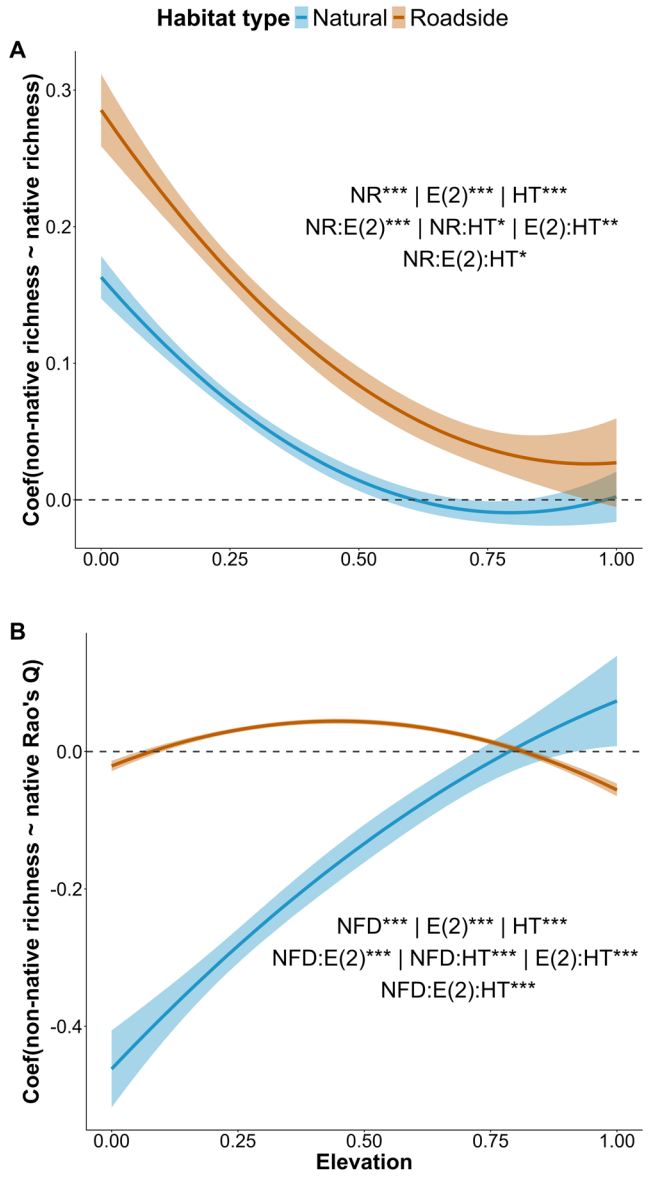


**FIGURE 3** | Relationship of non-native species richness to native species richness (A) and native Rao's Q (B) by elevation and habitat type at the global scale. The y-axis represents the coefficient of the relationship between non-native species richness and native diversity (species richness (A) and Rao's Q (B)), not the response variable. Positive relationships between non-native species richness and native diversity are above the gray dashed line and negative slopes are below. Line and ribbon colors indicate whether the community was in roadside (orange) habitats or natural (blue) habitats. Ribbons represent standard error. Coefficients of the non-native to native diversity relationships were extracted from the models with non-native species richness as response and native diversity (native richness: NR, native Rao's Q: FD), elevation (E or E(2) for the quadratic term), habitat type (HT), and their interactions as explanatory variables. At the global scale, the quadratic term for elevation provided a better fit than linear elevation for both models using a likelihood ratio test (native richness: $\chi^2 = 59.828$, $p < 0.001$, native Rao's Q: $\chi^2 = 75.246$, $p < 0.001$). Abbreviations inside the panels refer to significant effects ($p < 0.05$) resulting from these models. Only significant effects including native diversity (NR/FD) are mentioned. For the complete statistical results, see Tables S6–S8.

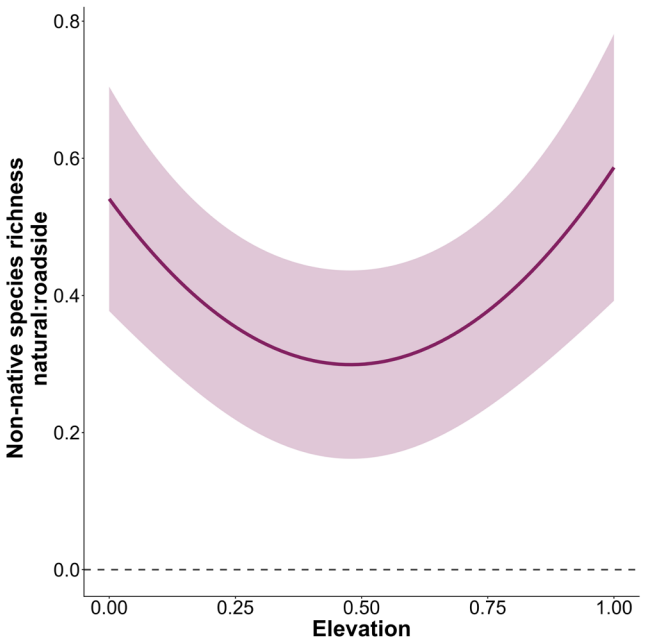


**FIGURE 4** | Ratio of non-native species found in natural habitats compared to roadside habitats by scaled elevation. The quadratic term for elevation was a better fit than linear elevation using a likelihood ratio test ($\chi^2 = 19.22$, $p < 0.001$). Ribbons represent 95% confidence intervals.

for the opposite case. Across regions, non-native species richness in (semi-)natural habitats was higher in more functionally diverse native communities, potentially signaling facilitation. This result goes in line with our second hypothesis assuming positive interactions at high elevations to support the establishment of non-native species. A higher native diversity can offer more possibilities for positive interactions, which are assumed to prevail under the harsh conditions present especially in the alpine zone and can help facilitate the establishment of non-native species (Cavieres 2021). This interpretation is supported by previous studies that demonstrate the ability of native species to create pockets of favorable microclimates, that is, nurse plant effects, which benefit non-native species in these harsh environments (Anthelme et al. 2012; Badano et al. 2007; Cavieres and Badano 2009). The increase in non-native species richness with higher native functional diversity may also suggest that communities with more diverse resource acquisition and growth strategies may provide more opportunities for non-native species to find such positive interactions. This facilitation may be more likely to be found in natural habitats, as they are often more vegetation dense, promoting close interaction among native and non-native species.

Surprisingly, and in contrast to the observed impact of native functional diversity, non-native species richness in high-elevation (semi-)natural communities was not significantly influenced by the number of native species. However, just over a third of regions showed a positive association between non-native species richness and native species richness, partially supporting our hypothesis about the role of facilitative interactions for non-native species establishment at high elevations in mountain regions (Duarte et al. 2021; O'Brien et al. 2019).

Interestingly, our findings for high-elevation (semi-)natural habitats did not align with the observed patterns for disturbed roadside habitats. While we recorded more non-native species in roadside communities with more native species, pointing again to facilitative interactions supporting non-native species' establishment, native functional diversity did not impact the number of non-native species in high-elevation roadside habitats. These diverging results, in combination with varying regional patterns, suggest that different scenarios of native diversity and environmental factors drive the establishment of non-native species in roadside habitats compared to semi-natural or natural habitats at high elevations and in the alpine zone. In the case of increasing non-native species richness with increasing native species richness, especially in regions where roads reach far into the alpine zone with harsh conditions (e.g., up to 4000 m a.s.l. in the Central Chilean and the Central Argentinian Andes where the treeline is at ca. 2200 m a.s.l.), higher native species richness can provide more opportunities for positive interactions. These results signal that communities at higher elevations, and even in alpine habitats, are not as protected from non-native species invasion as previously expected, and should be closely monitored for potential newly arriving species.

### 4.2 | Habitat-Dependent Interactions in the Lower Half of the Elevation Gradient

In the lower part of the elevation gradient, the observed relationship between non-native species richness and native diversity also depended on both the habitat type considered and the native diversity metric used. In low-elevation semi-natural habitats, we expected to find the strongest signals of biotic resistance (Hypotheses 1 and 3). This was confirmed by finding fewer non-native species in communities with high native functional diversity (H1), and by not finding native functional diversity to result in any type of biotic interaction impacting non-native species establishment in roadside habitats (H3). In an experimental study, Conti et al. (2018) found that native communities resisted invaders with functionally similar traits. This suggests that at larger scales, communities with high functional diversity may be more likely to repel a wide variety of non-native species (Delavaux et al. 2023), thus decreasing their overall establishment.

A potential limitation of our study is that our one-time assessment does not allow us to exclude the case that non-native invasion has already led to a decline in native species diversity and community recomposition (Hejda et al. 2009; Kuebbing and Nuñez 2016). In this case, a greater number of non-native species would not result from the lack of biotic resistance in a low-diversity native community, but rather the functionally poor native community would be the consequence of non-native species' establishment. However, for example, we found that native species richness did not decline over time despite non-native species invasions in a previous study in Tenerife (Teide) (Buhaly et al. 2025). Future studies using temporal data may help determine how community recomposition following invasion affects the relationships between non-native and native species richness.

Interestingly, we found the opposite response for non-native species richness in the lower part of the elevation gradient when using the number of native species as an indicator of native diversity. More non-native species were found in communities with high native species richness, both in roadside and (semi-)natural habitats. We can speculate that in these low-elevation habitats, greater structural complexity including forests with multiple vegetation layers of herbs, shrubs, and trees can lead to an increased habitat heterogeneity (Camacho et al. 2025), which can benefit both native and non-native species, possibly leading to increased species richness for both species groups. A species-rich native plant community can be a reflection of numerous ecological niches, also accommodating both native and non-native species.

An additional explanation for the unexpected positive correlation between non-native and native species richness is that disturbance might be relatively intense in lower-elevation areas (Elsen et al. 2020; Marini et al. 2009; Pauchard and Alaback 2004). These communities may include additional microsites and disturbance heterogeneity due to their proximity to human-induced disturbances, further increasing possible niche space (Berli et al. 2003; Lee and Power 2013). In cases of frequent mowing and use of herbicides, the competition among species may be substantially reduced. Both non-native and native species have been found to recolonize highly disturbed habitats (Chiuffo et al. 2018; Everingham et al. 2019; Jauni et al. 2015), which suggests the potential for simultaneous growth in disturbed environments. Our results underscore the role of disturbance and resource availability as dominant drivers of non-native species richness in these environments (Chiuffo et al. 2018).

Overall, our findings provide limited support for our first hypothesis, assuming biotic resistance in lowland habitats. We also found only partial support for Hypothesis 3, with natural habitats exhibiting stronger relationships between non-native species richness and native functional diversity; however, this was not apparent when examining native species richness. The strong relationships between non-native species richness and native species richness along disturbed roadsides may be driven more by mechanistic causes such as habitat heterogeneity as opposed to stronger interactive effects. This potential for diverging responses highlights the need to address abiotic factors and under which conditions they may play a role in the relationship between native species diversity and invasion by non-native species.

### 4.3 | Moving Beyond Species Richness

The expansion of the biotic resistance hypothesis to include more than species richness is important, as functional diversity seems to be a relevant measure in this context (Conti et al. 2018; Díaz et al. 2022; Grace et al. 2017; Li et al. 2022). Functionally diverse communities can make more complete use of available resources through a higher degree of niche complementarity among species (Godoy et al. 2020). Since functional diversity incorporates the real differences between individuals while ignoring species with similar traits, relying solely on taxonomic measures may overlook important mechanisms of biotic resistance, as it does not capture the resource-use efficiency and complementarity which functional diversity reflects. Since we found diverging responses depending on

how native diversity was assessed, we suggest that hypotheses should carefully consider the diversity metric tested. Then, elevation (degree of environmental harshness) can also be considered to distinguish potentially different responses of low and high-elevation communities. As meta-analyses such as Jeschke and Heger (2018) found only partial support for the biotic resistance hypothesis, and alpine communities are at higher risk of habitat reduction and endemic species loss (Dirnböck et al. 2011; Wershow and DeChaine 2018), it is important to determine more specific drivers of potential resistance and consider multiple metrics of diversity to help manage alpine communities in the face of climate change.

### 4.4 | Percolation Into Natural Habitats

We hypothesized that the ratio of non-native species between natural and roadside habitats would be higher at high elevations and in alpine areas due to the anticipated transition from competition to facilitation along the elevation gradient, and thus a higher likelihood that non-native species moved from roadsides into the adjacent (semi-)natural vegetation. We found that this ratio was relatively similar at high and low elevations, but at both ends of the elevation gradient the ratio was higher than at mid elevations, thus only partly confirming our expectations (Hypothesis 4). This high ratio at both low and high elevations is likely the result of two scenarios. Low elevations are the most common site for the introduction of non-native species and generally have the highest non-native species richness (Alexander et al. 2016; Q. Guo et al. 2018). This suggests that there is a larger pool of species to invade natural habitats from the roadside. However, the high ratio of non-native species between natural and roadside habitats at high elevations highlights that once non-native species reach high elevations and the alpine zone, having used roads as dispersal corridors, they can more easily spread into adjacent natural vegetation. This may also reflect species with specific functional traits that allow them to both shift along mountain roads, as well as into natural habitats (McDougall et al. 2018). This percolation into natural habitats occurs in conjunction with facilitative effects conferred by native functional diversity, suggesting that establishment in these new habitats may be aided by resident native species. This emphasizes the role of roads as key dispersal pathways for non-native plant invasions, particularly in high-elevation alpine environments, where their presence does not limit the spread of non-native species into surrounding vegetation.

### 4.5 | Conclusions

Our findings indicate a lack of biotic resistance at the upper end of elevation gradients reaching up to the alpine zone. Rather, we observed positive effects of native diversity on the number of established non-native species, signaling facilitation effects. While we observed some evidence of biotic resistance conferred by functional diversity in natural habitats at lower elevations, the high ratio of non-native species in natural to disturbed roadside habitats indicates that, once established, many non-natives can spread into adjacent more natural vegetation. Though high-elevation habitats, especially alpine zones, are not currently heavily invaded by non-native species (Alexander et al. 2011; McDougall et al. 2011), future environmental changes, including a rising number of propagules through increased traffic and climate warming, are likely to increase the risk of plant invasions into alpine habitats (Carboni et al. 2018; Pauchard et al. 2016; Petitpierre et al. 2016; Rew et al. 2020).

Our study results highlight the importance of monitoring and managing roads as key pathways for non-native species introductions into high-elevation ecosystems. Proactive measures to reduce propagule pressure, such as avoiding planting non-native species in highly disturbed sites or monitoring seed dispersal on vehicles, and mitigation of the effects of climate change are essential in preventing the spread of invasive species in especially vulnerable alpine environments.

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#### Conflicts of Interest

The authors declare no conflicts of interest.

#### Data Availability Statement

All data is published on Zenodo. Species abundance data and community functional diversity is available at https://doi.org/10.5281/zenodo.15749536 and at https://doi.org/10.5281/zenodo.15014188, respectively.

#### References

Alexander, J. M., C. Kueffer, C. C. Daehler, et al. 2011. "Assembly of Nonnative Floras Along Elevational Gradients Explained by Directional Ecological Filtering." *Proceedings of the National Academy of Sciences of*

*the United States of America* 108, no. 2: 656–661. https://doi.org/10.1073/pnas.1013136108.

Alexander, J. M., J. J. Lembrechts, L. A. Cavieres, et al. 2016. "Plant Invasions Into Mountains and Alpine Ecosystems: Current Status and Future Challenges." *Alpine Botany* 126, no. 2: 89–103. https://doi.org/10.1007/s00035-016-0172-8.

Anthelme, F., B. Buendia, C. Mazoyer, and O. Dangles. 2012. "Unexpected Mechanisms Sustain the Stress Gradient Hypothesis in a Tropical Alpine Environment." *Journal of Vegetation Science* 23, no. 1: 62–72. https://doi.org/10.1111/j.1654-1103.2011.01333.x.

Arel-Bundock, V., N. Greifer, and A. Heiss. 2024. "How to Interpret Statistical Models Using Marginaleffects for R and Python." *Journal of Statistical Software* 111, no. 9: 1–32. https://doi.org/10.18637/jss.v111.i09.

Arévalo, J. R., J. D. Delgado, R. Otto, A. Naranjo, M. Salas, and J. M. Fernández-Palacios. 2005. "Distribution of Alien vs. Native Plant Species in Roadside Communities Along an Altitudinal Gradient in Tenerife and Gran Canaria (Canary Islands)." *Perspectives in Plant Ecology, Evolution and Systematics* 7, no. 3: 185–202. https://doi.org/10.1016/j.ppees.2005.09.003.

Bacher, S., B. S. Galil, M. A. Nuñez, et al. 2023. "Chapter 4: Impacts of Invasive Alien Species on Nature, nature's Contributions to People, and Good Quality of Life." In *Thematic Assessment Report on Invasive Alien Species and Their Control of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*, edited by H. E. Roy, A. Pauchard, P. stoett, and T. Truong. IPBES Secretariat. https://doi.org/10.5281/zenodo.7430731.

Badano, E. I., E. Villarroel, R. O. Bustamante, P. A. Marquet, and L. A. Cavieres. 2007. "Ecosystem Engineering Facilitates Invasions by Exotic Plants in High-Andean Ecosystems." *Journal of Ecology* 95: 682–688.

Barajas Barbosa, M. P., D. Craven, P. Weigelt, et al. 2023. "Assembly of Functional Diversity in an Oceanic Island Flora." *Nature* 619, no. 7970: 545–550. https://doi.org/10.1038/s41586-023-06305-z.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67, no. 1: 1–48. https://doi.org/10.18637/jss.v067.i01.

Berli, M., J. M. Kirby, S. M. Springman, and R. Schulin. 2003. "Modelling Compaction of Agricultural Subsoils by Tracked Heavy Construction Machinery Under Various Moisture Conditions in Switzerland." *Soil & Tillage Research* 73, no. 1: 57–66. https://doi.org/10.1016/S0167-1987(03)00099-0.

Bertness, M. D., and R. Callaway. 1994. "Positive Interactions in Communities." *Trends in Ecology & Evolution* 9, no. 5: 191–193.

Botta-Dukát, Z. 2005. "Rao's Quadratic Entropy as a Measure of Functional Diversity Based on Multiple Traits." *Journal of Vegetation Science* 16, no. 5: 533–540. https://doi.org/10.1111/j.1654-1103.2005.tb02393.x.

Bruelheide, H., J. Dengler, O. Purschke, et al. 2018. "Global Trait–Environment Relationships of Plant Communities." *Nature Ecology & Evolution* 2, no. 12: 1906–1917. https://doi.org/10.1038/s41559-018-0699-8.

Buhaly, M., A. R. Backes, J. R. Arévalo, and S. Haider. 2025. "Temporal Variability in Native Plant Composition Clouds Impact of Increasing Non-Native Richness Along Elevational Gradients in Tenerife." *Perspectives in Plant Ecology, Evolution and Systematics* 66: 125845. https://doi.org/10.1016/j.ppees.2024.125845.

Camacho, L. F., N. Schwartz, and L. Avilés. 2025. "Vegetation Structural Complexity Across Elevational Gradients: Insights From the Tropical Andes." *Journal of Biogeography* 52, no. 5: e15102. https://doi.org/10.1111/jbi.15102.

Carboni, M., M. Guéguen, C. Barros, et al. 2018. "Simulating Plant Invasion Dynamics in Mountain Ecosystems Under Global Change Scenarios." *Global Change Biology* 24, no. 1: e289–e302. https://doi.org/10.1111/gcb.13879.

Catford, J. A., C. C. Daehler, H. T. Murphy, et al. 2012. "The Intermediate Disturbance Hypothesis and Plant Invasions: Implications for Species Richness and Management." *Perspectives in Plant Ecology, Evolution and Systematics* 14, no. 3: 231–241. https://doi.org/10.1016/j.ppees.2011.12.002.

Cavieres, L. A. 2021. "Facilitation and the Invasibility of Plant Communities." *Journal of Ecology* 109, no. 5: 2019–2028. https://doi.org/10.1111/1365-2745.13627.

Cavieres, L. A., and E. I. Badano. 2009. "Do Facilitative Interactions Increase Species Richness at the Entire Community Level?" *Journal of Ecology* 97, no. 6: 1181–1191. https://doi.org/10.1111/j.1365-2745.2009.01579.x.

Cavieres, L. A., C. L. Quiroz, M. A. Molina-Montenegro, A. A. Muñoz, and A. Pauchard. 2005. "Nurse Effect of the Native Cushion Plant *Azorella monantha* on the Invasive Non-Native *Taraxacum officinale* in the High-Andes of Central Chile." *Perspectives in Plant Ecology, Evolution and Systematics* 7: 217–226.

Chiuffo, M. C., M. C. Cock, A. O. Prina, and J. L. Hierro. 2018. "Response of Native and Non-Native Ruderals to Natural and Human Disturbance." *Biological Invasions* 20, no. 10: 2915–2925. https://doi.org/10.1007/s10530-018-1745-9.

Choler, P., R. Michalet, and R. M. Callaway. 2001. "Facilitation and Competition on Gradients in Alpine Plant Communities." *Ecology* 82, no. 12: 3295–3308. https://doi.org/10.1890/0012-9658(2001)082%5B3295:FACOGI%5D2.0.CO;2.

Compagnoni, A., and P. B. Adler. 2014. "Warming, Competition, and *Bromus tectorum* Population Growth Across an Elevation Gradient." *Ecosphere* 5, no. 9: Article 121. https://doi.org/10.1890/es14-00047.1.

Conti, L., S. Block, M. Parepa, et al. 2018. "Functional Trait Differences and Trait Plasticity Mediate Biotic Resistance to Potential Plant Invaders." *Journal of Ecology* 106, no. 4: 1607–1620. https://doi.org/10.1111/1365-2745.12928.

Davis, M. A., P. Grime, and K. Thompson. 2000. "Fluctuating Resources in Plant Communities: A General Theory of Invasibility." *Journal of Ecology* 88: 528–534.

Delavaux, C. S., T. W. Crowther, C. M. Zohner, et al. 2023. "Native Diversity Buffers Against Severity of Non-Native Tree Invasions." *Nature* 621, no. 7980: 773–781. https://doi.org/10.1038/s41586-023-06440-7.

Díaz, S., J. Kattge, J. H. C. Cornelissen, et al. 2016. "The Global Spectrum of Plant Form and Function." *Nature* 529, no. 7585: 167–171. https://doi.org/10.1038/nature16489.

Díaz, S., J. Kattge, J. H. C. Cornelissen, et al. 2022. "The Global Spectrum of Plant Form and Function: Enhanced Species-Level Trait Dataset." *Scientific Data* 9, no. 1: 755. https://doi.org/10.1038/s41597-022-01774-9.

Dirnböck, T., F. Essl, and W. Rabitsch. 2011. "Disproportional Risk for Habitat Loss of High-Altitude Endemic Species Under Climate Change." *Global Change Biology* 17, no. 2: 990–996. https://doi.org/10.1111/j.1365-2486.2010.02266.x.

Duarte, M., M. Verdú, L. A. Cavieres, and R. O. Bustamante. 2021. "Plant–Plant Facilitation Increases With Reduced Phylogenetic Relatedness Along an Elevation Gradient." *Oikos* 130, no. 2: 248–259. https://doi.org/10.1111/oik.07680.

Elsen, P. R., W. B. Monahan, and A. M. Merenlender. 2020. "Topography and Human Pressure in Mountain Ranges Alter Expected Species Responses to Climate Change." *Nature Communications* 11, no. 1: 1974. https://doi.org/10.1038/s41467-020-15881-x.

Elton, C. S. 1958. *The Ecology of Invasions by Animals and Plants*. Methuen.

Enders, M., F. Havemann, F. Ruland, et al. 2020. "A Conceptual Map of Invasion Biology: Integrating Hypotheses Into a Consensus Network."

*Global Ecology and Biogeography* 29: 978–991. https://doi.org/10.1111/geb.13082.

Enquist, B., R. Condit, R. K. Peet, M. Schildhauer, and B. M. Thiers. 2016. "Cyberinfrastructure for an Integrated Botanical Information Network to Investigate the Ecological Impacts of Global Climate Change on Plant Biodiversity." *PeerJ Preprints* 4: e2615v2. https://doi.org/10.7287/peerj.preprints.2615v2.

Espinoza-Guzmán, M. A., D. Aragonés Borrego, and F. J. Sahagún-Sánchez. 2023. "Evaluation of Recent Land-Use and Land-Cover Change in a Mountain Region." *Trees, Forests and People* 11: 100370. https://doi.org/10.1016/j.tfp.2023.100370.

Everingham, S. E., F. Hemmings, and A. T. Moles. 2019. "Inverted Invasions: Native Plants Can Frequently Colonise Urban and Highly Disturbed Habitats." *Austral Ecology* 44, no. 4: 702–712. https://doi.org/10.1111/aec.12719.

Falster, D., R. Gallagher, E. H. Wenk, et al. 2021. "AusTraits, a Curated Plant Trait Database for the Australian Flora." *Scientific Data* 8, no. 1: 254. https://doi.org/10.1038/s41597-021-01006-6.

Forman, R. T. T., D. Sperling, J. A. Bissonette, et al. 2003. *Road Ecology: Science and Solutions*. Island Press.

Fridley, J. D., J. J. Stachowicz, S. Naeem, et al. 2007. "The Invasion Paradox: Reconciling Pattern and Process in Species Invasions." *Ecology* 88, no. 1: 3–17.

Fuentes-Lillo, E., J. J. Lembrechts, L. A. Cavieres, et al. 2021. "Anthropogenic Factors Overrule Local Abiotic Variables in Determining Non-Native Plant Invasions in Mountains." *Biological Invasions* 23: 3671–3686. https://doi.org/10.1007/s10530-021-02602-8.

Godoy, O., L. Gómez-Aparicio, L. Matías, I. M. Pérez-Ramos, and E. Allan. 2020. "An Excess of Niche Differences Maximizes Ecosystem Functioning." *Nature Communications* 11, no. 1: 4180. https://doi.org/10.1038/s41467-020-17960-5.

Gómez-Aparicio, L., R. Zamora, J. M. Gómez, J. A. Hódar, J. Castro, and E. Baraza. 2004. "Applying Plat Facilitation to Forest Restoration: A Meta-Analysis of the Use of Shrubs as Nurse Plants." *Ecological Applications* 14, no. 4: 1128–1138. https://doi.org/10.1890/03-5084.

Grace, J. B., S. Harrison, and H. Cornell. 2017. "Is Biotic Resistance Enhanced by Natural Variation in Diversity?" *Oikos* 126, no. 10: 1484–1492. https://doi.org/10.1111/oik.04334.

Griffith, D. M., T. M. Anderson, and S. Goslee. 2019. "The 'Plantspec' R Package: A Tool for Spectral Analysis of Plant Stoichiometry." *Methods in Ecology and Evolution* 10, no. 5: 673–679. https://doi.org/10.1111/2041-210x.13143.

Guo, K., P. Pyšek, M. Chytrý, et al. 2024. "Stage Dependence of Elton's Biotic Resistance Hypothesis of Biological Invasions." *Nature Plants* 10, no. 10: 1484–1492. https://doi.org/10.1038/s41477-024-01790-0.

Guo, Q., S. Fei, Z. Shen, B. V. Iannone, J. Knott, and S. L. Chown. 2018. "A Global Analysis of Elevational Distribution of Non-Native Versus Native Plants." *Journal of Biogeography* 45: 793–803. https://doi.org/10.1111/jbi.13145.

Haider, S., J. J. Lembrechts, K. McDougall, et al. 2022. "Think Globally, Measure Locally: The MIREN Standardized Protocol for Monitoring Plant Species Distributions Along Elevation Gradients." *Ecology and Evolution* 12, no. 2: e8590. https://doi.org/10.1002/ece3.8590.

Hartig, F. 2024. *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models* [Computer software].

He, Q., M. D. Bertness, and A. H. Altieri. 2013. "Global Shifts Towards Positive Species Interactions With Increasing Environmental Stress." *Ecology Letters* 16: 695–706. https://doi.org/10.1111/ele.12080.

Hejda, M., P. Pyšek, and V. Jarošík. 2009. "Impact of Invasive Plants on the Species Richness, Diversity and Composition of Invaded Communities." *Journal of Ecology* 97, no. 3: 393–403. https://doi.org/10.1111/j.1365-2745.2009.01480.x.

Hulme, P. E., T. Ikeda, V. Vandvik, et al. 2023. "Chapter 3: Drivers Affecting Biological Invasions." In *Thematic Assessment Report on Invasive Alien Species and Their Control of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*, edited by H. E. Roy, A. Pauchard, P. Stoett, and T. Truong. IPBES Secretariat. https://doi.org/10.5281/zenodo.7430727.

Intergovernmental Panel on Climate Change (IPCC). 2023. *Climate Change 2022 – Impacts, Adaptation and Vulnerability: Working Group II Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press. https://doi.org/10.1017/9781009325844.

IPBES. 2018. *The IPBES Assessment Report on Land Degradation and Restoration*, 744. Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. https://doi.org/10.5281/zenodo.3237392.

Jauni, M., S. Gripenberg, and S. Ramula. 2015. "Non-Native Plant Species Benefit From Disturbance: A Meta-Analysis." *Oikos* 124, no. 2: 122–129. https://doi.org/10.1111/oik.01416.

Jeschke, J. M., and T. Heger. 2018. *Invasion Biology: Hypotheses and Evidence*. CABI.

Kalwij, J., M. Robertson, and B. van Rensburg. 2015. "Annual Monitoring Reveals Rapid Upward Movement of Exotic Plants in a Montane Ecosystem." *Biological Invasions* 17, no. 12: 3517–3529. https://doi.org/10.1007/s10530-015-0975-3.

Kattge, J., G. Bönisch, S. Díaz, et al. 2020. "TRY Plant Trait Database – Enhanced Coverage and Open Access." *Global Change Biology* 26, no. 1: 119–188. https://doi.org/10.1111/gcb.14904.

Kindt, R. 2020. "WorldFlora: An R Package for Exact and Fuzzy Matching of Plant Names Against the World Flora Online Taxonomic Backbone Data." *Applications in Plant Sciences* 8, no. 9: e11388. https://doi.org/10.1002/aps3.11388.

Körner, C. 2004. "Mountain Biodiversity, Its Causes and Function." *Ambio* 13: 11–17.

Körner, C. 2007. "The Use of "Altitude" in Ecological Research." *Trends in Ecology & Evolution* 22, no. 11: 569–574. https://doi.org/10.1016/j.tree.2007.09.006.

Körner, C., J. Paulsen, and E. Spehn. 2011. "A Definition of Mountains and Their Bioclimatic Belts for Global Comparisons of Biodiversity Data." *Alpine Botany* 121: 73–78. https://doi.org/10.1007/s00035-011-0094-4.

Körner, C., and E. Spehn. 2002. *Mountain Biodiversity. A Global Assessment*. Parthenon Publishing Group.

Kotlarski, S., A. Gobiet, S. Morin, M. Olefs, J. Rajczak, and R. Samacoïts. 2023. "21st Century Alpine Climate Change." *Climate Dynamics* 60, no. 1: 65–86. https://doi.org/10.1007/s00382-022-06303-3.

Kuebbing, S. E., and M. A. Nuñez. 2016. "Invasive Non-Native Plants Have a Greater Effect on Neighbouring Natives Than Other Non-Natives." *Nature Plants* 2, no. 10: 16134. https://doi.org/10.1038/nplants.2016.134.

Kueffer, C., K. McDougall, J. Alexander, et al. 2013. "Plant Invasions Into Mountain Protected Areas: Assessment, Prevention and Control at Multiple Spatial Scales." In *Plant Invasions in Protected Areas: Patterns, Problems and Challenges*, edited by L. Foxcroft, P. Pyšek, D. M. Richardson, and P. Genovesi, vol. 7, 89–113. Springer.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. "lmerTest Package: Tests in Linear Mixed Effects Models." *Journal of Statistical Software* 82, no. 13: 1–26. https://doi.org/10.18637/jss.v082.i13.

Laliberté, E., and P. Legendre. 2010. "A Distance-Based Framework for Measuring Functional Diversity From Multiple Traits." *Ecology* 91, no. 1: 299–305. https://doi.org/10.1890/08-2244.1.

Laliberté, E., P. Legendre, and B. Shipley. 2025. *Measuring Functional Diversity (FD) from Multiple Traits, and Other Tools for Functional Ecology* [R].

Lear, L., E. Hesse, K. Shea, and A. Buckling. 2020. "Disentangling the Mechanisms Underpinning Disturbance-Mediated Invasion." *Proceedings of the Royal Society B: Biological Sciences* 287, no. 1919: 20192415. https://doi.org/10.1098/rspb.2019.2415.

Lee, M. A., and S. A. Power. 2013. "Direct and Indirect Effects of Roads and Road Vehicles on the Plant Community Composition of Calcareous Grasslands." *Environmental Pollution* 176: 106–113. https://doi.org/10.1016/j.envpol.2013.01.018.

Lembrechts, J. J., J. M. Alexander, L. A. Cavieres, et al. 2017. "Mountain Roads Shift Native and Non-Native Plant Species' Ranges." *Ecography* 40, no. 3: 353–364. https://doi.org/10.1111/ecog.02200.

Li, S., P. Jia, S. Fan, et al. 2022. "Functional Traits Explain the Consistent Resistance of Biodiversity to Plant Invasion Under Nitrogen Enrichment." *Ecology Letters* 25: 778–789. https://doi.org/10.1111/ele.13951.

MacDougall, A. S., B. Gilbert, and J. M. Levine. 2009. "Plant Invasions and the Niche." *Journal of Ecology* 97, no. 4: 609–615. https://doi.org/10.1111/j.1365-2745.2009.01514.x.

Marini, L., K. J. Gaston, F. Prosser, and P. E. Hulme. 2009. "Contrasting Response of Native and Alien Plant Species Richness to Environmental Energy and Human Impact Along Alpine Elevation Gradients." *Global Ecology and Biogeography* 18: 652–661. https://doi.org/10.1111/j.1466-8238.2009.00484.x.

McDougall, K. L., J. M. Alexander, S. Haider, A. Pauchard, N. G. Walsh, and C. Kueffer. 2011. "Alien Flora of Mountains: Global Comparisons for the Development of Local Preventive Measures Against Plant Invasions." *Diversity and Distributions* 17: 103–111. https://doi.org/10.1111/j.1472-4642.2010.00713.x.

McDougall, K. L., J. Lembrechts, L. J. Rew, et al. 2018. "Running Off the Road: Roadside Non-Native Plants Invading Mountain Vegetation." *Biological Invasions* 20: 3461–3473. https://doi.org/10.1007/s10530-018-1787-z.

Mitchell, C. E., A. A. Agrawal, J. D. Bever, et al. 2006. "Biotic Interactions and Plant Invasions." *Ecology Letters* 9, no. 6: 726–740. https://doi.org/10.1111/j.1461-0248.2006.00908.x.

Mouchet, M. A., S. Villéger, N. W. H. Mason, and D. Mouillot. 2010. "Functional Diversity Measures: An Overview of Their Redundancy and Their Ability to Discriminate Community Assembly Rules." *Functional Ecology* 24, no. 4: 867–876. https://doi.org/10.1111/j.1365-2435.2010.01695.x.

Müllerová, J., M. Vítková, and O. Vítek. 2011. "The Impacts of Road and Walking Trails Upon Adjacent Vegetation: Effects of Road Building Materials on Species Composition in a Nutrient Poor Environment." *Science of the Total Environment* 409, no. 19: 3839–3849. https://doi.org/10.1016/j.scitotenv.2011.06.056.

O'Brien, M. J., L. F. T. De Menezes, K. A. Bråthen, G. Losapio, and F. I. Pugnaire. 2019. "Facilitation Mediates Species Presence Beyond Their Environmental Optimum." *Perspectives in Plant Ecology, Evolution and Systematics* 38: 24–30. https://doi.org/10.1016/j.ppees.2019.03.004.

Oksanen, J., G. L. Simpson, F. G. Blanchet, et al. 2025. *vegan: Community Ecology Package* (Version R package version 2.8-0) [Computer software]. https://vegandevs.github.io/vegan/.

Olsen, S. L., J. P. Töpper, O. Skarpaas, V. Vandvik, and K. Klanderud. 2016. "From Facilitation to Competition: Temperature-Driven Shift in Dominant Plant Interactions Affects Population Dynamics in Seminatural Grasslands." *Global Change Biology* 22, no. 5: 1915–1926. https://doi.org/10.1111/gcb.13241.

Pauchard, A., and P. B. Alaback. 2004. "Influence of Elevation, Land Use, and Landscape Context on Patterns of Alien Plant Invasions Along Roadsides in Protected Areas of South-Central Chile." *Conservation Biology* 18, no. 1: 238–248. https://doi.org/10.1111/j.1523-1739.2004.00300.x.

Pauchard, A., A. Milbau, A. Albihn, et al. 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, no. 2: 345–353. https://doi.org/10.1007/s10530-015-1025-x.

Pauchard, A., and K. Shea. 2006. "Integrating the Study of Non-Native Plant Invasions Across Spatial Scales." *Biological Invasions* 8: 399–413.

Payne, D., M. Snethlage, J. Geschke, E. M. Spehn, and M. Fischer. 2020. "Nature and People in the Andes, East African Mountains, European Alps, and Hindu Kush Himalaya: Current Research and Future Directions." *Mountain Research and Development* 40, no. 2: A1–A14.

Petitpierre, B., K. McDougall, T. Seipel, O. Broennimann, A. Guisan, and C. Kueffer. 2016. "Will Climate Change Increase the Risk of Plant Invasions Into Mountains?" *Ecological Applications* 26, no. 2: 530–544. https://doi.org/10.1890/14-1871.1.

Proß, T. 2023. *Spectroscopy script v6.8* [Computer software]. https://doi.org/10.5281/zenodo.10021217.

Pyšek, P., P. E. Hulme, D. Simberloff, et al. 2020. "Scientists' Warning on Invasive Alien Species." *Biological Reviews* 95, no. 6: 1511–1534. https://doi.org/10.1111/brv.12627.

Pyšek, P., D. M. Richardson, M. Rejmánek, G. L. Webster, M. Williamson, and J. Kirschner. 2004. "Alien Plants in Checklists and Floras: Towards Better Communication Between Taxonomists and Ecologists." *Taxon* 53, no. 1: 131–143. https://doi.org/10.2307/4135498.

R Core Team. 2024. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.

Rahbek, C., M. K. Borregaard, R. K. Colwell, et al. 2019. "Humboldt's Enigma: What Causes Global Patterns of Mountain Biodiversity?" *Science* 365, no. 6458: 1108–1113. https://doi.org/10.1126/science.aax0149.

Rao, C. R. 1982. "Diversity and Dissimilarity Coefficients: A Unified Approach." *Theoretical Population Biology* 21, no. 1: 24–43. https://doi.org/10.1016/0040-5809(82)90004-1.

Ratier Backes, A., C. Römermann, J. M. Alexander, et al. 2023. "Mechanisms Behind Elevational Plant Species Richness Patterns Revealed by a Trait-Based Approach." *Journal of Vegetation Science* 34, no. 1: e13171. https://doi.org/10.1111/jvs.13171.

Rew, L. J., K. L. McDougall, J. M. Alexander, et al. 2020. "Moving Up and Over: Redistribution of Plants in Alpine, Arctic, and Antarctic Ecosystems Under Global Change." *Arctic Antarctic and Alpine Research* 52, no. 1: 651–665. https://doi.org/10.1080/15230430.2020.1845919.

Rossignaud, L., M. O. Kimberley, D. Kelly, S. Fei, and E. G. Brockerhoff. 2022. "Effects of Competition and Habitat Heterogeneity on Native-Exotic Plant Richness Relationships Across Spatial Scales." *Diversity and Distributions* 28, no. 5: 1093–1104. https://doi.org/10.1111/ddi.13516.

Schickhoff, U., M. Bobrowski, S. Mal, N. Schwab, and R. B. Singh. 2022. "The World's Mountains in the Anthropocene." In *Mountain Landscapes in Transition: Effects of Land Use and Climate Change*, edited by U. Schickhoff, R. B. Singh, and S. Mal, 1–144. Springer International Publishing. https://doi.org/10.1007/978-3-030-70238-0_1.

Schrodt, F., J. Kattge, H. Shan, et al. 2015. "BHPMF—a Hierarchical Bayesian Approach to Gap-Filling and Trait Prediction for Macroecology and Functional Biogeography." *Global Ecology and Biogeography* 24, no. 12: 1510–1521. https://doi.org/10.1111/geb.12335.

Seebens, H., L. A. Meyerson, S. J. Rahlao, et al. 2023. "Chapter 2: Trends and Status of Alien and Invasive Alien Species." In *Thematic Assessment Report on Invasive Alien Species and Their Control of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*, edited by H. E. Roy, A. Pauchard, P. Stoett, and T. Truong. IPBES Secretariat. https://doi.org/10.5281/zenodo.7430725.

Shea, K., and P. Chesson. 2002. "Community Ecology Theory as a Framework for Biological Invasions." *Trends in Ecology & Evolution* 17, no. 4: 170–176.

Singmann, H., B. Bolker, J. Westfall, F. Aust, and M. Ben-Shachar. 2024. *afex: Analysis of Factorial Experiments* [Computer software].

Society for Ecological Restoration, International Network for Seed Based Restoration, & Royal Botanic Gardens Kew. 2023. *Seed Information Database (SID)* Available from:. https://ser-sid.org/. (February 2023).

Spooner, P. G. 2015. "Minor Rural Road Networks: Values, Challenges, and Opportunities for Biodiversity Conservation." *Nature Conservation Bulgaria* 11: 129–142. https://doi.org/10.3897/natureconservation.11.4434.

Tyser, R. W., and C. A. Worley. 1992. "Alien Flora in Grassland Adjacent to Road and Trail Corridors in Glacier National Park." *Conservation Biology* 6: 253–262.

von Holle, B., S. E. Weber, and D. M. Nickerson. 2020. "The Influence of Warming and Biotic Interactions on the Potential for Range Expansion of Native and Nonnative Species." *AoB Plants* 12, no. 5: plaa040. https://doi.org/10.1093/aobpla/plaa040.

Wershow, S. T., and E. G. DeChaine. 2018. "Retreat to Refugia: Severe Habitat Contraction Projected for Endemic Alpine Plants of the Olympic Peninsula." *American Journal of Botany* 105, no. 4: 760–778. https://doi.org/10.1002/ajb2.1042.

Yang, C., H. Xu, Q. Li, et al. 2025. "Global Loss of Mountain Vegetated Landscapes and Its Impact on Biodiversity Conservation." *Nature Communications* 16, no. 1: 8971. https://doi.org/10.1038/s41467-025-64449-0.

## Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Relationship of non-native species richness to native Shannon's diversity by elevation and habitat type at the global and regional scale. **Figure S2:** Relationship of non-native species richness to native species richness by elevation and habitat type at the regional scale. **Figure S3:** Relationship of non-native species richness to native Rao's Q by elevation and habitat type at the regional scale. **Figure S4:** Ratio of non-native species in natural habitats compared to roadsides by elevation and region at the regional scale. **Table S1:** Information on the length of the elevation gradients, the number of roads, the survey year, and the total number of native and non-native species for each region. **Table S2:** Prediction model details. Prediction models were created for each trait individually, using partial least squares regression (PLS regression). **Table S3:** Plant traits used in functional diversity analysis. Traits are divided into leaf economics spectrum (LES) traits, structural investment, and resource acquisition traits. **Table S4:** Results of the generalized linear mixed-effects models for species richness explained by elevation and habitat type. **Table S5:** Results of the linear mixed-effects models for native Shannon diversity and native Rao's Q explained by elevation and habitat type. **Table S6:** Results of the generalized linear mixed-effects models for non-native species richness explained by native species richness, native Shannon diversity and native functional diversity (Rao's Q). **Table S7:** Results of the generalized linear mixed-effects models for non-native species richness by native species richness, elevation, and habitat type for all regions individually. **Table S8:** Results of the generalized linear mixed-effects models for non-native species richness by native functional diversity for all regions individually. **Table S9:** Results of the generalized linear mixed-effects models for non-native species richness by native Shannon's diversity, elevation, and habitat type for all regions individually.