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# Global Homogenisation of Plant Communities Along Mountain Roads by Non-Native Species Despite Mixed Effects at Smaller Scales

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## ABSTRACT

**Aim:** Mountain ecosystems are experiencing increased invasion of non-native plants. These increases in non-native species put mountains at risk of biotic homogenisation and a reduction of biodiversity. Our study aims to test if non-native plant species are contributing to biotic homogenisation along roadways in mountain regions and how this changes along elevation gradients and across spatial scales.

**Location:** 18 globally distributed mountain regions.

**Time Period:** 2012–2023.

**Major Taxa Studied:** Vascular plants.

**Methods:** We used standardised vegetation surveys including species cover from 18 mountain regions worldwide to analyse whether the addition of non-native species to the native flora increased or decreased Bray–Curtis dissimilarity (i.e., beta-diversity) among roadside plant communities along elevation gradients ranging from 15 to 3919 m a.s.l. We tested this at the local, regional, continental and global scales using mixed-effects models and confirmed it using null models.

**Results:** In the New World, we mainly observed homogenisation across regions and scales, as beta-diversity was mostly lower with the addition of non-native species. This was particularly true for low elevations. In contrast, we predominantly found community differentiation in the Old World, specifically at smaller (i.e., local and regional) scales. At the global scale, communities became more similar through the addition of non-native species at all elevations.

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**Main Conclusions:** Large-scale homogenisation might be interpreted as a signal that high-elevation plant communities along roadways may become more similar as non-native species continue to spread upwards. Future studies should investigate the mechanisms driving the observed patterns of both homogenisation and differentiation by non-native species, and explore the potential consequences of these patterns for ecosystem function and resilience.

## 1 | Introduction

Non-native species are spreading throughout the globe at an increasing rate (Seebens et al. 2017), including into relatively pristine ecosystems like those found in mountains (Alexander et al. 2016). Non-native species richness has been shown to be considerably higher at low and mid-elevations, where most introductions occur, compared to high elevations (Alexander et al. 2016; Fuentes-Lillo et al. 2021; Haider et al. 2018; Marini et al. 2013). More recently, upward expansion of non-native species along elevation gradients was observed globally (Iseli et al. 2023). The expansion of agriculture, urban life and tourism into natural environments has led to the development of complex transportation networks (Ibisch et al. 2016), which serve as an efficient vector for the spread of non-native plant propagules into previously uninvaded habitats (Ansong and Pickering 2013; Lemke et al. 2019; McDougall et al. 2018; Mortensen et al. 2009; Sandoval et al. 2022).

A risk associated with the spread of non-native species is the homogenisation of plant communities (i.e., a reduction of beta-diversity between communities) (McKinney and La Sorte 2007; Winter et al. 2009). However, few studies have focused specifically on mountains where these effects may be in flux due to rapid elevational spread (Haider et al. 2018; Pauchard et al. 2013). Homogenisation of plant communities by non-native species has been found regardless of gains (Finderup Nielsen et al. 2019; Kortz and Magurran 2019) or losses (Smart et al. 2006; Stotz et al. 2019) in species richness. Gains are likely to occur more frequently, as relatively few non-native species are needed within a system to cause taxonomic homogenisation, indicating that the potential for homogenisation in any ecosystem is high (Kortz and Magurran 2019). In contrast, homogenisation through the loss of native species happens in later periods of the invasion process, potentially due to competition and can only be revealed through time-series analyses of the same plant communities.

Homogenisation of communities can lead to decreased landscape multifunctionality and ecosystem services at smaller spatial scales (Olden et al. 2004; van der Plas et al. 2016) because removing species with asynchronous responses leaves ecosystems vulnerable to disturbance and fluctuations in environmental conditions (Aussenac et al. 2017; De Mazancourt et al. 2013; Gross et al. 2014; Hautier et al. 2017; Isbell et al. 2015). Previous regional-scale studies in both grasslands (Wang et al. 2021) and forests (van der Plas et al. 2016) suggest a strong positive relationship between beta-diversity and ecosystem functioning, highlighting the need to conserve spatially diverse communities.

So far, the long-term effects of homogenisation are poorly understood, particularly in mountainous regions and the introduction of non-native species does not necessarily imply a reduction in the native community, specifically at larger scales (Lefebvre et al. 2024). Further, there is scarce information linking homogenisation by non-native species directly to threats to ecosystem functioning, likely due to the difficulty of long-term and multi-scale studies. Therefore, it is vital to create a baseline of potential homogenisation by non-native species to study these impacts in the future. Additionally, though homogenisation has been found at all spatial scales, it is unlikely that there is a singular cross-scale mechanism to explain all circumstances and more likely that there are nested mechanisms from small to large scales.

Biotic differentiation, as opposed to homogenisation, causes an increase in beta-diversity (McKinney 2004). Non-native species can create biotic differentiation, specifically at finer scales (Blowes et al. 2024; McKinney 2004). The impact of increased beta-diversity is also not well studied and some studies suggest it is a transitional phase to homogenisation, especially in disturbed areas (Kramer et al. 2023; Mori et al. 2018; Socolar et al. 2016). An increase in beta-diversity due to differentiation might strengthen and stabilise ecosystem processes, as shown in the field of biodiversity-ecosystem functioning research (Castillioni and Isbell 2023; Grman et al. 2018).

While studies have analysed homogenisation by non-native species at specific spatial scales, few have compared multiple scales, specifically in mountains, using standardised data (but see Haider et al. 2018). Here, we addressed local, regional, continental and global scales by analysing beta-diversity, as floristic dissimilarity, between plant communities along mountain elevation gradients to determine whether the addition of non-native species leads to homogenisation or differentiation at each scale. Mountain roads, though not necessarily representative of general mountain vegetation, were specifically selected as they represent the transition where non-native species can spread from low to high elevations. To achieve this, we utilised 18 regional standardised vegetation survey datasets sampled along 46 mountain roads (each road traversing an elevation gradient), collected and integrated by the Mountain Invasion Research Network (MIREN) (Haider et al. 2022; Kueffer et al. 2014) (Figure S1).

First, we test the hypothesis that the spread of non-native species is homogenising plant communities in mountains across all spatial scales, that is, from local to global scales. Second, we hypothesise that homogenisation is less pronounced at higher elevations, where non-native species are typically less frequent and abundant.

## 2 | Materials and Methods

### 2.1 | Vegetation Surveys

Vegetation survey data were collected in 18 mountainous regions using the Mountain Invasion Research Network (MIREN) standard protocol (Haider et al. 2022): the Australian Alps, the Central and South Chilean Andes, the Central and

South Argentinian Andes, the Rocky Mountains (Montana, United States), the Blue Mountains (Oregon, United States), the Austrian Alps, the Northern Scandes Mountains (Norway), the Krkonoše Mountains (Czech Republic), the Swiss Alps, the Himalayas (Kashmir, India), the Changbai Mountains (China), La Palma (Canary Islands, Spain), Tenerife (Canary Islands, Spain), the Maloti-Drakensberg (South Africa), the Cape Fold Mountains (South Africa) and the Hawaiian Islands (Hawaii, United States; Figure S1 and Table S1) (Seipel et al. 2022). These datasets were collected between 2012 and 2023, comprise all continents except Antarctica and range in latitude from 68.423°N (Norway) to 41.183°S (Argentina). A total of 2627 native and 563 non-native species were recorded. In each region, one to four elevation gradients (corresponding to roads; mostly, three elevation gradients) were selected for surveying. The majority of elevation gradients were open year-round, paved and used with moderate to high frequency by vehicles. The lowest point of a road was determined as the point at which there was no longer significant elevation change or beyond which sampling was not possible, while the uppermost point typically reached the highest point of the road. For information regarding the range of elevation for each region, see Table S1. Each elevation gradient (road) was divided into 20 equal sampling sites beginning at the lowest section of the elevation gradient and ending at the highest. One 50 m × 2 m plot was created parallel and adjacent to the road at each sampling site. These sampling sites adjacent to roadways represent primary introduction sites for non-native species. In total, 46 elevation gradients were surveyed across the 18 mountainous regions.

At each sampling site, all vascular plant species were identified and cover was recorded. Cover was estimated categorically in percentage bins; however, these classes varied between regions based on the protocol for the year in which they were sampled. For the Swiss Alps, the Krkonoše Mountains (Czech Republic), La Palma (Spain), Tenerife (Spain), both South African regions (Maloti-Drakensberg and Cape Fold Mountains) and the cover classes were as follows: 1—< 0.1%, 2-0.1-1%, 3-2-5%, 4-6-10%, 5-11-25%, 6-26-50%, 7-51-75% and 8-76-100%. All other regions were recorded as follows: 1—< 1%, 2-1-5%, 3-6-25%, 4-26-50%, 5-51-75%, 6-76-95% and 7-96-100%. For analyses, all bins were converted back to percentage by using the average of the bin range. Species names were harmonised using World Flora Online (R package 'WorldFlora') (Kindt 2020) and the Taxonomic Name Resolution Service (Boyle et al. 2021). Species were given a non-native or native status by the regional data contributors according to local references and databases. As a guideline, species introduced after CE 1500 are noted as non-native. While this may exclude some early introductions, this timeline reflects the widespread increase in non-native species due to extensive human migration (Nunn and Qian 2010).

### 2.2 | Statistical Analyses

All statistical analyses were carried out in R version 4.4.1 (R Core Team 2024). Among the elevation gradients, only sampling sites with both native and non-native species present were selected, because otherwise a comparison between community similarity of only native species and of native and non-native species together would not be possible. While removing sites with only native species limits the data slightly, it allows for direct testing of the addition of non-native species on community similarity. Species retained their status and contributed to analyses based on the region they were observed in. A species native to one region but non-native to another would contribute to the pairwise all-species community dissimilarity.

In total, 687 sampling sites across all regions were utilised in the final dataset. Sampling sites were pooled into three elevation categories for each spatial scale analysis. The categories were formed by dividing each elevation gradient into three equal portions and then scaling the average elevation of the sites in each category between 0 and 1. At the regional scale, high and low sites retained an elevation value of 1 and 0, respectively, and a new middle elevation value was calculated according to the entire regional elevation gradient. This was repeated at the continental and global scale. Although the elevation range strongly differed between regions, we believe that scaling is a valid approach because absolute elevations, or absolute temperatures, do not reflect the same environmental extremes across latitudinal gradients.

At all spatial scales, Bray–Curtis dissimilarity between sampling sites, as a robust metric for beta-diversity, was calculated using species cover data with the function 'beta.pair.abund' in the package Betapart (Baselga et al. 2021; Schroeder and Jenkins 2018). For beta-diversity calculations, the dataset was divided into a native-only dataset and an all-species dataset. This allowed us to interpret the effect of non-native species on beta-diversity in comparison to only native species. Additionally, Jaccard dissimilarity and its components, richness and replacement, were calculated using the beta.div.comp function in the package 'adespatial' in order to rule out the effects of differences in species richness on the comparison between native-only dissimilarity and all species values (Dray et al. 2025). The results of this additional analysis did not suggest a significant influence of species richness; therefore, the following analyses were conducted using Bray–Curtis dissimilarity due to the additional information of including species abundances. Detailed results and explanations can be found in the Methods S1 and Tables S2–S12.

At the smallest spatial scale, that is, the local scale, all pairwise comparisons of sampling sites within each elevation band of a single elevation gradient were calculated ($n = 3181$) (Figure 1). A linear mixed-effects model was fit using all pairwise beta-diversity values as the response variable, with the fixed effects including scaled elevation as a continuous variable (each elevational band in each gradient has a single scaled value), whether the value was from the native-only dataset or from the all-species dataset (species group) and region as well as all possible interactions. Three sets of random effects were included in the model in order to account for the sampling design as well as the non-independency inherent to pairwise dissimilarity calculations. As some sites within an elevation band are closer in elevation to each other than others, they are more likely to have similar communities. The following random effects were chosen in an effort to reduce this potential effect. These random effects were the name of the first sampling site used in the pairwise calculation nested in the elevation gradient (road) name (1|Road/Site1), the second sampling site name nested in the elevation

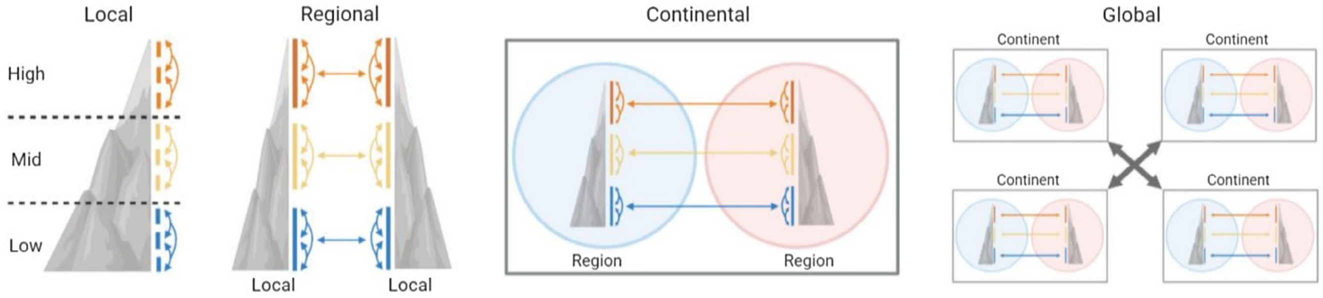

**FIGURE 1** | Methods of sampling site comparison at the local, regional, continental and global spatial scale. At all spatial scales, elevation gradients were divided into low, mid and high elevational bands. At the local scale, analysis was completed using sites within the same elevational band separately for each elevation gradient in each region. At the regional scale, analysis was completed using sites within the same elevational band across elevation gradients within each region. At the continental scale, analysis was completed using sites within the same elevation band across elevation gradients in the same continent. At the global scale, analysis was completed using all sites in the same elevation band for all elevation gradients. Created with BioRender.com.

gradient name (1|Road/Site2) and a combination of the sampling site names (1|SiteCombo). The linear mixed-effects model (LMM) was fit using the function 'lmer' in the package lmerTest (Kuznetsova et al. 2017). Model fit for this model and all following models was evaluated by visually assessing QQ plots and histograms of model residuals to ensure model assumptions were met. Because interactions including region were significant (Table S13), separate linear mixed-effects models were produced for each region. These individual models included the same fixed and random effects as listed above, with region removed as a fixed effect.

For the regional spatial scale, all possible pairwise combinations of sampling sites within the same elevation band were calculated using all elevation gradients within a region (*n* = 9984) (Figure 1). Regions with only one gradient were not used in this analysis. Similar to the local scale, an all-region LMM using scaled elevation, species group, region and all interactions was run. Random effects were similar to those noted above, but additionally included information relevant to comparing multiple elevation gradients ((1|Road1/Site1) + (1|Road2/Site2) + (1|RoadCombo/SiteCombo)). Separate models were created for each region because region identity was a significant interaction term in the general model (Table S14). Individual LMMs included the same fixed and random effects as the general model but without region as a fixed effect.

The continental spatial scale was analyzed using pairwise comparisons of sampling sites within the same elevation band across regions within the same continent (*n* = 25,848) (Figure 1). The island regions Tenerife and La Palma were placed with their geographic continent and categorised as Africa. The Australian Alps and the Hawaiian Islands (Hawaii, USA) were not utilised in this analysis as there was either only one region or they did not appropriately fit into another continent geographically. A LMM was fit with scaled elevation, species group and continent as the fixed effects. Information regarding regions was added to the previous random effects ((1|Region1/Road1/Site1) + (1|Region2/Road2/Site2) + (1|RegionCombo/RoadCombo/SiteCombo)). Continental models were also created to further analyze homogenisation at this scale due to continent being a significant interaction term (Table S15). Individual LMMs for each continent included the same fixed and random effects as the general model without continent as a fixed effect.

Finally, the global spatial scale was analyzed using pairwise comparisons of sampling sites in the same elevational band for all elevation gradients (*n* = 152,980) (Figure 1). This included all regions that were used in the local scale analysis. Scaled elevation and species group were used as fixed effects in the LMM with random effects including continental information ((1|Continent1/Region1/Road1/Site1) + (1|Continent2/Region2/Road2/Site2) + (1|ContinentCombo/RegionCombo/RoadCombo/SiteCombo)).

In addition to the LMMs, two null models were used to validate significant effects of non-native species in the linear mixed-effects models, which could have resulted from differences in species richness. For the first null model, this was achieved by randomising the native and non-native species within a sampling site and calculating 95% confidence intervals to determine whether the differences in beta-diversity values were simply from the addition of species or from an effect of non-native species (for details see Methods S2 and Figure S2). For the second null model, non-native species were replaced by random native species from the same region and elevation band and 95% confidence intervals were used to determine whether the addition of non-native species resulted in the same differences in beta-diversity as adding native species.

## 3 | Results

Across all regions, the number of non-native species generally declined with increasing elevation, though the proportion of non-natives to the total number of species was inconsistent (Figure S3). The percentage of sites each native and non-native species occurs in per region varied significantly between regions, with some species occupying less than 10% of sites and others occupying almost 100% (Figure S4). The highest number of non-native species shared between regions at the continental scale was 24 non-natives at both low and high elevations between the Rocky Mountains (Montana, USA) and the Blue Mountains (Oregon, USA) in North America (Figures S5–S11). At the global scale, the continents that shared the highest number of non-natives were Europe and South America at low elevations (62 species), with Europe generally sharing the highest number with all continents (Figure S10).

Across all scales, there was no consistent effect of elevation on the dissimilarity (beta-diversity) between communities, with beta-diversity showing either increasing, decreasing, or no response to elevation. This applied to communities of native species only, as well as to communities including both native and non-native species. In the following, we describe and interpret only those results which were supported by both the linear mixed-effects models as well as the two null models (See Section 2 and Methods S2 for details). Overall, while there is homogenisation of communities by non-native species at the global scale, both homogenisation and differentiation occur from the local to continental scales (Figure 2).

### 3.1 | Local Scale

The mean beta-diversity of native-only groups was 0.748 while the mean beta-diversity of all-species groups was 0.728. In the Australian Alps, the South Chilean Andes, the Central Argentinian Andes and the Blue Mountains (Oregon, USA), the addition of non-native species reduced differences between plant communities within the same road, as a greater beta-diversity was observed for the subset including only native species (Figures 2 and 3; Figure S11 and Tables S16–S18). According to the null models, this homogenising effect of non-native species was observed only at low elevations for the Central Argentinian Andes and the Blue Mountains (Oregon, USA), while in the Australian Alps and the South Chilean Andes, it was observed at mid (both regions) and high elevations (only Australia) (Figure S11). For the Australian Alps, this effect was the strongest at high elevations.

In contrast, in the Krkonoše Mountains (Czech Republic), the Swiss Alps, the Himalayas (Kashmir, India) and Tenerife (Spain), non-native species led to a differentiation between plant communities, indicated by a significantly lower beta-diversity for the native-only subset compared to including all species. This differentiating effect of non-native species was observed in all four of these regions at low elevations (Figure S11), but it mostly disappeared towards higher elevations according to the null models. Tenerife was the only region where community differentiation by non-native species was found within all three elevation bands.

For the South Argentinian Andes and the Rocky Mountains (Montana, USA), the effect of non-native species switched from homogenisation to differentiation with increasing elevation.

### 3.2 | Regional Scale

For the 15 regions including more than one elevation gradient, beta-diversity was calculated between communities within

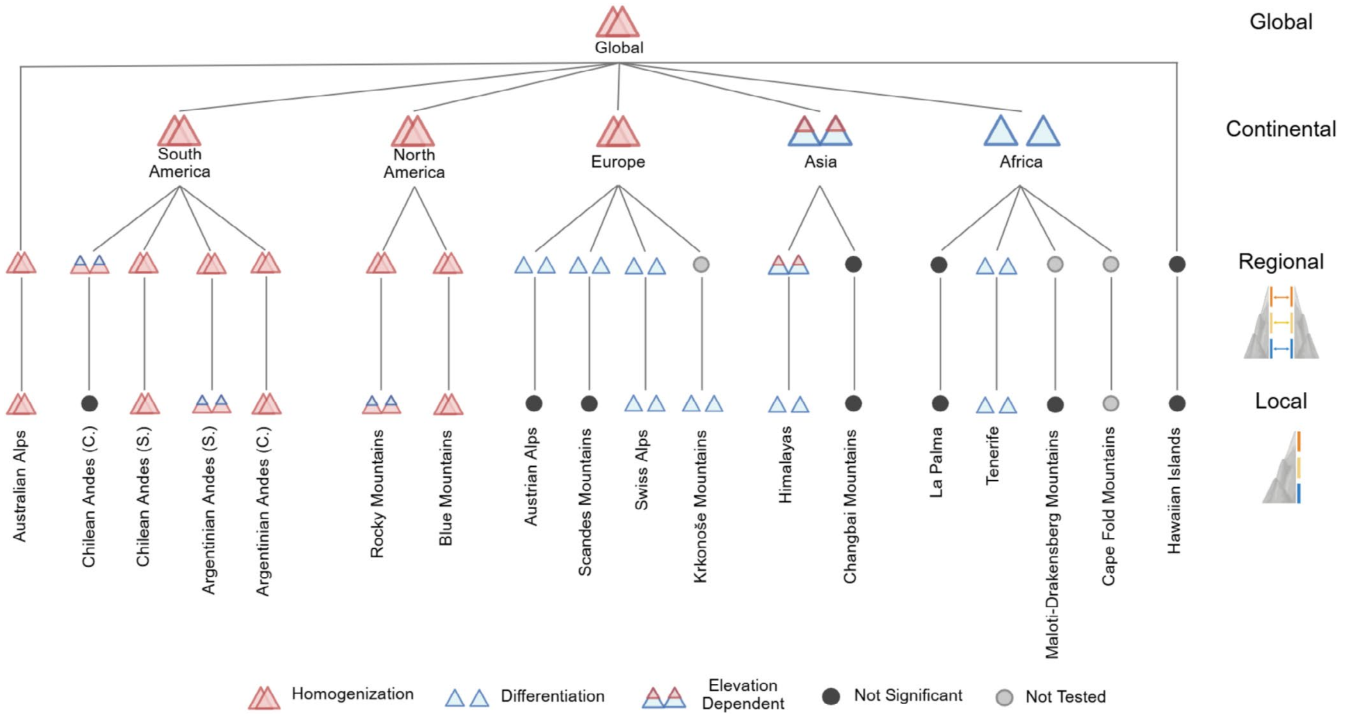

**FIGURE 2** | Overview of the directional effect of non-native species at the local, regional, continental and global scale. Red overlapping triangles indicate homogenisation, blue separate triangles indicate differentiation, blue and red adjacent triangles indicate an elevation dependent response (change in colour indicates direction of transition across elevation gradient), black circles indicate non-significant results and grey circles indicate where an analysis could not be done. This effect of non-native species was derived from a combination of the results of the linear mixed-effects models (Tables S6, S19, S22 and S25) and two null models (Tables S17, S18, S20, S21, S23, S24, S26 and S27). Detailed elevational results can be found in Figures S11–S13. Created with BioRender.com.

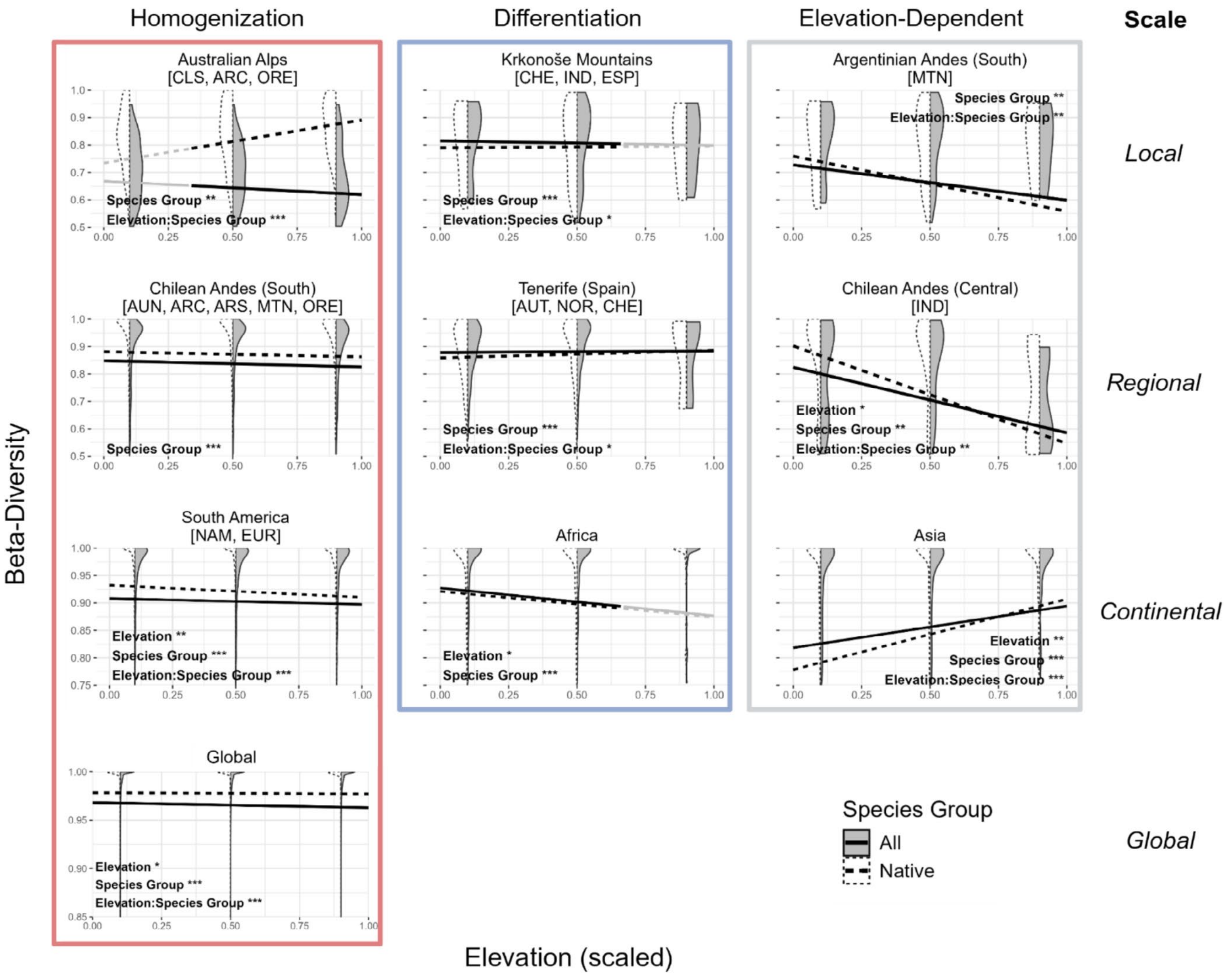

**FIGURE 3** | Beta-diversity of native only and all species by elevation and region at all spatial scales. Presented regions/continents are representative of trends at each scale (see all regions/continents in Figures S11–S13). Significant effects are listed in each panel (* < 0.05, ** < 0.01, *** < 0.001). Data points are only displayed at the local scale and not larger scales for pattern visibility. Regions/continents not represented by individual lines but following the same pattern as the one displayed: ARC, Argentinian Andes (Central); ASI, Asia; AUN, Australian Alps; AUT, Austrian Alps; CHE, Swiss Alps; CLS, Chilean Andes (South); ESP, Tenerife (Spain); IND, Himalayas (Kashmir, IND); MTN, Rocky Mountains (Montana, USA); NAM, North America; NOR, Scandes Mountains (Norway); ORE, Blue Mountains (Oregon, USA) The direction of the effect of non-native species is indicated by the coloured title on each panel (red—homogenisation, blue—differentiation, white—elevation dependent). Grey sections of the lines indicate results not confirmed by the null models. Widths were preset for violin plots to avoid overcrowding the plot, though this still allows for comparison of point densities within elevation bands. Created with BioRender.com.

elevational bands across the elevation gradients of that region. The mean beta-diversity of native-only groups was 0.821 while the mean beta-diversity of all-species groups was 0.812. Non-native species elicited homogenisation between communities in the Australian Alps, the South Chilean Andes, the Central Argentinian Andes, the South Argentinian Andes, the Rocky Mountains (Montana, USA) and the Blue Mountains (Oregon, USA; low and mid-elevations) as shown by the lower beta-diversity for comparisons including all species as compared to considering only native species (Figure 3; Figure S12 and Tables S19–S21).

In the Austrian Alps (mid-elevations), Scandes Mountains (Norway), Swiss Alps and Tenerife (Spain), non-native species led to differentiation between plant communities, indicated by lower beta-diversity of the native-only subset compared to all species (Figure S12).

In the Central Chilean Andes, the influence of non-native species changed from homogenisation at low elevations to differentiation at high elevations (Figure S12). In the Himalayas (Kashmir, India), the contrasting pattern occurred, with differentiation at lower elevations, switching to homogenisation with increasing elevation.

### 3.3 | Continental Scale

Sixteen regions (all except for Hawaii and Australia) were formed into five continental groups. The mean beta-diversity of native-only groups was 0.909, while the mean beta-diversity of all-species groups was 0.905. Non-native species led to continental-scale homogenisation in North and South America and Europe (low and mid elevations) (Figure 3; Figure S13 and Tables S22–S24). Differentiation by non-natives was found in Africa. For Asia, we observed the opposite pattern, with differentiation at low and mid elevations and homogenisation at high elevations.

### 3.4 | Global Scale

The mean beta-diversity of native-only groups was 0.986 while the mean beta-diversity of all-species groups was 0.972. At the global scale, non-native species homogenised plant communities in all elevation bands. Beta-diversity of the native-only subset was consistent along the elevation gradient while beta-diversity of all species decreased with elevation (Figure 3) (Tables S25–S27). It is important to note that while elevation was significant, the immensity of the dataset led to very small standard errors which may have resulted in statistically, but potentially not ecologically significant results.

## 4 | Discussion

In our multi-region study, we found evidence that non-native species homogenise roadside plant communities across elevations at the global scale. However, cases of community homogenisation and differentiation were surprisingly balanced. Further, we found striking differences between the Old and New World, with homogenisation being dominant in the New World and differentiation mainly occurring in the Old World.

These results represent the first global study focused specifically on mountain regions using data at the community level. However, it should only be considered a first step as our focus was on roadsides as primary dispersal pathways of non-native species within mountain systems (Lemke et al. 2019; Sandoval et al. 2022), and the results cannot be immediately transferred to mountain ecosystems in general. Still, it is well known that the non-native species pool at roadsides is the source for invasions into natural habitats (McDougall et al. 2018), and therefore, processes observed along roads might occur in further habitats at a later stage.

This loss of beta-diversity, that is, the increase in similarity between communities, results on one hand from the introduction of the same non-native species to multiple mountain regions, especially given the significant overlap between European species and mountain-dwelling non-natives across Australia, South and North America (Kalusová et al. 2017; Lenzner et al. 2022; McDougall et al. 2011; Yang et al. 2021). On the other hand, species invasions increase the taxonomic overlap between native and invasive ranges. Both processes increase the similarity of plant community compositions as the number of shared species increases, even though unique species might not be lost. Homogenisation is corroborated by several previous large-scale studies, suggesting that it is a common phenomenon associated with the spread of non-native species (Daru et al. 2021; Winter et al. 2009; Yang et al. 2021). We observed the homogenisation of plant communities at all spatial scales in our study, which, especially for the New World, overall confirms our first hypothesis. We also found a number of cases where non-native species led to differentiation of communities, most often at the local and regional scale. Community differentiation has been previously described (McKinney 2004) but not well documented in mountain regions. This suggests that homogenisation through the addition of non-native species may not be as common as originally thought, especially when analysing finer scales.

Across scales, we expected to find a stronger signal of homogenisation through non-native species at lower elevations (Hypothesis 2), because numerous studies have reported a decreasing number of non-native species with increasing elevation (Alexander et al. 2011; Guo et al. 2018; Marini et al. 2013). Using Figure 2 for a vote counting approach, we can see that from the local to the continental scale, the majority of regions display homogenisation through species invasions at low elevations. This proportion is constant across scales and in no case was there a shift to differentiation at low elevations and larger scales. In contrast, at high elevations, homogenisation was least visible at the local scale and most apparent at the continental scale. Taking elevation gradients as space for time substitutes, we might expect that ongoing non-native species' range expansions towards higher elevations (Dainese et al. 2017; Iseli et al. 2023), which are supported by climate warming (Mamantov et al. 2021) and higher propagule pressure (Rolls et al. 2023; Thompson et al. 2020), will more often lead to community homogenisation of high-elevation mountain vegetation, especially at the local scale.

Although we observed homogenisation at all scales, we do not expect a single cross-scale mechanism to cause this phenomenon. Rather, multiple drivers operating at a single or few scales are theorised to exist. In Australia, South and North America, we consistently found homogenisation of lowland plant communities at local through continental scales. This may be due to, first, the high number and proportion of non-native species both overall (Figure S3) and with regard to shared species within each continent (Figures S5, S8 and S9) following the shared invasion history (Lenzner et al. 2022); second, paralleling the wide-ranging distributions of non-native species in these continents (Ricklefs et al. 2008; Van Kleunen et al. 2015), non-native species often occurred on average in more plots than native species (Figure S4). Vice versa, the decrease of non-native species richness with increasing elevation as well as their scarce occurrence at high elevations (i.e., the same non-native species populating only few communities) might explain the switch to community differentiation at high elevations in Central Chilean and South Argentinian Andes and the Rocky Mountains (Montana, USA; Figure S3) (Averett et al. 2016; Fuentes-Lillo et al. 2023).

Consistent community differentiation through non-native species at the continental scale was only observed for Africa, while the effect of non-native species was elevation-dependent for Asia. Specifically for Africa, our study has a significant lack of data and the regions included cannot represent the whole continent. In the regions included in our study (two islands of the Canary archipelago and two distantly located South African mountain ranges), varying colonial histories and diverging global trade networks (Chapman et al. 2017; Lenzner et al. 2022) likely led to a distinct set of non-native species. Additionally, differences in the climatic conditions and vegetation types between the Maloti-Drakensberg and the Cape Fold Mountains (Canavan et al. 2021) led to different sets of non-native species within South Africa (Figure S7). The elevation-dependent result found in Asia likely reflects the pattern observed in the Himalayas. While low-elevation communities in the Himalayas became more different, we observed homogenisation at high elevations. It is possible that strong environmental filtering at elevations above 3000 m a.s.l. only allowed a pre-adapted subset of non-native species to establish there. In fact, at high elevations, the non-native floras in two Himalayan gradients were almost complete subsets of the third one's. At the local and regional scale, despite a higher number and proportion of non-native species within communities in Tenerife (Africa) and the Himalayas (Asia), the yet limited number of widespread non-native species might have prevented the homogenisation of lowland plant communities in these regions. Therefore, it is likely that we overestimated the importance of a high number of non-native species causing community homogenisation and that the frequency of non-native species may be more important (Blowes et al. 2024).

Interestingly, in Europe, non-native species led to community differentiation at local and regional scales, though many of the same non-native species were found across several mountain regions (Figure S6), leading to the homogenisation of plant communities at the continental scale (Finderup Nielsen et al. 2019; Marini et al. 2013; Winter et al. 2009). The consistent community differentiation within our European study regions might be explained by the low number of non-native compared to native species in a community (Figure S3) in combination with the limited number of widespread non-native species in these regions (Haider et al. 2018; Pyšek et al. 2017; Rolls et al. 2023; Van Kleunen et al. 2015), leading to a high turnover of non-native species between communities and sparse occurrences within a single elevation gradient or region. As biotic differentiation has been considered a transitional phase (Kramer et al. 2023; Mori et al. 2018; Socolar et al. 2016), it is possible that as non-native species continue to spread within individual regions, homogenisation may become more consistent across spatial scales.

With our multi-region study, the first to address the effects of non-native species on differences in roadside plant community composition separately for low and high elevations and from local to global scales, we can, despite some study limitations, draw several conclusions. First, the addition of non-native species can contribute to the homogenisation of roadside plant communities in mountain ecosystems. This phenomenon is partly driven by the number of non-native species but also by their frequency across multiple sites. It is important to consider that phylogenetic and functional homogenisation have been shown to occur concurrently with taxonomic homogenisation (Li et al. 2020; Tobias and Monika 2012; Tordoni et al. 2019; Winter et al. 2009), possibly increasing risks to ecosystem functioning and community resilience, though this was not directly tested in this study. In particular, the impact of homogenisation may vary if resulting from the replacement of native species versus the addition of non-native species. The latter can lead to an increase in alpha- and gamma-diversity, which might even strengthen ecosystem processes and stability if it aligns with an increase in functional diversity (Castillioni and Isbell 2023; Grman et al. 2018), though this requires further research. Homogenisation of communities through the replacement of native species may represent a more directly negative impact of non-native species spread as this is more likely to reduce ecosystem functioning and resistance to disturbance.

Interestingly, differentiation and homogenisation occurred in relatively equal amounts at local and regional scales, a finding which has not yet been described across multiple regions. This may be a temporary artefact, as non-native species may not have yet filled their potential niche space and/or ranges and may become more locally abundant (Iseli et al. 2023; Seebens et al. 2017). However, the exact impact of homogenisation, differentiation and the transition between these two stages is not yet well known due to the limited number of temporal studies. Differentiation of communities through the addition of non-native species may also be beneficial, especially in light of a changing climate, as it can potentially increase functional redundancy of communities (Pillar et al. 2013).

Additionally, shifts from differentiation to homogenisation with increasing geographic extent indicate that the potentially greater local species richness through the addition of non-native species exists in conjunction with increasing similarity of communities at large scales. This highlights both the importance of distinguishing between native and non-native diversity (Pauchard et al. 2018) and the consideration of several metrics of diversity (Santini et al. 2017) to prevent a misrepresentation of the effects of non-native species at larger spatial extents. Moreover, it is also important to note that there are multiple methods of calculating diversity and that these alternative approaches are useful in specific contexts. Finally, the effect of non-native species on community similarity differed between geographic regions. This emphasises the idiosyncrasy of biological invasions, which might be even more pronounced in mountain regions as, for example, the elevation of the highest impact of humans may differ across regions (Fuentes-Lillo et al. 2021; Irl et al. 2021). Future studies focusing on environmental and anthropogenic factors influencing invasion history may improve our understanding of these changes in community similarity in response to the addition of non-native species.

Our study is a first step towards a better understanding of how the impacts of the addition of non-native species on communities at local scales can translate into larger-scale consequences along roads in mountain regions. The inclusion of more mountain regions, especially in Africa and Asia, as well as more natural habitats, would further support a general understanding of the factors leading to homogenisation or differentiation at local and regional scales. In times of global change and novel ecosystems, this examination of the current status of community similarity in the wake of spreading non-native species will allow us to track future temporal shifts in homogenisation and differentiation, and the potential transition between states.

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## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

The data that support the findings are available in Zenodo at [https://doi.org/10.5281/zenodo.15749536], as well as the code [https://doi.org/10.5281/zenodo.15005206] following the acceptance of the article.

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Methods S1.** Jaccard dissimilarity. **Methods S2**. Null models. **Figure S1:** Map of the 18 study regions. **Figure S2:** Example of null model confidence intervals for native removal model. **Figure S3:** Number and proportion of non-native species per plot by elevation band in each region. **Figure S4:** Percent of plots each species occurs in by species status and elevation band in each region. **Figure S5:** Number and proportion of shared species that contribute to homogenisation between regions in South America at low and high elevations. **Figure S6:** Number and proportion of shared species that contribute to homogenisation between regions in Europe at low and high elevations. **Figure S7:** Number and proportion of shared species that contribute to homogenisation between regions in Africa at low and high elevations. **Figure S8:** Number of shared species that contribute to homogenisation between regions in North America at low elevations and high elevations. **Figure S9:** Number of shared species that contribute to homogenisation between regions in Asia at low elevations and high elevations. **Figure S10:** Number and proportion of shared species that contribute to homogenisation between continents at low and high elevations. **Figure S11:** Local-scale beta-diversity of only native and all species by elevation and region. **Figure S12:** Regional scale beta-diversity of native only and all species by elevation and region. **Figure S13:** Continental scale beta-diversity of native only and all species by elevation and region. **Table S1:** Overview of elevation gradients in each region. **Table S2:** Results of local scale general linear mixed-effects model of Jaccard dissimilarity. **Table S3:** Results of the regional scale general linear mixed-effects model of Jaccard dissimilarity. **Table S4:** Results of the continental scale general linear mixed-effects model of Jaccard dissimilarity. **Table S5:** Local scale linear mixed-effects model results for Jaccard dissimilarity by region. **Table S6:** Regional scale linear mixed-effects model results for Jaccard dissimilarity by region. **Table S7:** Continental scale linear mixed-effects model results for Jaccard dissimilarity by region. **Table S8:** Results of the global scale linear mixed-effects model of Jaccard dissimilarity. **Table S9:** Local scale generalised linear mixed-effects model results for the proportion of the richness component of Jaccard dissimilarity by region. **Table S10:** Regional scale linear mixed-effects model results for the proportion of the richness component of Jaccard dissimilarity by region. **Table S11:** Continental scale linear mixed-effects model results for the proportion of the richness component of Jaccard dissimilarity by region. **Table S12:** Results of the global scale general linear mixed-effects model for the proportion of the richness component of Jaccard dissimilarity. **Table S13:** Results of local scale general linear mixed-effects model of Bray–Curtis dissimilarity. **Table 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**Table S34:** Results of the global scale linear mixed-effects model of Ruzicka dissimilarity. **Table S35:** Results of local scale general linear mixed-effects model of Morisita-Horn dissimilarity. **Table S36:** Results of the regional scale general linear mixed-effects model of Morisita-Horn dissimilarity. **Table S37:** Results of the continental scale general linear mixed-effects model of Morisita-Horn dissimilarity. **Table S38:** Local scale linear mixed-effects model results for Morisita-Horn dissimilarity by region. **Table S39:** Regional scale linear mixed-effects model results for Morisita-Horn dissimilarity by region. **Table S40:** Continental scale linear mixed-effects model results for Morisita-Horn dissimilarity by region. **Table S41:** Results of the global scale linear mixed-effects model of Morisita-Horn dissimilarity.