



Research Letters

Homogenization and differentiation of Andean ecoregion floras driven by non-native plants: the role of political and environmental factors

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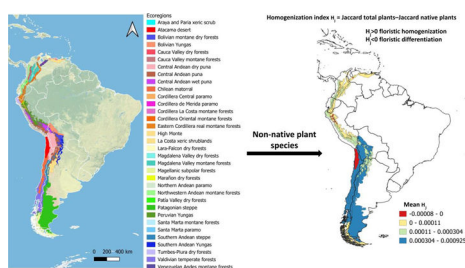
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HIGHLIGHTS

- Non-native plants drive both floristic homogenization and differentiation between Andean ecoregions.
- Floristic similarity declined with geographic and climatic distances and political dissimilarity.
- Geographic distance and political dissimilarity more strongly affect non-native similarity.

GRAPHICAL ABSTRACT



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ABSTRACT

Non-native plants can drive either homogenization or differentiation of plant communities; however, studies examining these effects at regional scale remain limited. Here, we assessed whether non-native plant introductions contribute to increasing or decreasing floristic similarity between 34 Andean ecoregions and evaluated the role of geographic, climatic, and political factors associated with these patterns. We compiled ecoregion plant composition from the GBIF and GRIIS databases, distinguishing native and non-native plant species. For each pair of ecoregions, we calculated the Jaccard similarity index separately for native and non-native plants and derived a homogenization index for 496 ecoregion pairs. We then regressed the Jaccard indices of native and non-native plants against geographic and climatic distances and political dissimilarity (the proportion of non-shared countries between ecoregion pairs). Both homogenization (37.7% of cases) and differentiation (34.7%) processes were found. Both native and non-native floristic similarity declined with geographic and climatic distances and political dissimilarity. The effect of political dissimilarity on non-native plants was the strongest, but it varies with the geographic distance. These interactions between biogeographic and sociopolitical factors contribute to a better understanding of ongoing floristic change across complex transnational mountain regions.

Introduction

There is evidence of an accelerating rate of non-native species introductions beyond their natural distribution ranges (Roy et al., 2024).

When non-native species remain confined to relatively small ranges, they may increase biotic differentiation between regions (Olden and Poff, 2003); when these species establish self-sustaining populations over extensive areas, they can promote biotic homogenization

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(McKinney and Lockwood, 1999; Olden et al., 2004). Taxonomic homogenization, defined as increased similarity in species composition between communities or regions (Olden and Rooney, 2006), is the most extensively studied in relation to non-native plants. Often, the Jaccard Similarity Index was used to quantify these effects (e.g., McKinney, 2004; Wani et al., 2023) in various ecosystems and spatial scales, yielding contrasting outcomes (e.g., McKinney, 2004; Qian and Ricklefs, 2006; Dar and Reshi, 2015; Qian and Qian, 2022; Keck et al., 2025). Understanding this process at regional scales is essential for assessing ongoing reshaping of biogeographic patterns, but it has been relatively underexplored (e.g., Wani et al., 2023).

Whether non-native species contribute to floristic homogenization or differentiation among regions may depend on the degree of climatic, geographic, and political distances between them. Geographically closer regions tend to share more similar non-native floras, and human-mediated dispersal can weaken the natural decay of floristic similarity with distance (Yang et al., 2021; Gulzar et al., 2024). Biotic homogenization driven by non-native species spread tends to increase between areas with similar climatic conditions, even when geographically distant (Capinha et al., 2015; Daru et al., 2021; Yang et al., 2021). Moreover, floristic homogenization has been found to be stronger between regions with shared or historical political ties, suggesting that administrative relationships, trade intensity, and policy harmonization contribute to the similarity of non-native species (Yang et al., 2021). Therefore, considering geographic, climatic and political distances between ecoregions might help understanding the biogeographic consequences of non-native species spread.

The influence of non-native species on floristic homogenization and differentiation has received limited attention in biodiversity hotspots, where the impacts may be especially important (e.g., Wani et al., 2023). One such region is the Andes mountain range in South America, a global biodiversity hotspot that spans over 8,000 km across seven countries. Its tropical portion was home of major pre-Columbian civilizations and later became the site of some of the earliest and most intensive European colonization (Grau et al., 2024), and currently faces different changes including climate, land-use, and biotic changes such as biological invasions (Tovar et al., 2022; Fuentes-Lillo et al., 2023).

Numerous studies have analyzed the ecology and biogeography of Andean non-native plants (e.g., Pauchard and Alaback, 2004; Fuentes-Lillo and Pauchard, 2019; Fuentes-Lillo et al., 2023; Fernandez et al., 2025) but few of them have focused on their local effects on biotic homogenization or differentiation (e.g., Castro and Jaksic, 2008; Hurtado-M et al., 2021). A regional-scale evaluation of homogenization or differentiation encompassing the full Andean range is lacking. Thus, our study aims to provide the first regional assessment of whether non-native plant introductions are associated with floristic homogenization or differentiation among Andean ecoregions.

We use the global biodiversity data (GBIF) and the Global Register of Introduced and Invasive Species for the Andes region (GRIIS) I to assess whether non-native plant introductions contribute to floristic homogenization or differentiation and II) to compare the relationship between similarity of non-native and native plants and three potential contributing factors: (a) geographic distance, (b) climatic distance and (c) political dis-similarity (i.e. number of countries shared between pairs of Andean ecoregions).

We expect plant similarity between Andean ecoregions to decline with geographic distance, but this decline will be less pronounced for non-native species than for native ones due to human-mediated dispersal. We also expect the decay in similarity associated to ecoregion's climatic differences will be stronger for native species, as their distributions are more tightly constrained by long-term adaptation to local environments while many non-native species tend to be generalists or related to human activities that may bypass natural climatic barriers. Political boundaries influence environmental governance and non-native plant introductions (Montti et al., 2024). Ecoregions that span many countries are subject to distinct cultural legacies, national

priorities, legal frameworks, and conservation policies, likely affecting introduction, establishment and spread of non-native plant species. Thus, we expect non-native floras will be more similar between ecoregions that share the similar political context (i.e., they are included in the same countries); similarity of native species, however, is expected to be largely independent of political boundaries.

Methods

Study area

The Andean region extends for more than 8,000 km along the western side of South America (from 10°N to 55°S), including parts in Venezuela, Colombia, Ecuador, Perú, Bolivia, Argentina and Chile; an elevational range up to c. 7000 masl, extreme rainfall gradients and huge topographic, edaphic and geomorphological heterogeneity, which results in high levels of biodiversity and endemisms (Borsdorf and Stadel, 2015) and a variety of ecoregions. We utilized the Terrestrial Ecosystems of the World (TEOW) dataset developed by WWF-US (Olson et al., 2001) as the reference for ecoregions. To focus on the Andes, we adopted the delimitation of the Andean region from Tovar et al. (2022) strictly as a geographic mask (Fig. 1). Ecoregions are areas with relatively homogeneous environmental conditions or species assemblages (Loveland and Merchant, 2004), often used as references for conservation planning.

List of native and non-native plants for the Andean ecoregions

To obtain the list of plant species with geographic coordinates, we used the Global Biodiversity Information Facility (GBIF) database (accessed in June 2024; see Table S1 in Supporting Information). We then identified the non-native plant species of the Andean ecoregions by crossing the list of plant species from GBIF with the list of introduced and invasive species from the Global Register of Introduced and Invasive Species (GRIIS; Ries and Pagad, 2020; accessed in June 2024; see Table S1 in Supporting Information). Non-native species identities were taxonomically validated using the Kew Database of World Plants by matching their scientific names as listed in GBIF. To ensure data quality, we followed the cleaning protocol established by Ribeiro et al. (2022), which addresses common errors and inconsistencies in occurrence records. This protocol includes a pre-filtering stage that removes records without scientific names, with geographically impossible or incoherent coordinates, with non-standard record bases (e.g., fossil records), or with missing georeferencing but with locality information that can be used to infer coordinates. Next, we performed a taxonomic cleaning by standardizing species' names based on the taxonomic authority provided by the Plants of the World Online (POWO, 2024). Finally, we removed duplicated entries and records with low coordinate precision (fewer than three decimal), as well as those located in institutions, herbaria, GBIF nodes, capitals, and centroids. We systematized and integrated plant species records from both databases (GBIF and GRIIS) using the *bdc* package (Ribeiro et al., 2022). Plant species richness per ecoregion, including totals and counts of native and non-native plant species, is detailed in Supplementary Table S2.

Data analysis

Floristic similarity and homogenization index among Andean ecoregions

To analyze the similarity of plant species among Andean ecoregions we used the Jaccard Index (J , the number of species shared by each pair of ecoregions divided by the total number of species recorded across the two ecoregions. McKinney, 2004; Qian and Qian, 2022). For each pair of ecoregions, we calculated the J for native plants (J_{native}), for non-native plants ($J_{\text{non-native}}$), and for native plus non-native plants (J_{total}). Then, we estimated the homogenization index as $H_J = J_{\text{total plants}} - J_{\text{native plants}}$, to

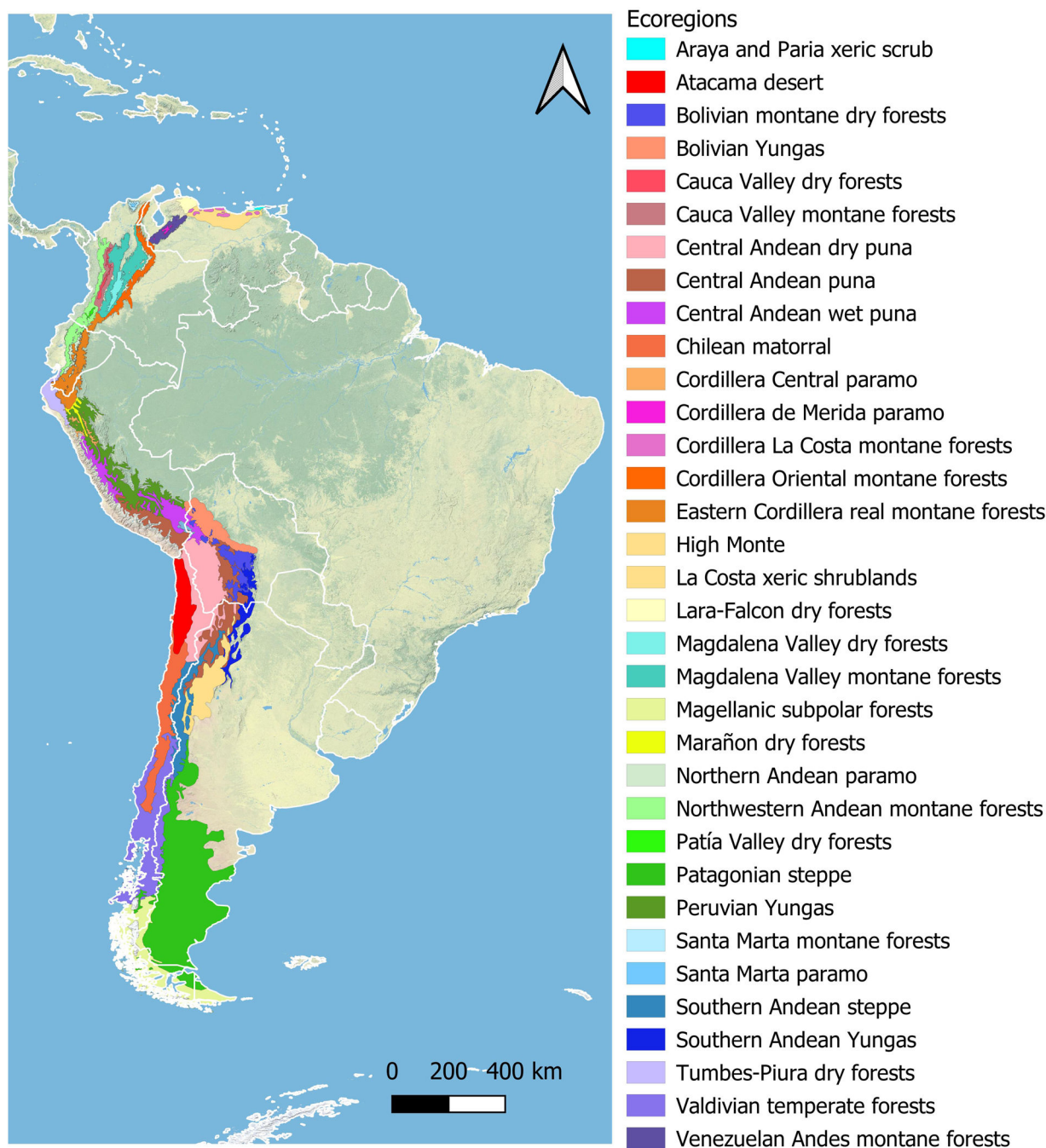


Fig. 1. Map showing the different Andean ecoregions considered in the study.

determine if a pair of Andean ecoregions has been homogenized or differentiated with the addition of non-native plants. Since the Santa Marta paramo ecoregion had no records of native species and the Lara-Falcon dry forests ecoregion had no records of non-native species in GBIF, they were excluded from the analysis. H_j ranges from -1 to 1; positive H_j values indicate biotic homogenization (i.e., increase similarity of plant communities between ecoregions) and negative H_j values indicate biotic differentiation (Qian and Ricklefs, 2006).

Effects of geographic and climatic distances and political dissimilarity between pairs of Andean ecoregions on floristic similarity

To evaluate the effects of geographic and climatic distances, and political dissimilarity on floristic similarity, we performed Generalized

Linear Models (GLM) with the Gaussian family. Geographic distance was the Euclidean distance between the centroids of each pair of Andean ecoregions using the “feature to point” and “Add XY Coordinates” modules in QGIS 3.34 (QGIS Development Team, 2023) (<https://www.esri.com/en-us/arcgis>). Then we used the `distm()` function from the `geosphere` package (Hijmans, 2024) which estimates the geospatial distance between them. The climatic distance was computed as the Euclidean distance of the following six climatic variables: annual temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, temperature seasonality, and annual precipitation; variables recognized as key factors influencing plant distribution (Qian and Qian, 2022; Wani et al., 2023). We obtained climate data from the WorldClim BIO Variables V1 dataset, available through the Earth Engine Data Catalog, and processed using Google Earth Engine

to calculate the average value of each variable for each ecoregion (Table S3). The political dissimilarity was evaluated as one minus the Jaccard index, that is, the proportion of non-shared countries between each pair of ecoregions. To this end, each ecoregion was encoded as a binary presence–absence vector of country occupancy, and dissimilarity scores were computed as the number of countries unique to either ecoregion divided by the total number of countries occupied. Thus, scores range from 0 (identical country sets) to 1 (no shared countries between ecoregions).

For native and non-native assemblages separately, we fitted (i) three single-predictor GLMs (one for each standardized predictor) and (ii) one full GLM that included the three main effects plus all possible interaction terms among them. For each single-predictor GLM, we used the t-statistic of the interaction coefficient (estimate / standard error) and its p-value to assess whether the slope for native plants composition differs significantly from that for non-native plants composition. All statistical analyses were performed using R (R Core Team, 2024).

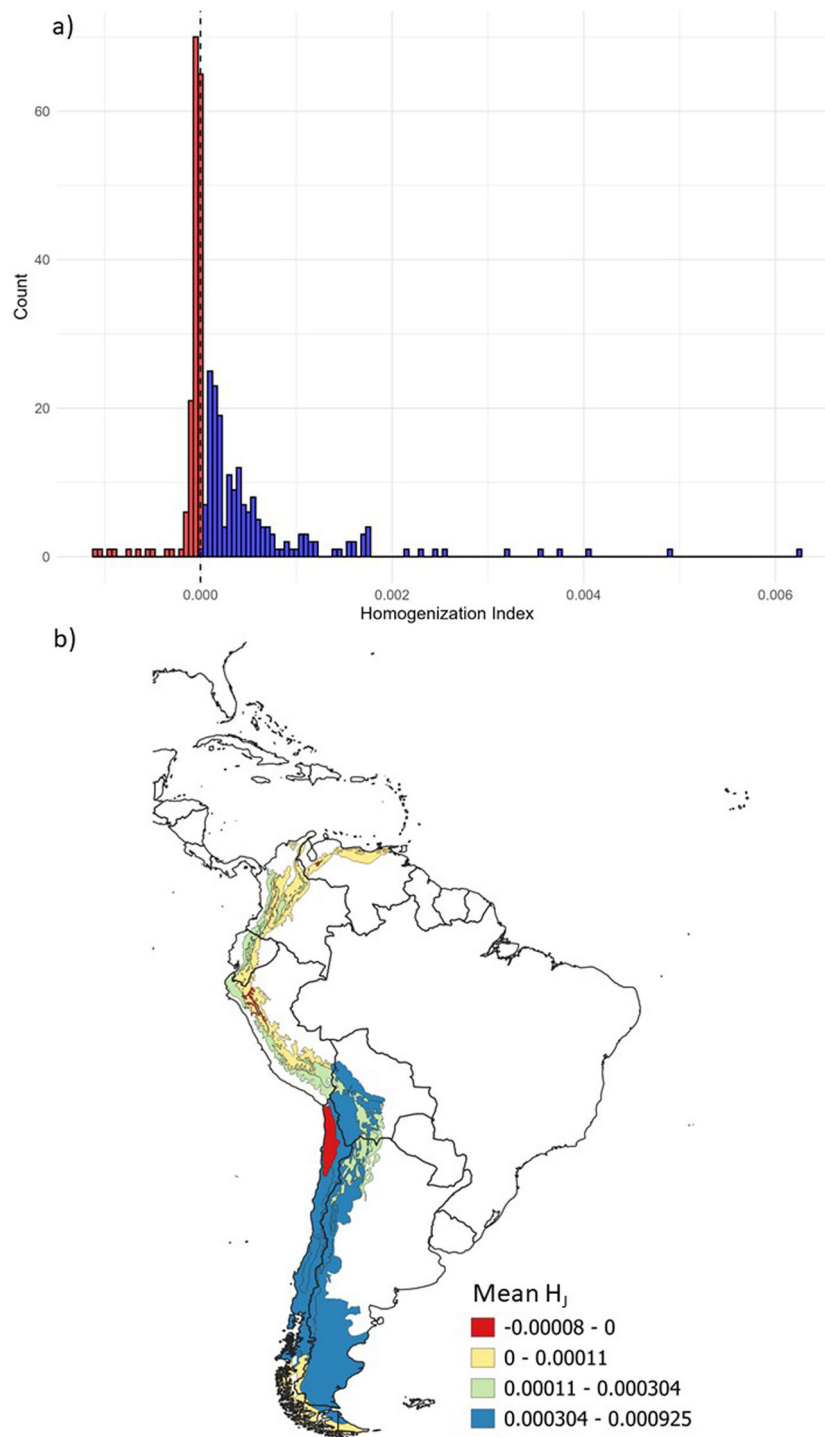


Fig. 2. Histogram (a) of the homogenization index (H_j) between Andean ecoregion pairs. The positive H_j values (blue bars) indicate biotic homogenization and the negative H_j values (red bars) indicate biotic differentiation. Zero values were excluded for clarity. The map (b) shows mean H_j values per Andean ecoregion (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Results

Floristic similarity and homogenization index among Andean ecoregions

Among the 561 pairs of Andean ecoregions the similarity index in native plant species varied from 0 to 0.50 (mean = 0.09), while the similarity index in non-native plant species ranged from 0 to 0.82 (mean = 0.12). Since there were no records of native or non-native for two ecoregions, we obtained the Homogenization index for 496 pairs. The homogenization index (H_J) ranged from -0.001 to 0.006, indicating the occurrence of both floristic homogenization and differentiation processes as a result of the introduction of non-native plants in Andean ecoregions (Fig. 2). Among the 496 ecoregion pairs, 187 (37.7%) had positive H_J values (i.e., floristic homogenization), 172 (34.7%) showed negative H_J values (i.e., floristic differentiation), and 137 (27.6%) had an H_J value of zero (Fig. 3). The most frequent class was of “slight differentiation”, but the homogenization classes reached more extreme values (Fig. 3). Based on the mean H_J values, most ecoregions in the Southern Andes exhibited positive values (i.e., floristic homogenization). The ecoregions with the highest positive means were the Central Andean dry puna, Chilean matorral, High Monte, and Southern Andean steppe. In contrast, the four ecoregions with negative mean H_J values were distributed across the Northern, Central, and Southern Andes: the Atacama Desert, Cordillera de Mérida páramo, Cordillera Central páramo, and Marañón dry forests.

Effects of geographic and climatic distances, and political dissimilarity between pairs of Andean ecoregions, on floristic similarity

Geographic distance, climatic distance, and political dissimilarity were all negatively related with floristic similarity for both native and non-native species. The regression model for non-native plants exhibited a higher intercept at zero distances than that for native plants (Fig. 4a–c). The effects of geographic distance ($p = 0.03$) and political dissimilarity ($p < 0.001$) on Jaccard index differ significantly between native and non-native plants across ecoregion pairs, whereas no significant difference was found for climatic distance ($p = 0.13$) (Fig. 4a–c). In the case of non-native plants, we found a significant interaction between political and geographic distance ($\beta = 0.650$, $p = 0.002$): at short geographic distances, increasing political dissimilarity was associated with decreased non-native plant similarity (Table 1). However, at larger geographic distances, this effect diminished and even reversed, with politically dissimilar ecoregions showing higher similarity in non-native flora (Table 1; Fig. S1).

Discussion

Our study provides novel insights into the role of non-native plant introductions in shaping floristic patterns across a large heterogeneous and transnational region, as well as a global biodiversity hotspot. Contrary to the previous findings of a strong process of floristic homogenization related to non-native plants across regions of one or a few countries (e.g. Qian and Qian, 2022; Wani et al., 2023) we found similar levels of both floristic homogenization and differentiation processes occurring between Andean ecoregions as a result of non-native plant

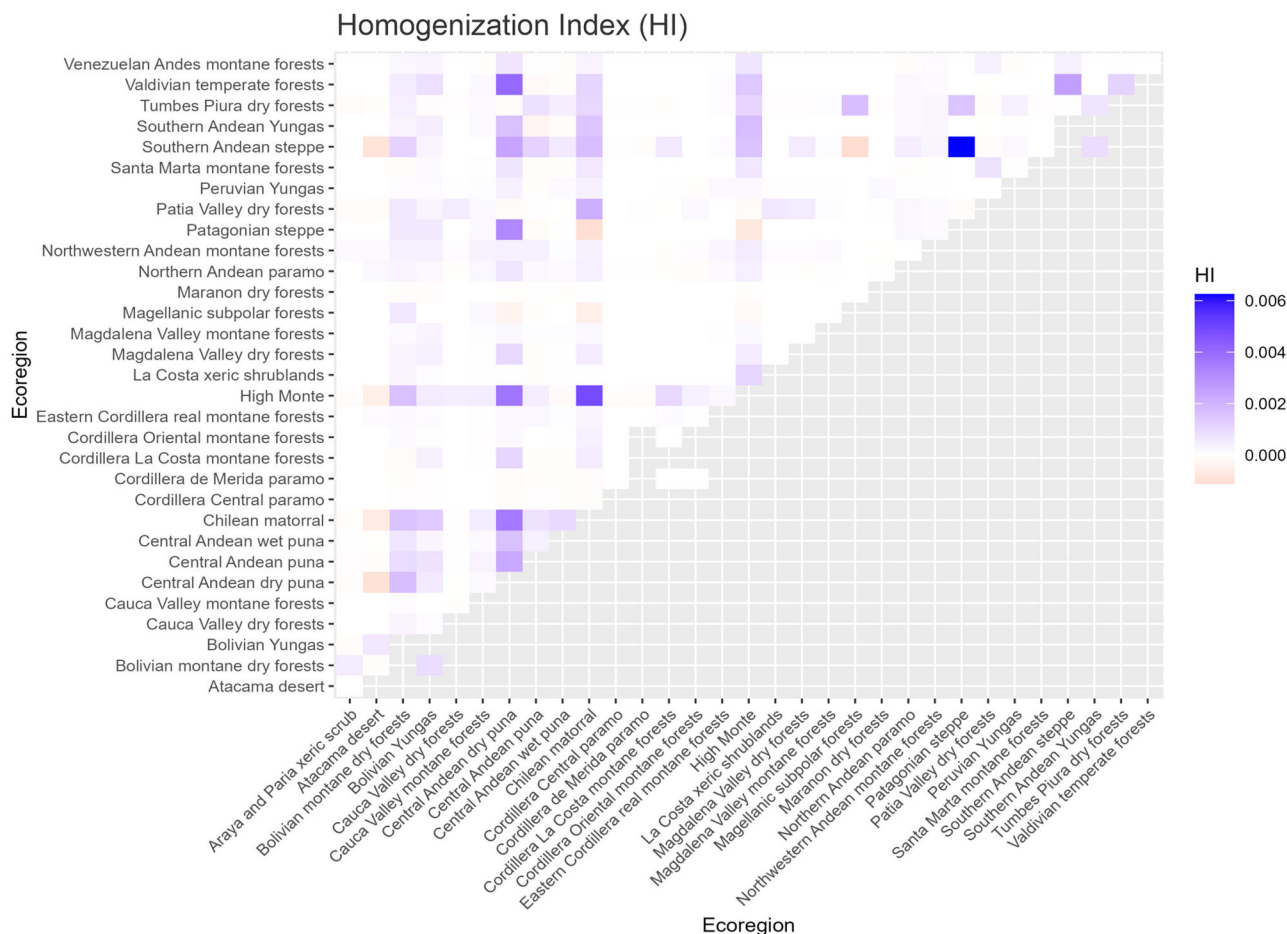


Fig. 3. homogenization index (H_J) among pairs Andean ecoregions.

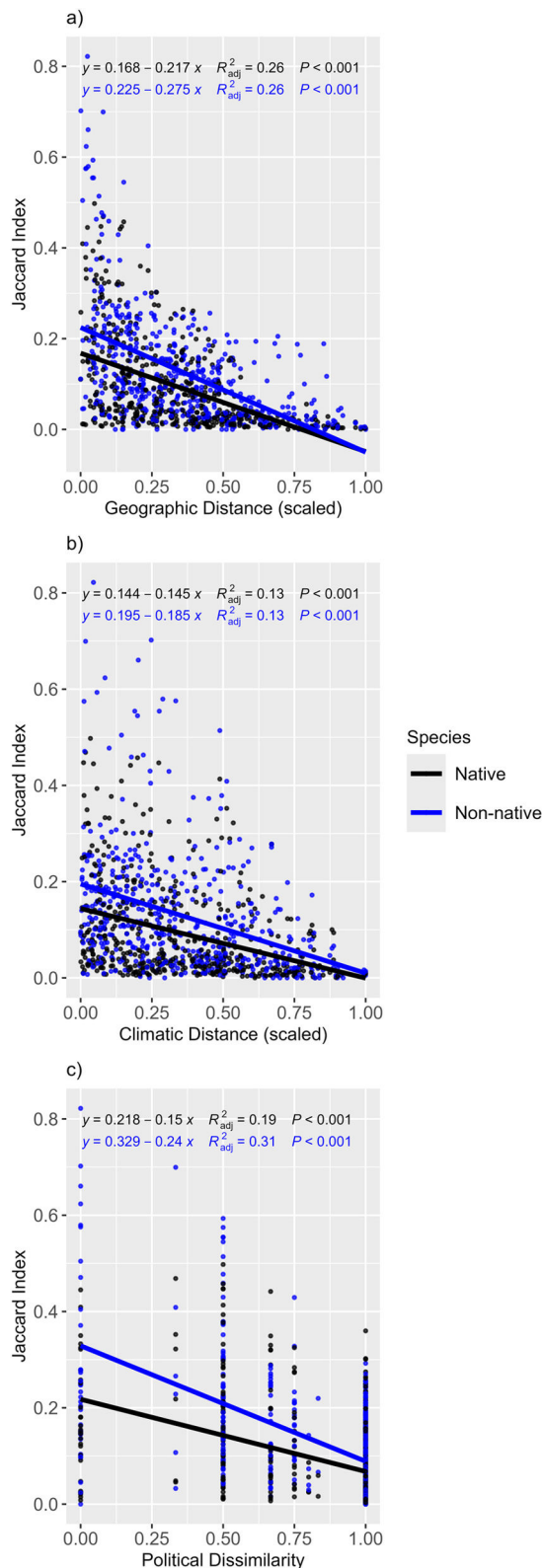


Fig. 4. Linear regression models of the Jaccard index of similarity with geographic distance (a), climatic distance (b) and political dissimilarity (c) for the native (black line) and non native plants (blue line) in the Andean region. Solid lines represent separate linear regressions (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

introductions. Approximately one-third exhibited positive HJ values (i. e., homogenization), another third showed negative values (i. e., differentiation), and the rest showed no net change, implying that the introduction of non-native species can drive contrasting biogeographic patterns depending on regional environmental and social conditions (Guo et al., 2018).

The observed pattern in mean homogenization index (H_J) values reveals regional differences in how non-native plant introductions are influencing floristic composition across the Andes. Ecoregions in the Southern Andes—such as the Central Andean dry puna, Chilean matorral, High Monte, and Southern Andean steppe—showed slightly positive mean H_J values, suggesting a subtle tendency toward floristic homogenization. Southern Andes have experienced long-standing human settlement and development, particularly in regions like the Chilean matorral, which may have facilitated the repeated introduction and establishment of the same non-native plants (Pauchard and Alaback, 2004; Fuentes-Lillo and Pauchard, 2019; Fuentes-Lillo et al., 2023). Regarding the ecoregions with negative mean H_J values—such as the Atacama Desert, Cordillera de Mérida páramo, Cordillera Central páramo, and Marañón dry forests—these span the three major Andean regions (Northern, Central, and Southern Andes), suggesting that floristic differentiation is not strictly a latitudinal pattern but rather the result of local ecological constraints, such as extreme aridity (Atacama Desert) or high-elevation climatic specialization (páramos). However, given that the index values remain close to zero, these results should be interpreted with caution, as they could be influenced by biases associated to uneven sampling intensity or availability of non-native plants records across Andean ecoregions.

Consistently with classic distance-decay expectations due to dispersal limitation and spatial turnover (Nekola and White, 1999), geographic distance was negatively associated with similarity in both native and non-native floras). However, contrary to our prediction, the slope of the relationship was significantly steeper for non-native than for native species (Fig. 4a), highlighting a distinct spatial structure in the distribution of non-native plant species. For non-native plant species, we found that the effects of geographic distance and political dissimilarity were not independent, but interacted significantly. Specifically, the negative effect of political dissimilarity on non-native plant similarity was stronger among geographically proximate ecoregions, suggesting that neighboring ecoregions governed by different countries may result in different policies, cultural practices, or introduction pathways that reduce floristic similarity. For example, differences in import regulations, biosecurity measures, and horticultural or agricultural preferences between countries likely contribute to this pattern. In contrast, at large geographic distances, this pattern reversed: greater political dissimilarity was associated with increased non-native floristic similarity. This reversal may reflect the influence of globalized economic and cultural processes that operate beyond national policies. Widely traded ornamental and crop species are often exchanged through international markets and follow similar introduction pathways worldwide. Consequently, distant regions with distinct political systems may still accumulate comparable sets of non-native plants, as large-scale socioeconomic forces—such as international trade and the circulation of agricultural and horticultural species (e.g., Montti et al., 2024)—may override local political differences and promote convergence in introduced floras.

While climatic distance accounted for a greater proportion of the variance in native plant species similarity compared to non-native plant species, the similarity in the slopes of these relationships suggests that climatic distance between regions exerts a comparable influence on both groups. In the case of native plant species, their long-term evolutionary and biogeographic history has been shaped by climate, leading to stronger spatial structuring (Ricklefs, 2004). Non-native species, although generally more ecologically flexible, are still subject climatic filtering after introduction, which limits their successful establishment to ecoregions with more similar climatic conditions (Thuiller et al.,

Table 1

Estimates, standard errors, t-values, and p-values from linear regressions testing the effects of political dissimilarity (pol. disim), climatic distance (clim. dist), geographic distance (geo. dist), and their interactions on the similarity of native and non-native plants across Andean ecoregions ($p < 0.001$).

Terms	Native plants				Non-native plants			
	Estimate	SE	t value	p	Estimate	SE	t value	p
(intercept)	0.2704	0.025	1.062	<2e-16	0.4496	0.029	15.24	<2e-16
pol. disim.	-0.0843988	0.032	-2.637	0.008	-0.25700	0.037	-6.927	1.38E-11
clim. dist	-0.1576851	0.085	-1.849	0.065	-0.27691	0.098	-2.801	0.005
geo. dist	-0.3853367	0.178	-2.158	0.031	-0.80656	0.207	-3.897	0.0001
pol.disim.:clim.dist.	0.0002	0.096	0.002	0.998	0.1316	0.112	1.174	0.241
pol.disim.:geo.dist.	0.1665	0.183	0.91	0.363	0.6497	0.212	3.063	0.002
clim.dist.:geo.dist.	0.1739	0.637	0.273	0.785	0.5454	0.739	0.738	0.461
pol.disim.:clim.dist.:geo.dist.	0.0192	0.639	0.03	0.976	-0.43575	0.741	-0.588	0.557

2005; Bradley et al., 2012; Capinha et al., 2015). Overall, our results are in line with those found in previous global studies that showed how regions with similar climatic conditions shared more non-native plant species (Yang et al., 2021; Capinha et al., 2023).

Our study has certain limitations. First, our analyses with Jaccard index are based on presence-absence data at a single point in time, which does not capture temporal dynamics or abundance differences—both of which are important to fully understand the trajectory and impact of invasions (Olden and Poff, 2003; Wani et al., 2023). Second, sampling effort and data completeness are uneven across the Andes, particularly for non-native species (Tovar et al., 2022), which might induce biases in spatial patterns detected (Pino et al., 2009). Third, our analysis did not account for specific socio-ecological characteristics of the ecoregions. Ecoregion-specific ecological, biogeographic, and anthropogenic variables such as elevation range, land use, habitat heterogeneity, disturbances, connectivity, trade volume, and human population density may influence the establishment and spread of non-native species, as well as the degree of floristic homogenization or differentiation.

Despite these limitations, our study is the first to assess floristic homogenization and differentiation driven by non-native plants across the Andes, a heterogeneous mountain system spanning seven countries. Our results show that with the introduction of non-native plants some Andean ecoregions increase their floristic similarity while others increase their differentiation, and that political borders and geographic distance play a significant role controlling these trends. Future research should consider the functional traits of non-native plant species such as growth form that contribute to homogenization (Dar and Reshi, 2015), as well as incorporate ecoregion-specific environmental, land use and socio-economic variables. Such efforts will be useful for anticipating the long-term consequences of biological invasions and for informing coordinated conservation and management strategies across this biodiverse region.

Data availability statement

Datasets of plant species downloaded from the GBIF and GRIIS databases for the Andes region are included as *Supporting Information Table S1*. Climatic characteristics of the Andean ecoregions, obtained from the WorldClim BIO Variables V1 dataset, are included as *Supporting Information Table S2*. Data and code for the Jaccard index, homogenization index, climatic distance, and regression analysis are available on GitHub: https://github.com/YohanaJ/HJ_Andes/tree/main.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.pecon.2026.01.003>.

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