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Linking Migration Flows With the Prevalence of Exotic Plant Species in the Andes

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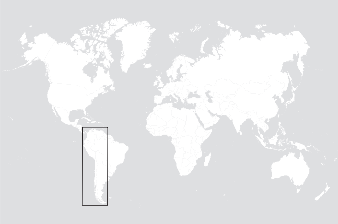

Human mobility and connectivity between cities are key features of globalization that foster urban expansion, landscape transformations, and changes in species distributions. Andean ecosystems, which function as biodiversity reservoirs, are vulnerable to environmental changes and to the introduction of exotic species. Through this study, we assess the association of migratory flows and other socioenvironmental characteristics with the prevalence of exotic woody species in the Andean region. We collected data on urban and demographic dynamics, migration proxies, and topographic and climate indicators for every first-order administrative unit of the Andean region. We used global biodiversity databases to obtain occurrence records of woody plants and estimated the proportion of exotic species records in each administrative unit. We performed multiple regression models that assessed the association of this prevalence with socioenvironmental information, and we compared them using the Akaike information criterion. We obtained 2,461,168 records of native species and 891,579 records of exotic species. Topography, climate, and immigration were included in the 10 best models, suggesting that the social connectivity of administrative units (through immigration) is a driver of changes in species composition of local communities. We consider that the prevalence of exotic species in woody plant composition is highly influenced by cultural drivers through the introduction of exotic species and through their use in urban and periurban environments.

Keywords: *human migration; Andes; exotic woody plants; nighttime lights; urban growth.*

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Introduction

Human migration, which entails social and cultural connectivity between regions, may drive ecological changes and influence ecosystem functioning and biodiversity. In South America, human migration is directed toward urban systems, which host around 80% of the population, and drives biophysical and demographic changes far beyond urban areas, modifying socioecological systems (Donoso and Sarmiento 2021). Urban areas, which function as an intertwined network connected through flows of people, material, money, and information (Seto et al 2012), usually constitute focal points for the introduction of exotic species (Spear et al 2013). As a result, tree communities in urban areas present a limited subset of native species and an overrepresentation of exotic species (McKinney 2006; Cadotte et al 2017), which may turn invasive under certain conditions (Pauchard et al 2016).

Exotic species constitute one of the main threats to the functioning of Andean ecosystems, which present relatively low proportions of rural population and reduced likelihood of deforestation (Aide et al 2019). In South America, urban areas have played a significant role in driving socioecological change, because of their increased connection with global and local markets and because of human migration (Aide and Grau 2004). Urbanization and urban growth are expected to continue, and projections indicate that 90% of people will live in cities by 2050 (Parés-Ramos et al 2013), posing significant challenges to the sustainability of socioecological systems (Branca and Haller 2021). The Andean region constitutes a biodiversity hotspot characterized by complex topography and reduced accessibility due to geographic barriers, such as mountains and the Amazon forests (Stadel 2000). While South American moist lowland forests currently undergo deforestation and degradation, forest recovery often occurs at high elevations and on slopes (Nanni et al 2015). Thus, the introduction of exotic species with invasive potential poses a significant concern because of their capacity to disrupt species composition, ecosystem functioning, and the provision of essential ecosystem services (Jimenez et al 2021).

The relationship of species composition (native and exotic) and species richness with socioeconomic conditions is a hot topic in human–nature studies (eg Guo et al 2012). The association of international migration with the

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TABLE 1 Comparison and characterization of the migration dynamics and demographics between Andean countries.

Country	Population (million inhabitants in 2021; World Bank n.d.)	Number of administrative units included (FAO 2015)	Percentage of international migration flows (Schultz 2014)	Percentage of records of native woody plants	Percentage of records of exotic woody plants	Prevalence of exotic plants
Argentina	45.8	13	5.0	0.6	5.5	0.01
Bolivia	12.1	8	1.4	6.1	7.8	0.02
Colombia	46.3	24	3.7	68.9	64.6	0.71
Ecuador	17.8	21	4.4	7.5	11.1	0.03
Peru	29.5	25	3.7	15.9	9.6	0.02
Venezuela	28.2	15	4.7	0.7	1.5	0.003

introduction of exotic species has been addressed in previous analyses focusing on trade dynamics and climate change (Chapman et al 2016), but the association of exotic trees and human migration at the local scale has frequently been disregarded. Most studies on introductions of exotic species are carried out in wealthy regions of the world (Capinha et al 2023). This is especially concerning because tropical and subtropical zones present high biodiversity and are located in developing countries that have fewer economic resources for research and conservation (Nuñez and Pauchard 2010; Early et al 2016). Further, local variability is often neglected (Lopez-Angulo et al 2018) leading to inadequate conservation strategies.

Although urban processes influence the diversity of native and exotic species (Fischer et al 2016; Cadotte et al 2017; Mehraj et al 2018), the extent to which this influence is explained by human mobility is unclear, owing to a lack of high-resolution homogeneous migratory data at regional scales. The goal of this study was to assess the influence of human mobility and the social connectivity of cities on the prevalence of exotic woody species (estimated as the proportion of their occurrence) in Andean environments. To achieve this goal, we (1) collected data on the occurrence of native and exotic woody plants in the Andean region obtained from global biodiversity databases, (2) developed metrics of immigration from 2010 (last census) and urban development for each major administrative unit, and (3) evaluated the influence of human movement and urban development on the proportion of exotic species in each, considering other socioenvironmental variables that may influence this ratio. Human migration indicates the level of connectivity and globalization of cities where migrants arrive and bring cultural values, skills, remittances, or even plants that ultimately influence their surroundings.

Material and methods

Study area

This study was carried out in 6 Andean countries: Argentina, Bolivia, Colombia, Ecuador, Peru, and Venezuela (Table 1), classified as low- and middle-income countries according to the World Bank (n.d.). In this study, we considered every first-order administrative unit taken from the Global Administrative Unit Layers database (FAO 2015) whose boundaries overlapped our study area. Within these countries, we selected the administrative units that belonged to the Andes region following the classification of Tovar et al (2022). The Andes are a mountain range spanning over 9000 km in length and reaching over 6000 m in elevation (Tovar et al 2022) that encompasses diverse ecosystems and hosts almost 10% of the vascular plant species in the world (Pérez-Escobar et al 2022).

The socioecological system studied experienced growth of urban areas with increasing concentrations of population and economic activity between 1950 and 2010 (Buytaert and Bievre 2012; Cerrutti and Parrado 2015). The study area encompasses different stages of urban transition (the shift from low to high urban development related to history and the country's economic development; Álvarez-Berríos et al 2013). Urban transitions range from Bolivia and Ecuador, with a low to medium proportion of urban population and high urban growth, to Argentina, Colombia, and Peru, where urban growth has slowed down (Álvarez-Berríos et al 2013; Bernard et al 2017).

Data

An overview of all data used is provided in Table 2. The table also explains their relevance for our study.

Woody species data: Information on woody species records was collected during February and March of 2023 from several databases (Table 2): the Global Biodiversity Information Facility (GBIF 2023a, 2023b), the Botanical Information and Ecology Network (Enquist et al 2016), Integrated Digitized Biocollections (Michonneau and Collins 2017), and Species Link (Thiers et al 2022). In this study, we only included woody plants (trees and bushes), since these plants tend to thrive in urban areas because of human intervention and management practices (Ossola et al 2020).

To systematize and integrate records from different databases, we used the bdc package of the R software (Ribeiro et al 2022). Species names were standardized according to the Leipzig Vascular Plants Catalogue (Freiberg et al 2020). We classified every plant species based on its origin (native or exotic) using the GlobalTreeSearch Species List (Beech et al 2017). For every first-order administrative unit, we estimated the proportion of exotic woody plant records in relation to the total number of woody species records (Figure 1).

TABLE 2 Overview of data selected; their relevance is related not only to prevalence of exotic woody plants but also to the mountain context in which the analysis takes place. (Table continued on next page.)

Information	Time frame	Dataset	Relevance
Biodiversity	1601–2023	GBIF (2023a, 2023b), BIEN (Enquist et al 2016), iDigBio (Michonneau and Collins 2017), and Species Link (Thiers et al 2022)	The prevalence of exotic species in cities can be measured through woody plant frequencies, allowing uses such as cropland and grazing pastures (mainly herbs) to be isolated. As a result of climate change and anthropic activities, mountain regions face rapid change in biodiversity, especially because of changes in species composition coupled with biological invasion. Understanding these patterns in exotic woody plant distribution is of vital importance in biodiversity hotspots, such as the Andes. Every species whose native range intersected any South American country was considered native. This criterion was useful to avoid discrepancies between national checklists of exotic plants and because the limits of plant ranges may be fuzzy and inconsistent across countries. The proportion of exotic woody plants as the ratio between exotic occurrences and total occurrences allows sampling bias to be controlled among administrative units because of greater occurrence records.
Migration	2010	Migration flows (Ceaușu et al 2019)	Migration is a result and an indicator of the cultural, economic, and social connection of urban centers within global systems. More-connected areas are more likely to receive and use exotic species to design cities that are functional to human needs and preferences (Higgs 2017). This social connectivity can be measured through the flows of internal immigration weighted by international immigration of each country.
Urbanization	2000–2021	Harmonized global nighttime light dataset 1992–2018 (Li et al 2020) and population counts data (World Bank n.d.)	Land use change is another key driver of change in mountain areas like the Andes, including rapid urbanization related to demographic growth and economic development. Most introductions of exotic species occur in urban areas. The growth of cities involves increasing concentrations of people (population density).
History	1600–1950	Foundation years of cities (Grau and Foguet 2021)	The age of cities determines the length of time cities have been transforming landscapes and when they have been receptive to exotic species and importation of plants (Yang et al 2015). Cities in the Andes have diverse foundation dates because of increasing interconnection with external markets and accessibility since European colonization. This increasing connectivity of mountain cities will have profound impacts on the prevalence of exotic plants.
Climate	1981–2010	Precipitation and temperature from CHELSA (Brun et al 2022)	Climate conditions are a key driver of species composition change because of their role in the successful establishment and survival of exotic plants. Changes in biophysical conditions lead to shifts in the distribution ranges of species. Climate conditions are the main driver of transformations in mountains, affecting the capacity of their biodiversity to support human populations.
Topography	2010	Digital elevation models from GMTED2010 (Danielson and Gesch 2011)	Elevation determines different biophysical conditions, while the range of the elevational gradient determines the diversity of environments available for colonization by exotic woody plants. High elevation has a negative effect on the prevalence of exotic plants because of low human disturbance and extreme climate conditions; cold environments are considered resistant to the entrance of exotic plants (Nievas et al 2019).

Note: GBIF, Global Biodiversity Information Facility; BIEN, Botanical Information and Ecology Network; iDigBio, Integrated Digitized Biocollections; CHELSA, Climatologies at high resolution for the earth's land surface areas; GMTED2010, Global Multi-Resolution Terrain Elevation Data 2010.

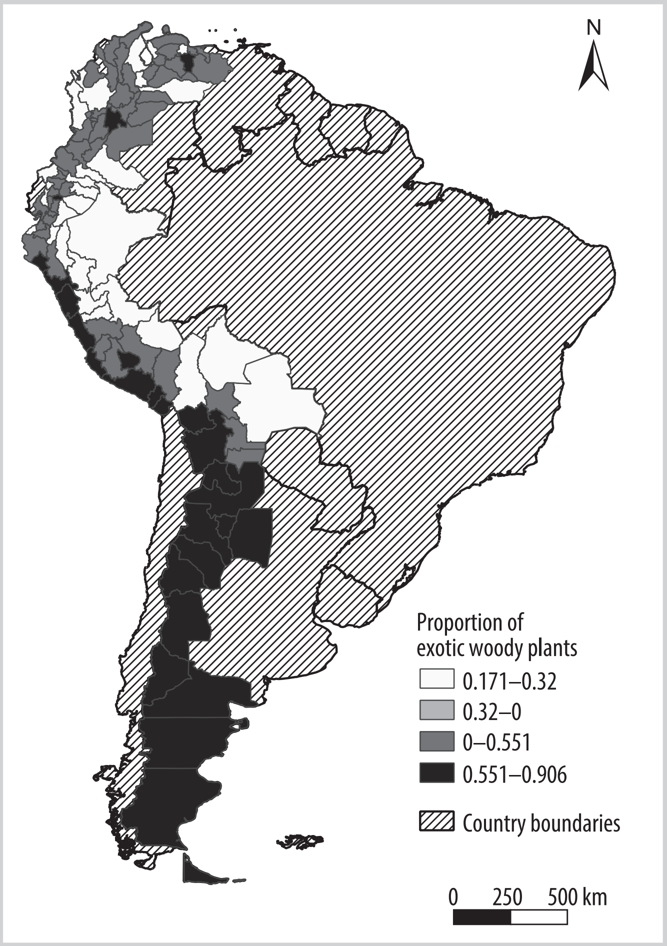


FIGURE 1 Exotic woody plants in proportion to the total number of woody species by first-order administrative unit in the Andean region.

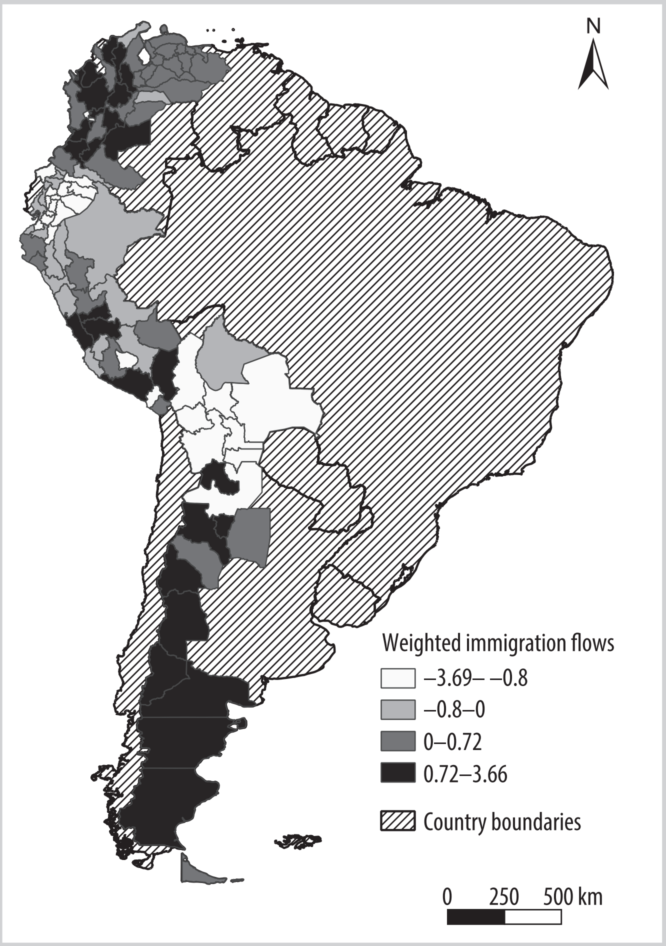


FIGURE 2 Index of weighted immigration flows by first-order administrative unit in the Andean region.

Migration data: We obtained migration data from WorldPop Hub, a portal of open spatial demographic data and dynamics that includes over 40,000 datasets. The dataset on migration flows (Ceaușu et al 2019) comprises migrant stocks obtained from censuses from 2010. Migrants are people whose administrative unit of residence changed in the previous 5 years (Ceaușu et al 2019). We estimated a migration index for each administrative unit that combined internal and international migration. Because of the size of values and variation, we estimated the logarithm of international migrant flows and multiplied it by the logarithm of internal migration for each country to obtain a weighted immigration flow index (Figure 2). This immigration index constitutes an integral indicator of local and international human social mobility (Table 2).

Urban development: We estimated different metrics of urban development that may affect the prevalence of exotic species. We used the most recent census for each administrative unit to estimate its population. The time since the city's foundation is deemed to indicate the period of urban interconnection (Table 2), so we used the foundation date of cities (Grau and Foguet 2021).

We used the harmonized global nighttime light dataset (Li et al 2020) to characterize the urban dynamics from 2000 to 2021 (Table 2). This dataset comprises sensor-detected nighttime light data from 2000 to 2021, making it possible to delineate urban expansion. Nighttime light values range from 0 to 63, and values over 20 are considered reliable urban pixels (Li et al 2020). We estimated the trend in nighttime lights by regressing yearly radiance against the calendar year. Finally, we calculated nighttime lights per inhabitant (Table 2) by dividing the population of each administrative unit by the number of urban pixels in 2020.

Natural environment: Since environmental conditions, such as climate and topography, can influence plant distributions and establishment, we included mean elevation, the standard deviation of elevation, mean precipitation, precipitation range, and mean temperature of each administrative unit in the analysis (Table 2).

Data analysis

To identify the most important variables to explain exotic woody species' prevalence, we performed multiple linear regression models. We considered all the linear combinations of explanatory variables (mean temperature, mean precipitation, precipitation range, mean elevation, standard deviation of elevation, foundation date, nighttime lights per inhabitant, nighttime light trends, total population, weighted immigration flows; Table 2) to explain the prevalence of exotic woody plants within each administrative unit. We conserved the most parsimonious

TABLE 3 Best 10 models with their predictors and the predictors' significance in each model.

Model	Weighted immigration flows	Mean temperature	Precipitation range	Mean elevation	Standard deviation of elevation	Mean precipitation	Nighttime lights per inhabitant	Total population	Nighttime lights trend	Foundation date
1	0.04***	−0.15***	−0.03*	−0.09***	0.02	−0.05***	—	—	—	—
2	0.04***	−0.15***	−0.02*	−0.08***	—	−0.06***	—	—	—	—
3	0.04***	−0.14***	−0.03**	−0.08***	0.02	−0.06***	0.01	—	—	—
4	0.04***	−0.14***	−0.02*	−0.07***	—	−0.06***	0.01	—	—	—
5	0.04***	−0.15***	—	−0.08***	—	−0.075***	—	—	—	—
6	0.04***	−0.16***	−0.03*	−0.09***	0.02	−0.05***	—	0.002	—	—
7	0.04***	−0.15***	−0.02*	−0.08***	—	−0.06***	—	0.005	—	—
8	0.04***	−0.16***	−0.03*	−0.09***	0.02	−0.05***	—	—	0.002	—
9	0.04***	−0.15***	−0.03*	−0.09***	0.02	−0.06***	—	—	—	0.002
10	0.04***	−0.14***	—	−0.07***	—	−0.08***	0.01	—	—	—

*** $P < 0.001$; ** $P < 0.05$; * $P < 0.1$.

models (the ones that were within 2 units of the Akaike information criterion [AIC]; Vrieze 2012) with respect to the best model. AIC is a metric that indicates the balance between data adjustment and model complexity. We averaged the most parsimonious models to assess the effect of each explaining variable on exotic prevalence (Symonds and Moussalli 2010). We also evaluated the frequency of each variable in the most parsimonious models to assess their consistency. All these analyses were performed using R software (R Core Development Team 2021).

Results

We collected 2,461,168 records of 10,365 native woody species across our study area. Of these native occurrences, 68.9% were from Colombia (1,698,175), 15.9% from Peru (392,990), 7.5% from Ecuador (186,760), 6.1% from Bolivia (150,292), 0.7% from Venezuela (18,320), and 0.6% from Argentina (14,631).

We gathered 891,579 records of 14,149 exotic species across the same 6 countries. Of these total occurrences, 64.6% were from Colombia (576,239), 9.6% were from Peru (85,031), 11.1% were from Ecuador (98,682), 7.8% were from Bolivia (69,319), 1.5% were from Venezuela (13,384), and 5.5% were from Argentina (48,874) (Table 1).

After model comparison ($n = 511$ possible models; see Table S1, *Supplemental material*, https://doi.org/10.1659/mrd.2023.00017.S1) we conserved 10 models (AIC between −175,233 and −173,233; Table 3). These models included immigration flows alongside climate indicators as predictive variables. Moreover, most of the models included at least one additional social variable such as total population, nighttime light trends, nighttime lights per inhabitant, and foundation date (see Table S2, *Supplemental material*, https://doi.org/10.1659/mrd.2023.00017.S1). Model averaging showed that the prevalence of exotic species increased in association with weighted immigration flows. Additionally, there was a positive correlation concerning the standard deviation of elevation as well as nighttime lights per inhabitant (Figure 3). In contrast, the prevalence of exotic woody plants exhibited a decrease relative to mean temperature, mean elevation, and mean precipitation (Figure 3).

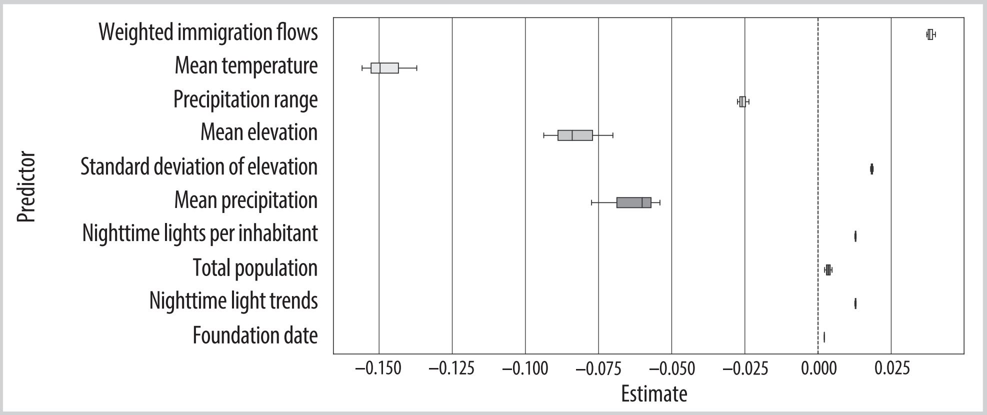
Discussion

Migrants do not come empty-handed

Since woody plants are long-lived organisms that can persist for many years, the current species composition and their dynamics are a legacy of anthropogenic disturbance and human mobility (Kowarik and von der Lippe 2008; Pemberton and Liu 2009). Our results showed that social connectivity plays a significant role in shaping species composition and abundance in Andean ecosystems. Human mobility, assessed through an immigration indicator, was a better predictor of exotic species prevalence in woody vegetation communities than other plausible socioeconomic indicators such as population or the date the city was founded (although they also played some role). The effect of migration on species composition is likely explained by 3 different processes: (1) Increased human mobility is associated with more frequent introductions of exotic species, which can establish viable populations and eventually become invaders (Mack and Lonsdale 2001; Hulme 2009). (2) Immigrating people can influence the cultural values of local communities and promote or suppress the use of certain species in managed urban landscapes (Reichard and White 2001; García Lerena et al 2018). (3) Immigrating people may foster urban expansion and increase disturbance frequency and intensity (eg road construction, natural cover fragmentation), which provide new places where pioneer species with high propagule pressure may thrive (Mehraj et al 2018).

Migration patterns in the Andes have undergone a shift from rural–urban to interurban migration, primarily from small towns to larger cities (Medina et al 2016). This transformation is propelled by the pursuit of better opportunities, although in certain instances, migration is influenced by the expansion of agricultural frontiers. For example, in Ecuador, migration flows are concentrated toward the Amazonian lowlands (driven by the search for

FIGURE 3 Main results of regression models between the proportion of exotic woody plants and different socioenvironmental predictors.



farmlands) and close to the capital city, Quito, in the highlands, motivated by urban amenities (Medina et al 2016). In Colombia, human mobility has been shaped by political and economic changes, such as the eradication of armed conflict and improved economic growth (Ramírez 2012). Although immigration is usually considered a relevant driver of population distribution and landscape modification (Bernard et al 2017; Royuela and Ordóñez 2018), the assessment of the association of migration flows and the prevalence of exotic plant species remains relatively unexplored. Our results highlight that human mobility, an indicator of the connectivity of a region, is associated with higher proportions of exotic species records (Figure 4). Moreover, using the combination of data on internal and international migration, we were able to overcome the problem associated with scarcity and reduced accessibility to information, which usually hinders studies on the association between human migration and species composition.

Invasibility patterns in the Andes: climate and people moving plants

The Andean region presents a high diversity of biophysical conditions (eg topography, climate, and land cover) that interact with Andean societies (eg through exotic species introductions and changes in land use and disturbance regimes) to determine their invasibility. Invasibility refers to traits of the receiving communities that enable the establishment and expansion of exotic species (Vicente et al 2010). Most arrivals of exotic plants involve connections with remote places; however, the establishment of new plant populations is moderated by the interaction of species characteristics and biophysical conditions (Furlan et al 2016). For instance, in mountain areas, the prevalence of exotic species decreases with elevation because of adverse biophysical conditions and reduced accessibility (Marini et al 2013). The latitudinal gradient also plays a role, for example, in low latitudes, characterized by less-stressing environmental conditions (eg high temperature and precipitation) and diverse native communities that may act as biological barriers reducing invasibility (Naeem et al 2000; Sax and Gaines 2008).

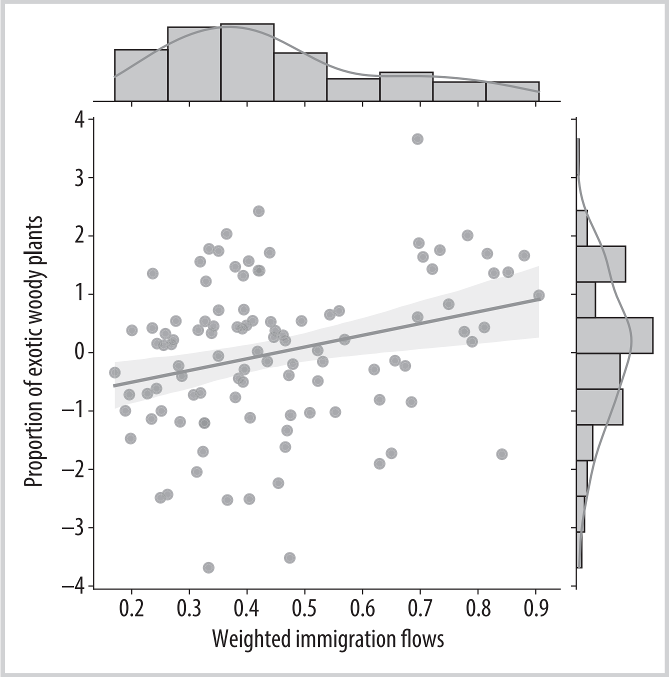
Because of their geographic isolation and steep slopes, which are associated with wide gradients of environmental conditions, mountains are extremely vulnerable to climate change. Climate warming and human interventions are likely to eliminate the barriers to the upward migration of exotic woody plants. This phenomenon is particularly evident in lowland cities, where changing temperature and precipitation patterns are weakening the limits to exotic plant migration upward (Payne et al 2020; Jimenez et al 2021). In addition, in higher latitudes there is a widespread use of exotic species (Egerer et al 2019) for aesthetic, recreational, and productive purposes, especially when native communities are present in small patches or when native species are undervalued for human uses (Sjöman et al 2016). For example, in harsh regions, cultivated cosmopolitan plants, such as *Pinus*, *Ulmus*, and *Eucalyptus*, are more likely to be used (Furlan et al 2016) to overcome resource scarcity with regard to specific purposes, such as silviculture (Thuiller et al 2006) or agriculture, as with *Prunus persica* in the puna region (Stampella et al 2013). In conclusion, it is likely that at least part of the increased prevalence of exotic species in harsher environments is explained by their adaptive traits, acclimatation capacity, and tolerance to adverse conditions that have been widely used for human purposes.

Ecosystem services and disservices of exotic plants in the Andes

The functioning of Andean ecosystems and the provision of ecosystem services depends on their identity and structural complexity. Alteration in species composition can disrupt the predictability of these ecosystem services and increase the vulnerability of local communities (eg exotic plants associated with fire regimes because of their traits; Contreras et al 2011) through alteration of dynamics in native plant communities (increased fire frequency) that are valuable for ecosystem services provision, such as water regulation.

At present, exotic species do not reach high densities in high elevations, but their presence in these environments, even at low densities, may disrupt ecosystem functions (Morales and Aizen 2002; Pauchard et al 2009). It is important to note that exotic plants can also offer ecosystem benefits, as they can host certain invertebrates (Salisbury et al 2017) or provide additional services. Exotic forest expansion in the surroundings of urban centers and low-residential areas enhances water regulation services and the capacity to sequester atmospheric carbon dioxide, showcasing the complex interactions between exotic and native species in Andean ecosystems (Jimenez et al 2023).

FIGURE 4 Correlation between the proportion of woody plants and weighted immigration flows. The solid line represents the fitted regression line. Bars indicate the deviations (residuals) between the observed values and those predicted by the regression. Smaller deviations represent a more accurate fit.



Big data: advantages and biases

Our study explored the role of socioeconomic development on the prevalence of exotic woody species using a novel approach that combines indicators of human migration with massive biodiversity data. Migration data are scarce, so we built an indicator of human mobility using the highest-resolution regional dataset available and combining it with emerging datasets on biodiversity.

Recent years have witnessed a significant increase in available biodiversity data, providing new opportunities to explore patterns and processes governing exotic plant dynamics. Biodiversity records, georeferenced by museums, herbaria, and citizens, are aggregated in regional and global datasets (Franklin et al 2017). However, challenges persist in handling these data, including geolocation and taxonomic uncertainties and sampling biases. For example, sampling is uneven across geographical space: with most sampling concentrated near roads and cities in the lowlands, the Andes tend to be underrepresented (Hughes et al 2021). Quantitative modifications to avoid these biases, such as evaluating the proportion of exotic species, rather than their raw abundance, must be implemented. In addition, the northern Andes (eg Colombia with 60% of exotic occurrences), which has higher native biodiversity, has more information about species occurrences. It is crucial to recognize the limitations of biodiversity records to avoid drawing inaccurate conclusions about vegetation patterns and dynamics; for example, range maps or diversity maps with erroneous records may lead to inaccurate results. These biases may be explained by a combination of factors: (1) inventories are usually restricted to forest vegetation, (2) exotic species lists underestimate the number of exotic species in each country (eg Global Register of Introduced and Invasive Species [GRIIS]; Seebens and Kaplan 2022), and (3) there is an overrepresentation of urban trees in citizen science studies (Ossola et al 2020). In this study, the inclusion of all the exotic woody species rather than only those included in GRIIS allowed us to generate a more complete database.

Final considerations and future perspectives

Social connectivity and human disturbance have led to changes in ecosystems where exotic species (eg woody plants) can accumulate and increase local biodiversity. The migration of people from diverse backgrounds introduces a myriad of perspectives, experiences, and values that significantly influence the development and construction of the biophysical environment. In some cases, species introductions turn into biological invasions, leading to unexpected outputs in the provision of ecosystem services. These complex processes need to be analyzed along with other socioeconomic changes (eg urbanization, land use changes, climate warming) and biophysical patterns.

Considering that global human migration is expected to increase by up to 200 million by 2050 (Black et al 2011), it is likely that the exchange of plants outside their current distribution range will increase. This will raise the risk of biological invasions. The emergent pattern could be universal and can be identified in cities of different sizes, cultures, and geographies. This is an exploratory and initial insight into what is hopefully a new research agenda, where we can explore the environmental impacts of migratory movements as part of urban processes. Human migration is far more complex and multifaceted, but, by identifying drivers of exotic woody plant introductions, this study aims to contribute to a solid basis for understanding the impacts of human mobility on biodiversity.

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Supplemental material

TABLE S1 Comparative analysis of performance scores among top regression models.

TABLE S2 Estimation of mean and range for the set of predictor variables employed.

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