Going up the Andes : patterns and drivers of non-native plant invasions across latitudinal and elevational gradients

Reference:
Fuentes Lillo Eduardo, Lembrechts Jonas, Barros Agustina, Aschero Valeria, Bustamante Ramiro O., Cavieres Lohengrin A., Clavel Jan, Herrera Ileana, Jimenez Alejandra, Tecco Paula, ...- Going up the Andes : patterns and drivers of non-native plant invasions across latitudinal and elevational gradients
Biodiversity and conservation / Malaysian Society of Pathologists - ISSN 1572-9710 - Dordrecht, Springer, 32(2023), p. 4199-4219
Full text (Publisher's DOI): https://doi.org/10.1007/S10531-023-02697-6
To cite this reference: https://hdl.handle.net/10067/1993070151162165141

Going up the Andes: patterns and drivers of non-native plant invasions across latitudinal and elevational gradients.

Short title: Plant invasions across the Andes

Eduardo Fuentes-Lillo[1,2,3,4], Jonas J. Lembrechts[4], Agustina Barros[5], Valeria Aschero[5], Ramiro Bustamante[2,6], Lohengrin A. Cavieres,[2,7], Jan Clavel[4], Ileana Herrera[8,9], Alejandra Jiménez[1,2], Paula Tecco[10], Philip E. Hulme[11], Martín A. Núñez[12], Ricardo Rozzi[2,13,14], Rafael A. Garcia[1,2], Daniel Simberloff[15], Ivan Nijs[4], Aníbal Pauchard[1,2*].

[1]Laboratorio de Invasiones Biológicas, Facultad de Ciencias Forestales, Universidad de Concepción, Chile

[2]Institute of Ecology and Biodiversity (IEB), Santiago, Chile

[3]School of Education and Social Sciences, Adventist University of Chile, Chile

[4]Research Group of Plants and Ecosystems (PLECO), Department of Biology, University of Antwerp, Belgium

[5]Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), CONICET, CCT-Mendoza, Argentina.

[6]Departamento de Ecología. Facultad de Ciencias. Universidad de Chile.

[7]Departamento de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Concepción, Chile

[8]Escuela de Ciencias Ambientales, Universidad Espíritu Santo, 091650, Guayaquil, Ecuador.

[9] Sección Botánica, Instituto Nacional de Biodiversidad (INABIO), 170501, Quito, Ecuador

[10] Instituto Multidisciplinario de Biología Vegetal (IMBiV-CONICET-UNC); Facultad de Ciencias Exactas Físicas y Naturales, Universidad Nacional de Córdoba, Argentina.

[11]Bio-Protection Research Centre, Lincoln University, Canterbury, New Zealand

[12]Grupo de Ecología de Invasiones, INIBIOMA, CONICET-Universidad Nacional del Comahue, Bariloche, Argentina.

[13]Universidad de Magallanes, Punta Arenas, Chile

[14]Department of Philosophy, University of North Texas, TX, USA

[15]Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN, USA.

***Correspondence: Anibal Pauchard**

Email: pauchard@udec.cl

Abstract

The Andes mountain range in South America has a high level of endemism and is a major source of ecosystem services. The Andes is increasingly threatened by anthropogenic disturbances that have allowed the establishment of non-native plants, mainly in the lower elevation areas. However, synergies between climate change and anthropogenic pressure are promoting the spread of non-native plants to higher elevation areas. In this article, we evaluate and identify the main non-native plants which are invading Andean ecosystems, and assess their taxonomic families, growth forms and distribution patterns. Based on a systematic literature review, we analyze the importance of climatic and anthropogenic factors as drivers of non-native species establishment in Andean ecosystems and the main impacts of non-native plants in the Andes and identified research gaps across each biogeographic region in the Andes. Finally, we highlight key elements to better tackle the problem of non-native plant invasions in Andean ecosystems, including a systematic monitoring of invasion patterns and spread (e.g. MIREN protocol) and a common policy agenda for prevention and management of non-native plants in this highly vulnerable region across international borders.

Keywords: Non-native plants, Andes mountain range, MIREN protocols, anthropogenic disturbance, invasive species prevention and management.

Introduction

Biological invasions are one of the main factors contributing to the loss of biodiversity worldwide, affecting ecosystems in all biomes (Pyšek et al. 2020). Although biological invasions by plants are currently largely concentrated in lowlands, climate change and human activities are increasingly funneling species upwards towards higher elevations (Alexander et al. 2016; Lembrechts et al. 2016; Dainese et al. 2017). Similarly, non-native species are moving toward higher latitudes, even into subpolar and polar areas (Pauchard et al. 2016; Lembrechts et al. 2017). The last two decades have seen a rapid increase in the number of studies of invasions into Arctic and alpine areas, starting to fill the critical gap in our understanding of plant invasions into mountain environments (Alexander et al. 2016; Fuentes-Lillo and Pauchard 2019). We now know that the patterns of invasion in mountain ecosystems are mainly conditioned by four key factors: propagule transport, abiotic conditions, biotic interactions and disturbance processes (Colautti et al. 2006; Pauchard et al. 2009, 2016). Unfortunately, many of these studies of invasive plant species in mountain areas focus on Europe and North America, with only a minority of studies from other continents such as South America (Alexander et al. 2016). Indeed, the latter continent has seen fewer than 200 publications on the topic during the last two decades, with 50% of these articles stemming from the mountain ecosystems of Chile and Argentina alone (Fuentes-Lillo and Pauchard 2019). This has left a considerable knowledge gap on mountain invasions in the páramo and puna (Barros and Pickering 2015; Fuentes-Lillo and Pauchard 2019).

The Andes is the main mountain range in South America (~500 to ~7,000 m.a.s.l). It has a geographical extent of more than 8,000 km, starting in the north of South America in Venezuela, at 8° N and extending all the way south to 69° S (Arroyo and Cavieres 2013). It comprises about 13% of the mountainous areas worldwide in a total area of 3,000,000 km² and with its highest peak reaching 6.962 m a.s.l (Insel et al. 2010). It hosts ecosystems with a high biodiversity of both flora and fauna due to the compression of climatic zones through elevational and latitudinal gradients (Pérez-Escobar et al. 2022) . Historically, the Andes have been divided into three biogeographic zones. Firstly, the páramo, which includes the Andes from Venezuela (11°N) to the northern region of Peru (8°S), found in tropical latitudes. Secondly, the puna, which extends from the northern region of Peru (8°S) to the northern part of Chile (27°S), encompassing tropical to mid-temperate latitudes. Finally, the southern Andean steppe, located in temperate latitudes from northern Chile (27°S) to Patagonia (55°S) (Arroyo and Cavieres 2013). It also has a high level of endemism resulting from the speciation and migration that occurred during the last glacial period (Pallardy 2002). Indeed, with 6.7% of worldwide plant diversity and 23% of species considered endemic, the Andes Mountain range is one of the main hotspots of biodiversity worldwide (Barros and Pickering 2015; Barros et al. 2015). Nevertheless, these vulnerable ecosystems have experienced an increase in plant invasions, with more than 100 non-native plant species recently reported in mountain ecosystems in the Central and Southern Andes (Alexander et al. 2016; Fuentes-Lillo and Pauchard 2019).

On average, the increase in temperature pushes plant species upwards on mountains at a rate of 1.1 m yr^{-1}, although species do not necessarily move unidirectionally (Chen et al. 2011; Lenoir and Svenning 2015). Upward expansion of non-native plants is however likely much faster, especially when facilitated by anthropogenic disturbances (Marini et al. 2011; Lembrechts et al. 2016). Anthropogenic disturbances, through industrial development, agriculture, livestock, tourism or mining (Barros et al. 2013a, 2014), are indeed one of the main drivers of the arrival and establishment of non-native plants in the Andes (Pauchard et al. 2016). Over the next few years, land use change in the Andes is expected to increase further, with direct implications for the establishment and dispersal of non-native plants (Pauchard et al. 2016; Bramer et al. 2018). Greater anthropogenic disturbance of these vulnerable ecosystems, combined with the impacts of climate change predicted for the coming decades, will likely jointly contribute to an accelerated upward migration of non-native plants in the Andes (Hernández-Lambraño et al. 2017; Fuentes-Lillo and Pauchard 2019). However, few studies have explored the distribution patterns of non-native plants along elevational and latitudinal gradients under different climate change scenarios, especially in Andean ecosystems (Lenoir et al. 2017; Fuentes-Lillo and Pauchard 2019).

The unique environmental and topographic characteristics of the Andes as a continent-spanning mountain range allow us to investigate how the factors of disturbance and climate change could favor the arrival, establishment and expansion of non-native plants at local, regional and continent-wide levels (Pauchard et al. 2009; De Frenne et al. 2013). This would allow not only a better understanding of the dynamics of these invasions, but also the development of multiscale protocols for the prevention and management of the growing diversity of non-native plants that threaten the biodiversity of these ecosystems. This is particularly relevant in higher elevation areas with higher endemism and where the level of protection (percentage of protected areas) is still not adequate (Pauchard et al. 2009; Alexander et al. 2016; Elsen et al. 2018).

Almost 15 years ago, a comprehensive research agenda was proposed to study biological invasions in mountain ecosystems (Pauchard et al. 2009). Until now, however, a unified evaluation for the Andes is lacking. Thus, we aim to identify the research gaps, summarize existing knowledge, and guide future efforts in the management of non-native plants in this highly vulnerable region. We use a systematic review to summarize current trends in plant invasions in different biogeographic areas of the Andes, taking advantage of the long latitudinal and steep elevational gradients of the mountain range as a natural experiment to advance the understanding of this global phenomenon in a rapidly changing world. Furthermore, we investigate the relative role of climate and anthropogenic disturbance as drivers of these distributional patterns, hypothesize about the future of plant invasions under a changing climate in the Andes, and summarize the limited evidence on the impacts of plant invasions in the system. Finally, we formulate a research agenda to inform protocols for the prevention and management of non-native plants in the region.

Methods

To determine non-native plant species richness patterns along both elevational and latitudinal gradients in the Andes, species richness data were extracted from both published and unpublished sources (the latter mostly data from the database from the Mountain Invasion Research Network (MIREN, http://www.mountaininvasions.org) and the biological invasions laboratory from the University of Concepcion, Chile (LIB, http://www.lib.udec.cl/). To obtain the published articles, a bibliographic search was carried out on Web of Science (WoS) and Google Scholar using the following keywords (and Spanish translations thereof): ((invasiv * OR non * native OR introduced * OR alien * OR exotic) NEAR plant), ('' high elevation ' 'OR' 'high-elevation' '), ("Colombia", "Venezuela", "Ecuador", "Peru", "Bolivia", "Argentina" and "Chile") and ("Andean", "mountains", "Andes mountain range") (Alexander et al. 2016; Fuentes-Lillo and Pauchard 2019). This search in a total of 185 scientific articles, of which 25 articles were selected based on the criterion that they presented a) a record of non-native plants associated with an elevational gradient, b) a focus on community studies and not on a single non-native species and c) sampling sites along an elevation gradient. For each of the selected articles, the occurrence data of non-native plants associated with each elevation were extracted. A total of 34 plots from nine studies were available for the páramo, 20 plots from six studies for the puna, and 120 plots from ten studies for the southern Andean steppe. The data obtained for both the páramo (Venezuela and Ecuador) and the southern Andean steppe (Argentina, central Chile, and southern Chile) correspond to studies that implement the MIREN sampling methodology, which primarily assesses non-native plant communities near mountain roads (Fig 1) (Haider et al. 2022).This resulted in a total of 101 non-native species richness records, from seven distinct Andean regions that cover a latitudinal range from 8°N to 37°S and incorporate an elevational range from 300 to 4,700 m.a.s.l. Additionally, 369 non-native plant species richness records were added from unpublished data (LIB database) concentrated in the southern Andes (36° to 53°S), across an elevational range from 337 to 1,665 m.a.s.l.

We divide the Andes mountain range into three biogeographic zones based on the classification proposed by Arroyo and Cavieres (2013). We analyze elevational patterns in the species richness of non-native plants within each zone. A generalized linear mixed-effects model (GLMM) was used to test whether non-native plants richness changed as a function of elevation (linear and quadratic) and latitude (linear and quadratic) and their interactions. The model was adjusted to a Poisson distribution error with logit link; the biogeographic zone was used as a random effect. This model was built with the function "*lmer*" using the R statistical package "*lmer4*" (v1.1-31; Bates et al. 2015), The predicted values from the model were extracted using the package "*ggeffect*" (v1.2.0; Lüdecke 2018). To model the nonlinear changes in the richness of non-native plants along latitudinal gradients in both the southern and northern hemispheres simultaneously, we used a cubic b-spline polynomial with a single knot at 0 degrees latitude. This approach allowed us to determine distinct distribution patterns of non-native plants in both the northern and southern hemispheres (Guo et al. 2021). To create the cubic b-splines matrix, we employed the *"bspline"* function from the *"splines2"* package (v0.5.0; Wang and Yan 2021).

To analyze the similarities between the non-native plant species communities in each Andean country, a Jaccard similarity index was calculated using the function "*vegdist*" using the beta diversity obtained with the function "*betadiver*" (both from the "*vegan*" package). The significance level of the dendrogram was calculated based on the 95% of the pseudo similarity values obtained using bootstrapping with 10,000 iterations (v2.6-4Oksanen 2009).

All graphs were created with the package *"ggplot2"* (v3.4.1; Wickham 2008).

Results

The literature review indicated that for the Páramo, only Venezuela (8°N) and Ecuador (0°S) had records of non-native plants along elevation gradients. For the Puna, records were found only in Bolivia (16°S). In contrast, for the Southern Andean Steppe, the majority of records were concentrated in Chile, particularly in central Chile (37°S) and southern Chile (36-39°S) and subantarctic Chile (53°S).

Our survey of non-native plants indicated that the Páramo Andes host 42 non-native plants of which 29% are from the Poaceae family, 12% from the Asteraceae family and the remaining 59% from 16 other families (Table S1, Fig S1).

In the Puna, a total of 60 non-native plants were registered, 25% from the Poaceae family, 18% from the Fabaceae family and 8% from the Rosaceae family; the remaining 49% came from 22 families (Table S1, Fig S1).

Finally, for the Southern Andean steppe, 99 non-native plants were registered, of which 21% are from the Asteraceae family, 19% from the Poaceae family and 11% from the Fabaceae family, with the remaining 49% from 22 families (Table S1, Fig S1). Only four of the non-native plants were present in all three biogeographic zones: *Dactylis glomerata (Poaceae)*, *Plantago lanceolata* (Plantaginaceae), *Taraxacum officinale (Asteraceae)* and *Rumex acetosella* (Polygonaceae) (Table 1). Additionally, 17 species were present in at least two of the biogeographic zones (Table 1). Of the 20 most common species, 35% belonged to the Poaceae family and 15% were from the Fabaceae family, and 70% have an European origin (Table 1). In the páramo, 62% of species have a forb growth form, 28% are graminoids and 4% are shrubs (Table S1). In the puna , 41% are forbs, 25% are graminoids, 18% are trees and 15% are shrubs (Table S1). Finally, for the Southern Andean steppe, 68% are forbs, 19% are graminoids, 7% are shrubs and 6% are trees (Table S1).

Table 1 The 20 most common non-native plant species present in the Andes mountain range, their growth form, biogeographic region of origin and countries of occurrence. For the complete list of species present in the Andes mountains, see Table S1.

Family	Species	Growth form	Biogeographic origin	*Country
Fabaceae	*Acacia dealbata*	Tree	Oceania	ChC, ChS
Poaceae	*Agrostis capillaris*	Graminoid	Europe	EC, ChC, ChS
Poaceae	*Dactylis glomerata*	Graminoid	Europe	EC, BO, Ven, ChC, ChS
Poaceae	*Echinochloa crus-galli*	Graminoid	Europe	Arg, ChC, ChS
Poaceae	*Holcus lanatus*	Graminoid	Europe	EC, BO, ChC, ChS
Juncaceae	*Juncus bufonius*	Forb	Europe	ChC, ChS
Poaceae	*Lolium perenne*	Graminoid	Europe/Africa	Arg, ChC, ChS
Asteraceae	*Matricaria recutita*	Forb	Europe	ChC, ChS
Poaceae	*Pennisetum clandestinum*	Graminoid	Africa	EC, BO
Pinaceae	*Pinus radiata*	Tree	North America	ChC, ChS
Plantaginaceae	*Plantago lanceolata*	Forb	Europe	EC, Ven, ChC
Poaceae	*Poa annua*	Graminoid	Europe	EC, Ven, BO, ChC, ChS, Arg
Lamiaceae	*Prunella vulgaris*	Forb	Europe/Asia	EC, BO, ChC
Pinaceae	*Pseudotsuga menziesii*	Tree	North America	ChC, ChS
Polygonaceae	*Rumex acetosella*	Forb	Europe	EC, BO, ChC, ChS
Caryophyllaceae	*Sagina procumbens*	Forb	Europe	EC, BO, ChC
Caryophyllaceae	*Silene gallica*	Forb	Europe	EC, BO, ChS
Asteraceae	*Taraxacum officinale*	Forb	Europe	EC, BO, Ven, ChC, ChS
Fabaceae	*Trifolium dubium*	Forb	Europe	EC, Arg, ChC, ChS
Fabaceae	*Trifolium repens*	Forb	Europe	EC, Ven, Arg, ChC, ChS

*Páramo: Ven=Venezuela, EC=Ecuador; Puna: BO=Bolivia, South Andean Steppe, Arg=Argentina, ChC=Central Chile, ChS=South Chile.

Jaccard's similarity analysis determined three groups of non-native plant communities: the first consisting of Venezuela and Bolivia, the second of Ecuador, Argentina and Central Chile, and the third of South and subantarctic Chile (Fig 2).

Within each of the three biogeographic zones of the Andes, we found a reduction in the richness of non-native plant species with increasing elevation, however with a strong latitudinal interaction. Non-native plant species richness peaked in the mid-latitudes, at around 39°S (driven by high species richness in Chile and Argentina in the northern half of the Southern Andean steppe, Fig 3A, C, Table 2). Both in the páramoand the southern Andes (mainly in south Chile), we observed a greater richness of non-native species growing above the treeline, than in the central Chile(Fig 3A). In the páramo, a weak decrease in the richness of non-native plants at low elevations (<1,500 m.a.s. l) was also observed (Fig 3A).

Table 2. Estimates, standard errors and significance (P-values) of the effect of elevation, latitude, quadratic equations of elevation (Quad Elev) and latitude (Quad Lati) and their interactions on the richness of non-native plants, based on a Generalized Linear Mixed Model. All estimates are significant *($P < 0.05$).*

	Estimate	***Std. error***	***p-Values***
Intercept	2.1099	0.264	**<0.001**
Elevation	-0.517	0.038	**<0.001**
Quad Elev	-0.064	0.026	**0.016**
Latitude	-0.437	0.122	**<0.001**
Quad Lati	-0.155	0.053	**0.003**
Elevation: Latitude	-0.205	0.058	**<0.001**
Quad Elev: Quad Lat	-0.003	0.004	0.511

Table 3. Overview of reported impacts (i.e. selected examples) of non-native plant species on mountain ecosystems in the Andes, based on a literature review.

Impact type	Non-native species	Impact	Reference
Water stock	*Pennisetum clandestinun*	Changes in the flow of water and runoff from peatlands, reducing the availability of water in the Colombian Andes. 16% reduction in water availability for low elevation urban areas in the Ecuadorian Andes.	Etter et al., 2008 Garavito et al., 2012
Biotic homogenization	*P. clandestinun* *Pinus patula* *Pinus radiata*	Changes in the composition of native species along the elevational gradients in the Venezuelan Andes.	Ataroff, 2003 Ataroff & Rada, 2000 Hofstede et al.,2002 Balthazar et al.,2015.
Recruitment and regenerations of native species	*P. radiata*	Changes in the recruitment and regeneration patterns of native understory species (e.g., *Baccharis latifolia, Cordia cylindrostachya, Dunalia solanacea*) in the Colombian Andes.	Cavalier & Santos, 1999.
Change in richness and abundance of native species	*Pinus contorta*	Changes in the patterns of richness and abundance of native species of the Patagonian steppe (*Festuca pallescens, Baccharis concava, Discaria chacaye*) in the subantarctic Andean ecosystems of Chile.	Franzese et al., 2017
	Ulex europeus	Change in the richness of native shrubs in the Colombian Andes, affecting the richness of native bird species (*Turdus fuscater and Colaptes rivolii*)	Amaya-Villareal & Renjifo, 2010
	Pinus sp	Changes in the richness and abundance of arthropod species, reducing the decomposition of litter and organic matter in the Colombian Andes over 3000 m.a.s.l.	Leon-Gamboa et al., 2010
	Taraxacum officinale	Reduces abundance of native species *Chaetanthera lycopodioides, Montiopsis potentilloides, Oxalis compacta, Phacelia secunda* and *Viola philippi*	Cavieres et al., 2005
Pollination patterns	*T. officinale*	The high density of individuals of T. officinale generates a change in pollination patterns, which translates into a reduction in pollination events of the native species *Hypochaeris thrincioides* and *Perezia carthamoides* in the Andes of central Chile.	Muñoz & Cavieres, 2008.
Phylogenetic diversity	*Pinus ponderosa*	Changes in the phylogenetic structure of arbuscular fungi of native species possibily affecting growth and development of native species in the Andes of Argentina.	Gazol et al., 2016.
	Taraxacum officinale	Reduces abundance of native species *Chaetanthera lycopodioides, Montiopsis potentilloides, Oxalis compacta, Phacelia secunda* and *Viola philippi*	Cavieres et al., 2005
Microclimatic conditions	*Pinus contorta*	Changes in soil temperature patterns, associated with greater vegetation cover in the Patagonian steppe of the subantarctic Andes.	García A et al., 2023 Franzese et al., 2017
	Ligustrum lucidum	Reduction of soil moisture and nutrient cycling in the Argentinean Andes.	Aragon et al., 2014
	Morus sp.	Reduction of soil moisture and litter decomposition in the Argentinean Andes.	Aragon et al., 2014

Discussion

Plant invasions in the Andean region mirrors global mountain patterns

The overarching patterns of invasion found in the Andes resemble with observations across the globe. Indeed, the Poaceae, Asteraceae and Fabaceae families were identified as the most common non-native families, while more than 63% of non-native species globally have an origin in Europe versus 70% in the Andes (Alexander et al. 2016). Regarding Jaccard´s similarity index, these results are similar to the results obtained by (Seipel et al. 2012), showing that plant community similarities between regions may be driven by similarities in climatic conditions. Under this context, the grouping formed by Bolivia and Venezuela may be conditioned by the bioclimatic similarities associated with an orotropical biome, which could be determining the presence of similar non-native plants (Rivas-Martínez 2010; Arroyo and Cavieres 2013). The same occurs in the grouping of Ecuador, Argentina, and central Chile, where the predominant dry season may function as an environmental filter, selecting the most drought-tolerant non-native plants (Rivas-Martínez 2010; Deil et al. 2011; Sandoya et al. 2017). Finally, regarding the grouping observed between southern Chile and Subantarctic Chile, this can be mainly explained by the climatic similarities in terms of temperature (with annual averages of 0-5°C) and precipitation, ranging from 717 mm in southern Chile to 1350 mm in Subantarctic Chile. Similar to other areas in the Andes, this can function as an environmental filter that favors non-native plants adapted to these low temperatures (Rivas-Martínez 2010; Arroyo and Cavieres 2013).

The observed declines along the elevational gradient in the Andes is in agreement with the observed global patterns of non-native plant species richness, where the highest richness of non-native plants is often found at low elevations (Pauchard et al. 2009; Alexander et al. 2011; McDougall et al. 2018). These patterns have been explained by the increasingly extreme climatic conditions and decreasing anthropogenic disturbance towards higher elevations (Pauchard et al. 2009; Alexander et al. 2011; Marini et al. 2011; Lembrechts et al. 2016). An exception often observed to the decline of non-native richness with elevation occurs in tropical regions, where non-native plant richness usually peaks at intermediate elevations due to high temperatures and drought in low elevation zones (Arévalo et al. 2005; Seipel et al. 2012).This pattern was also observed in the páramo, where a (weak) peak in abundance occurs at intermediate altitudes (Fig 3A).

The decrease in non-native plant richness at higher altitudes can be attributed to the extreme climatic conditions in that region (Rew et al. 2020). On the other hand, in lower altitude zones, the high diversity of native plants may act as a biotic filter, preventing the establishment of non-native species, which explains the low richness in these areas. Meanwhile, the high number of non-native plants observed in mid-altitude zones (2500-3000 meters above sea level) is associated with both the presence of human settlements, which facilitates their dispersal and establishment as well as moderate climatic conditions that resemble temperate conditions of most European generalist non-native species (Sandoya et al. 2017).

The higher non-native plant species richness at intermediate latitudes observed in this study coincides with the global pattern (Guo et al. 2021) where a greater richness of non-native plant species is found at mid latitudes 40°S (Guo et al. 2021). This pattern of peak in non-native plant species richness at intermediate latitudes is likely associated with the higher density of human populations and anthropogenic activities (concentration of agriculture, tourism, mining etc.), which results in a higher propagule pressure in these ecosystems (Pauchard and Alaback 2004; Barros et al. 2015; Guo et al. 2021). On the other hand, the decline in richness of non-native plants in the páramo can be explained by biotic resilience resulting from the high native species richness per unit area (Guo et al. 2021); rapid ecosystem recovery after disturbances due to high diversity (Guo et al. 2021); lack of functional traits associated with shade tolerance (Fine 2002); and low colonization rate (low propagule pressure) (Fine 2002; New et al. 2007). In the Southern Andes (above 50°S), the lower richness may be associated with extreme climatic conditions, low population density and fewer anthropogenic activities (Pauchard et al. 2016; Guo et al. 2021).

Both the elevational and latitudinal distribution patterns can depend substantially on sampling effort, which is lower in the paramo and puna than in the South Andean steppe. Therefore, the observed distribution patterns of non-native plants, primarily between latitudes 11°N and 27°S, should be treated with caution, as there is a significant information gap regarding the richness of non-native plants along elevation gradients, particularly in countries like Colombia and Peru. Increasing the sampling intensity and coverage of elevation gradients in the páramo and puna could reveal a higher richness of non-native plants in these regions, potentially altering the current distribution patterns of non-native plants in the Andes.

Factors determining invasion: the importance of the human footprint in the Andes

In general, most invasions reported from the Andean region are highly associated with anthropogenic factors, such as forest-agricultural areas in the páramo and areas used for tourism and livestock grazing in the Central and Southern Andes (e.g., Barros et al., 2015). As in any other biome, human disturbance in mountains can affect the three other major constraints for plant invasions: abiotic conditions, biotic interactions and propagule pressure (Colautti et al. 2006; Pauchard et al. 2009), with multiple types of disturbance often favoring generalist species (Barros and Pickering 2014; Vásquez et al. 2015; Sandoya et al. 2017).

Recent decades have seen, there has been a progressive increase in the intensity of human disturbances in mountainous areas of South America resulting in a loss of pristine areas (Barros et al. 2014). Consequently, pristine areas are increasingly restricted to protected areas,, which are often surrounded by agriculture and urban development (Fuentes-Lillo et al. 2021). Protected areas in the Ecuadorian and Colombian Andes are mainly located around population centers (Bax and Francesconi 2019). Furthermore, the anthropogenic development of mountainous areas in the Andes is associated with an increase in tourist activities within protected areas and their surroundings, including hotels, ski resorts and vacation homes (Barros and Pickering 2014; Barros et al. 2015).

Roads act as one of the main drivers of invasion into the Andes (Pauchard et al. 2009; Seipel et al. 2012). At the intersection of land use changes, roads connect agriculture, urban areas and tourism activities, turning them into key drivers for the introduction of non-native plants to these ecosystems and into protected areas (Pauchard and Alaback 2004; Barros and Pickering 2014). Dispersal mechanisms include transporting seeds attached to car tires, clothing and domestic livestock (Ansong and Pickering 2013), by. Roads also cause altered soil properties, including higher nutrient levels, changes in soil pH, increased drainage and more extreme microclimatic conditions (Forman and Alexander 1998; Müllerová et al. 2011; Alexander et al. 2016). Finally, they can reduce competition from native species and thus favor non-native plant establishment through niche expansion (Bolnick et al. 2010; Lembrechts et al. 2014, 2016). The facilitative effects of roads towards plant invasions have been documented for several roads in South America, including in Ecuador (Sandoya et al. 2017); Bolivia (Fernández-Murillo et al. 2015); the Central Andes (Argentina and Chile) (Haider et al. 2018); the South-central Andes (Pauchard and Alaback 2004; McDougall et al. 2011; Haider et al. 2018) and Argentina (Haider et al. 2018; McDougall et al. 2018). A similar, yet smaller, impact has been observed for hiking trails in Chile, which to a some extent also increase propagule pressure, alter abiotic conditions and reduce competitive interactions (Liedtke et al. 2020).

In the central Andes of Peru, an example of the role of disturbance is the establishment of the *Pennisetum clandestinum*, a non-native African grass, associated with the elimination of vegetation above 3.800 m.a.s.l caused by the introduction of cattle (Urbina and Benavides 2015). The introduction of cattle in the Peruvian Andes also facilitated the establishment of *Pinus patula* and *Pinus radiata* species at 4.000 m.a.s.l (Raboin and Posner 2012). In the Bolivian Andes, the establishment of the non-native tree *Eucalyptus globulus* and the grasses *Sorghun halepense* and *Cynodon lemfuensis* has been favored by fire disturbance (Thomas et al. 2010). In the Central Andes of Chile and Argentina, the presence of non-native herbs *Taraxacum officinale, Lactuca sativa, Rumex. acetosella* and *Convolvulus arvensis* is associated with the disturbance caused by tourism (formation of informal trails) and cattle (Muñoz and Cavieres 2008; Barros and Pickering 2014). In the southern Andes, the establishment of the evergreen shrub species *Ulex europaeus* is associated with fragmentation of the Andean forests (Altamirano et al. 2016). In this same context, the invasive pine *Pinus contorta* was favored by anthropogenic disturbance, including fragmentation and anthropogenic land use (Franzese et al. 2017).

In the Andes, most of the protected areas are located at intermediate elevation (~ 1000-2000 m a.s.l) (Elsen et al. 2018), while anthropogenic activities (agricultural, livestock, tourism and mining activities) are increasingly affecting higher elevation areas, generating higher propagule pressure, changes in abiotic conditions and reduction of biotic resistance across the whole elevation gradient (Barros et al. 2015; Pauchard et al. 2016; Fuentes-Lillo and Pauchard 2019). It is thus necessary to generate biosecurity protocols to avoid the arrival of new species and develop plans and mechanisms to increase the extent of protected areas at higher elevations, especially given that these areas have a great taxonomic diversity and high levels of endemism (Ansong and Pickering 2013).

Factors determining invasion: is climate a limiting factor?

Mountains are ecosystems with steep gradients of abiotic factors such as temperature, precipitation, UV radiation, nutrient availability and growing season length, which have functioned as an abiotic filter preventing the establishment of non-native plants in higher elevations (Pauchard et al. 2009). The invasion process at high elevations and latitudes is thus limited to non-native plants that are pre-adapted to extreme climatic conditions or show very flexible climate niches (Alexander et al. 2011; Lembrechts et al. 2016). These climatic limitations supposedly largely drive the characteristic decline in non-native plants with elevation observed in mountain systems worldwide (Alexander et al. 2011; Seipel et al. 2012; McDougall et al. 2018). However, in the Andes we observed that a large number of non-native plants managed to grow above the treeline (Fig 3A). We speculate that these occurences could be explained by the presence of anthropogenic disturbances (i.e. roads, human settlements) that modify abiotic conditions (Lembrechts et al. 2016; Fuentes-Lillo et al. 2021). Some examples of non-native plants that grow above the tree line in the Andes include *Acacia dealbata*, *Lupinus polyphyllus*, *Verbascum virgatum* and *Echium vulgare*, which grow in the highest elevation areas above the tree limit (Fig 1).

It is important to note that these non-native plants, in addition to growing above the treeline, are subjected to low temperatures, high radiation, extreme drought, and nutrient-poor, underdeveloped soils (primarily volcanic) (Fuentes-Lillo et al. 2021). Therefore, the presence of anthropogenic activities by modifying soil conditions (nutrient addition) and increasing water availability these patterns. For example, a correlation has been found between the nutrient content (nitrogen, phosphorus and potassium) and the presence of *T. officinale* in the Central Andes, where nutrient-poor soils would be key to limiting the establishment of this non-native plants (Quiroz et al. 2011). In the Peruvian Andes, water availability was identified as the main limitation for the establishment of non-native plants above 3.700 m.a.s.l (Thomas et al. 2010). In the Colombian Andes, low water availability and low nutrients levels were key to limiting the establishment of the non-native species *Anthoxanthum odoratum*, *Hypochaeris raditaca*, and *Holcus lanatus* above 3.500 m.a.s.l (Valencia et al. 2013). Other abiotic conditions might also be saffected by disturbance (Lembrechts et al. 2016).

Climate change: predicted effects on the patterns of non-native plants in the Andes

The effects of climate change are less well documented in the Andes than in other mountain areas of the world (Pauchard et al. 2016; Fuentes-Lillo and Pauchard 2019). Nevertheless, current climatic models for the Andes indicate a warming rate of approximately 0.34°C per decade, similar to what is forecasted for both the Arctic and the Antarctic, and higher than the global average (Bozkurt et al. 2017). These higher temperatures are likely to be accompanied by increased precipitation in the páramo and by complex changes in precipitation in the Central and Southern Andes, for both rain and snow (Bozkurt et al. 2017b). These changes in temperature and precipitation will directly affect species redistribution as they track their climatic niche (Petitpierre et al. 2016; Pauchard et al. 2016; Dainese et al. 2017). For the páramo, several studies have determined that increases in temperature can move species distribution limits upwards in the mountains. For example, it is expected that every 3°C temperature increase will result in upward shift of 600 meter in species range limits (Arzac et al. 2011; Bramer et al. 2018; Rew et al. 2020). In addition, climate change will have major indirect impacts on Andean ecosystems. For example, predicted increases in annual precipitation levels will result in increased erosion processes and land displacement that may favor the establishment of non-native plants over the native community (Ruiz et al. 2008; Ansong and Pickering 2013). For the Central Andes, it has been predicted that climate change may increase drought events, which would favor the establishment of non-native species adapted to drought conditions (Molina-Montenegro et al. 2011).

The warming climate directly affectthe upward expansion of non-native plants (Petitpierre et al. 2016). This change in the elevational patterns is mainly associated with an improvement in abiotic conditions as well as a significant improvement in dispersal patterns, associated with higher seed production, which significantly increases the probability of establishment of non-native plants (Teller et al. 2016). In the paramo Andes (e.g., Colombian and Peruvian Andes), the expected increased precipitation might also lift one of the main limitations for the establishment of non-native plants in the region (Thomas et al. 2010; Valencia et al. 2013).

Forthe ecosystems of the Andes, we are aware of only one study that evaluates the future distribution of non-native plants along elevational and latitudinal gradients. This study models the potential niche of *Taraxacum officinale* and *Ulex europeus* under a climate change scenario in 2050, predicting an expansion of the potential niche, generating the redistribution of these species from the valley towards higher elevation areas, especially for the Andes of Chile and Argentina (Hernández-Lambraño et al. 2017).

Considering that the redistribution of non-native plants could be directed towards highlands and high latitudes due to the projected increase in temperatures and precipitation in the Andes, generating more experimental studies (e.g use of open top chambers (OTC)), coupled with modeling (Species Distribution Modeling and Ecological Niche Modeling) for different non-native plants is necessary to fully understand how future climate scenarios will affect the patterns of distribution of non-native plants in the Andes (Ebeling et al. 2008; Bellard et al. 2013). This will allow identifying the future areas occupied by non-native plants, which will help to generate biosecurity protocols to manage, control and prevent future expansion of non-native species (Faulkner et al. 2020). In this context, generating hybrid (i.e. mechanistic and correlative) models that include microclimatic (high-resolution data) and anthropogenic variables could provide a more realistic approximation of the future distribution of non-native plants (Lenoir et al. 2017; Lembrechts et al. 2020).

Impacts

The impact of non-native plants on the ecosystems of the Andes has been poorly studied in comparison to other alpine ecosystems (Alexander et al. 2016). Mainly, compared to other regions in the southern hemisphere, such as South Africa with the impact of *Pinus* species on mountain fynbos (van Wilgen 2012), *Pilosaella officinarum* in Australia (Alexander et al. 2016), and *Pinus* species in New Zealand (Tomiolo et al. 2016)

Most of the studies in the Andes pertain to tree non-native plants that invade large areas (e.g., *Pinus radiata*, *P. patula*, *P. contorta*) (Table 3). These studies are often focused on evaluating the effect of non-native species on the reduction of biodiversity, due to changes in the richness and abundance of native species, effects on pollination regimes or biotic homogenization (Table 3). It is important to note that during the last

10 years, only 10 publications reported on the impact of non-native plants in the Andes, with the majority belonging to the páramo (Fuentes-Lillo and Pauchard 2019).

Prevention and management of invasive plants in the Andes: do we need a common policy framework?

Although studies have shown that, invasive non-native plants are a major threat to biodiversity and ecosystem services in South America (Table 3), the concern of the state and citizens regarding invasive plants is lower than in other continents such as Oceania, Europe, or North America (Speziale et al. 2012; Pyšek et al. 2020). The magnitude of other threats to biodiversity in South America (IPBES, 2018) may contribute to the underestimation of the role of invasive species and particularly plants in the biodiversity crisis. More than two decades ago, most South American countries agreed to create an international committee to address climate change and ratified the United National Framework Convention on Climate Change (Dimitrov 2010); Comisión Europea, 2019). In addition, all countries ratified the Convention on Biological Diversity (CBD), which includes an explicit mandate to prevent, control, and eradicate non-native plants that pose a threat to local biodiversity. Although most countries where the Andes occur are signatories to various biodiversity conventions and sustainable development strategies, public policies in South American countries related to the prevention and control of invasive species is poor, and reflects the low political and social understanding and interest. Research on invasive species and most efforts to control invasive plants are directed toward species that are economic pests or have socioeconomic impacts (Speziale et al. 2012; Aizen et al. 2019; Fuentes-Lillo and Pauchard 2019).

There are, however, important differencess among South America countries in the policies to tackle invasive species. For example, Ecuador has a legal basis that supports the management of non-native species, mainly in the Convention on Biological Diversity (CBD) article 8-h that promotes the prevention, control and eradication of non-native species. Additionally, Ecuador presents a strategic plan that seeks to identify pathways of introduction, prioritize non-native species and reduce the impacts of non-native species in both terrestrial and aquatic ecosystems by 2019 (MAATE 2019). During the last decades, Colombia has made significant progress in protecting ecosystems from invasive species, moving from a national code of renewable natural resources (CNRN law 2811 of 1974) that allowed the introduction of non-native species to the country with a special permit from the state, to a management plan for the prevention and management of introduced, transplanted and invasive species that aims to prevent, identify routes of introduction and reduce the impacts of non-native species (MADS, 2011). Both Peru and Bolivia have national action plans on non-native species led by the Ministry of Environment (MINAM) in Peru and the Ministry of Environment and Water in Bolivia (MMAYA). These plans seek to coordinate technical groups to evaluate the risk of non-native species, identify routes of introduction and reduce the impact of these species on ecosystem services, and have goals to be met by 2035.

In Argentina, the Ministry of Environment and Sustainable Development has a national strategy on invasive non-native species (ENEEI) that aims to minimize the impact on national resources, biodiversity, ecosystem services, the economy, public health and culture. This national strategy seeks to develop a framework to strengthen governance and effective protection of biodiversity, enhance the socioeconomic benefits that include natural resources and ecosystem services, and promote research on the impacts of invasive species to generate effective public policies to control their impact.

Finally, Chile has a national biodiversity strategy with a vision for the year 2030 that involves the objectives of the CBD. Within this national strategy, the aim is to promote good practices in the agricultural and forestry sector sector associated with the use of non-native species, in order to prevent the introduction, release and dispersal of invasive non-native species and/or potentially invasive non-native species to the natural environment. The strategic objectives also include promoting basic and applied research on invasive species, mainly on prevention, control and/or eradication and restoration mechanisms, increasing awareness and information to the public on invasive species and developing environmental education strategies related to biological invasions and their effects on national biodiversity. It is expected that by the 2030s that efficient biosecurity protocols will be implemented, with prioritization of non-native species, identification of introduction routes and finally at least ten restoration plans in areas that have been invaded by non-native species (MMA 2017).

Unfortunately, aside from variation in national public policies and regulations there is additional variation in the enforcement of these instruments across regions and taxa (Aizen et al., 2019; Comisión Europea, 2019). Most public policies, national strategies and regulatory frameworks do not apply specifically to the Andes Mountains, but these ecosystems are equally represented by each of these regulatory systems associated with each country that includes the Andes mountains (Aizen et al. 2019). Because these ecosystems have a high level of endemism, are important biodiversity hotspots, and that protected areas protect an inadequate proportion of the Andes (Castillo et al. 2020), it is necessary to generate specific public policies for these ecosystems. Nonetheless, for most environmental agencies, mountain environments are low priority in terms of prevention and control of invasive species, including because of the perception that the rugged terrain and inaccessibility of the Andes mountains makes them seen as less prone to invasions.

This review has highlighted that it is necessary to move towards a regulatory framework or regional strategy, including all the countries that make up the Andes, to develop, standardize and prioritize policies to identify introduction routes, prioritize non-native species for their control, and reduce the drivers causing non-native species introduction and spread. A common multinational framework across the Andes could reduce the regional impact of non-native species in the region Generating bilateral and multinational strategies to prevent the spread and enhance the management of invasive non-native plants in the Andes is critical. These strategies should move towards implementing joint risk assessments before introducing any non-native species, as European countries have adopted (Aizen et al. 2019). An example in the region includes the coordinated efforts between Chile and Argentina to create a bilateral strategy for vertebrates such as for the control of the beaver (*Castor canadensis*) in Tierra del Fuego in southern Patagonia (Sanguinetti et al. 2014; Aizen et al. 2019).

No less important for the prevention and management of invasive plants in the Andes is the extremely limited "on the ground" expertise and experience about control methods for these species. Although some agencies have conducted experimental initiatives, these efforts have been limited and usually confined to specific taxa. For example, for invasive tree species a few studies have been conducted for *Pinus* spp. control in Chile and Argentina (Pauchard et al. 2016), and for *Ligustrum lucidum* (glossy privet) in Argentina (Valfré-Giorello et al. 2019), but the amount of research and scope of operational scale actions are considerably lower than countries such as New Zealand (Edwards et al. 2021) and Australia (Pyšek et al. 2020). For shrub species the situation is similar, with some effort on a few species receiving most of the attention as with *Ulex europaeus* control in Colombia (Gómez-Ruiz et al. 2013) and Chile (Norambuena et al. 2000), while for herb species there is no reported experience in control.

Conclusions

Our review challenges the paradigm that extreme climatic conditions are the main limitation for the redistribution of non-native plants in the Andes, instead shifting the focus to the role of anthropogenic factors on the redistribution of non-native plants, both at latitudinal and elevational extremes. An improved understanding of the effect of anthropogenic factors on invasions in the region will assist to reduce the arrival of non-native plants in the higher elevation areas.

Given that climate change may have implications for altitudinal and latitudinal redistribution (i.e., shifting towards higher latitudes), it is crucial to enhance the study of the climate change effect on the patterns of redistribution of non-native plants. This will provide valuable information for developing biosecurity protocols and efficient management plans to mitigate future impacts of non-native plants on mountain ecosystems and their native biodiversity.

Increasing the understanding of the impacts of non-native plants on mountain ecosystems and ecosystem services is of utmost importance, considering that it is one of the aspects of plant invasions in mountains that has received insufficient attention and the importance of the Andes for biodiversity conservation and as a source of important ecosystem services (e.g., water) for the people who inhabit or depend on these areas.

Unfortunately, even though invasive plant species have been recorded as an important threat to biodiversity in the Andes, especially under climate change scenarios, countries have not responded accordingly in terms of prevention and management policies. Future efforts must address the multinational nature of invasion processes. Coordinated policies across neighbouring countries will increase the chances for successful intervention. In this regard, research gaps on prevention and management tools must urgently be addressed. In addition, and to minimize the impacts from anthropogenic use that favors plant invasions, strengthening protected areas systems and improving management for biodiversity conservation is critical in the Andes.

Finally, we urge the scientific community to unify methodological studies that allow us to have a better understanding of the invasion process both along the elevational and latitudinal gradients of the Andean ecosystems, considering that the Andes functions as a natural laboratory to evaluate ecological processes related to biological invasions along the gradients of climate and anthropogenic disturbance inherently present in the system.

STATEMENTS & DECLARATIONS

FUNDING

The idea behind this manuscript was initiated by AP, AB, RB, PH, RR and DS in the Malalcahuello plant invasions workshop funded by ICM P05-002 in May 2014. EFL, LC and AP funded by Fondecyt grants 1180205 and 1231616, grant ANID/BASAL FB210006 and ACT210038. EFL was funded by ANID doctoral scholarship 375957. JJL acknowledges funding by the Research Foundation Flanders (grants OZ7828 and OZ7916) and the University of Antwerp (grant FFB190028).

COMPETING INTERESTS

The authors have no relevant financial or non-financial interests to disclose

AUTHORS CONTRIBUTIONS

All author contributed to the study conception and design. Data analysis was undertaken by Eduardo Fuentes Lillo, Jonas J. Lembrechts and Ramiro Bustamante. The first draft of the manuscript was written by Eduardo Fuentes Lillo, Anibal Pauchard and Jonas J Lembrechts. Editing by all authors. All authors read and approved the final manuscript.

References

Aizen MA, Smith-Ramírez C, Morales CL, et al (2019) Coordinated species importation policies are needed to reduce serious invasions globally: The case of alien bumblebees in South America. J Appl Ecol 56:100–106. https://doi.org/10.1111/1365-2664.13121

Alexander JM, Kueffer C, Daehler CC, et al (2011) Assembly of nonnative floras along elevational gradients explained by directional ecological filtering. Proc Natl Acad Sci U S A 108:656–661. https://doi.org/10.1073/pnas.1013136108

Alexander JM, Lembrechts JJ, Cavieres LA, et al (2016) Plant invasions into mountains and alpine ecosystems: current status and future challenges. Alp Bot 126:89–103. https://doi.org/10.1007/s00035-016-0172-8

Altamirano A, Cely JP, Etter A, et al (2016) The invasive species Ulex europaeus (Fabaceae) shows high dynamism in a fragmented landscape of south-central Chile. Environ Monit Assess 188:. https://doi.org/10.1007/s10661-016-5498-6

Ansong M, Pickering C (2013) Are weeds hitchhiking a ride on your car? A systematic review of seed dispersal on cars. PLoS One 8:1–11. https://doi.org/10.1371/journal.pone.0080275

Arévalo JR, Delgado JD, Otto R, et al (2005) Distribution of alien vs. native plant species in roadside communities along an altitudinal gradient in Tenerife and Gran Canaria (Canary Islands). Perspect Plant Ecol Evol Syst 7:185–202. https://doi.org/10.1016/j.ppees.2005.09.003

Arroyo MTK, Cavieres LA (2013) High-Elevation Andean Ecosystems. Encycl Biodivers Second Ed 4:96–110. https://doi.org/10.1016/B978-0-12-384719-5.00428-7

Arzac A, Chacón-moreno E, Llambí LD (2011) DEL ECOTONO BOSQUE PARAMO EN LOS ANDES TROPICALES DISTRIBUTION OF PLANT LIFE FORMS IN THE UPPER LIMIT OF THE FOREST PARAMO ECOTONE IN THE TROPICAL ANDES. 24:26–46

Barros A, Gonnet J, Pickering C (2013a) Impacts of informal trails on vegetation and soils in the highest protected area in the Southern Hemisphere. J Environ Manage 127:50–60. https://doi.org/10.1016/j.jenvman.2013.04.030

Barros A, Gonnet J, Pickering C (2013b) Impacts of informal trails on vegetation and soils in the highest protected area in the Southern Hemisphere. J Environ Manage 127:50–60. https://doi.org/10.1016/j.jenvman.2013.04.030

Barros A, Monz C, Pickering C (2015) Is tourism damaging ecosystems in the Andes? Current knowledge and an agenda for future research. Ambio 44:82–98. https://doi.org/10.1007/s13280-014-0550-7

Barros A, Pickering C, Renison D (2014) Short-term effects of pack animal grazing exclusion from andean alpine Meadows. Arctic, Antarct Alp Res 46:333–343. https://doi.org/10.1657/1938-4246-46.2.333

Barros A, Pickering CM (2015) Impacts of experimental trampling by hikers and pack animals on a high-altitude alpine sedge meadow in the Andes. Plant Ecol Divers 8:265–276.

https://doi.org/10.1080/17550874.2014.893592

Barros A, Pickering CM (2014) Non-native plant invasion in relation to tourism use of aconcagua park, Argentina, the highest protected area in the southern hemisphere. Mt Res Dev 34:13–26. https://doi.org/10.1659/MRD-JOURNAL-D-13-00054.1

Bates D, Mächler M, Bolker BM, Walker SC (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:. https://doi.org/10.18637/jss.v067.i01

Bax V, Francesconi W (2019) Conservation gaps and priorities in the Tropical Andes biodiversity hotspot: Implications for the expansion of protected areas. J Environ Manage 232:387–396. https://doi.org/10.1016/j.jenvman.2018.11.086

Bellard C, Thuiller W, Leroy B, et al (2013) Will climate change promote future invasions? Glob Chang Biol 19:3740–3748. https://doi.org/10.1111/gcb.12344

Bolnick DI, Ingram T, Stutz WE, et al (2010) Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. Proc R Soc B Biol Sci 277:1789–1797. https://doi.org/10.1098/rspb.2010.0018

Bozkurt D, Rojas M, Boisier JP, Valdivieso J (2017a) Climate change impacts on hydroclimatic regimes and extremes over Andean basins in central Chile. Hydrol Earth Syst Sci Discuss 17:1–29. https://doi.org/10.5194/hess-2016-690

Bozkurt D, Rojas M, Boisier JP, Valdivieso J (2017b) Climate change impacts on hydroclimatic regimes and extremes over Andean basins in central Chile. Hydrol Earth Syst Sci Discuss 17:1–29. https://doi.org/10.5194/hess-2016-690

Bramer I, Anderson BJ, Bennie J, et al (2018) Advances in Monitoring and Modelling Climate at Ecologically Relevant Scales. Adv Ecol Res 58:101–161. https://doi.org/10.1016/bs.aecr.2017.12.005

Castillo LS, Correa CA, Matallana CL, et al (2020) Connectivity of Protected Areas: Effect of Human Pressure and Subnational Contributions in the Ecoregions of Tropical Andean Countries. Land 9:1–19

Chen IC, Hill JK, Ohlemüller R, et al (2011) Rapid range shifts of species associated with high levels of climate warming. Science (80-) 333:1024–1026. https://doi.org/10.1126/science.1206432

Colautti RI, Grigorovich IA, MacIsaac HJ (2006) Propagule pressure: A null model for biological invasions. Biol Invasions 8:1023–1037. https://doi.org/10.1007/s10530-005-3735-y

Dainese M, Aikio S, Hulme PE, et al (2017) Human disturbance and upward expansion of plants in a warming climate. Nat Clim Chang 7:577–580. https://doi.org/10.1038/NCLIMATE3337

De Frenne P, Rodríguez-Sánchez F, Coomes DA, et al (2013) Microclimate moderates plant responses to macroclimate warming. Proc Natl Acad Sci U S A 110:18561–18565. https://doi.org/10.1073/pnas.1311190110

Deil U, Alvarez M, Bauer EM, Ramírez C (2011) The vegetation of seasonal wetlands in extratropical and orotropical South America. Phytocoenologia 41:1–34. https://doi.org/10.1127/0340-269X/2011/0041-0491

Dimitrov RS (2010) Inside Copenhagen: The state of climate governance. Glob Environ Polit 10:18–24. https://doi.org/10.1162/glep.2010.10.2.18

Ebeling SK, Welk E, Auge H, Bruelheide H (2008) Predicting the spread of an invasive plant: Combining experiments and ecological niche model. Ecography (Cop) 31:709–719. https://doi.org/10.1111/j.1600-0587.2008.05470.x

Edwards P, Sprague R, Stahlmann-Brown P (2021) Removing invasive conifers-considerations, complexity and costs. Environ Res Commun 3:. https://doi.org/10.1088/2515-7620/ac13c7

Elsen PR, Monahan WB, Merenlender AM (2018) Global patterns of protection of elevational gradients in mountain ranges. Proc Natl Acad Sci U S A 115:6004–6009. https://doi.org/10.1073/pnas.1720141115

Faulkner KT, Robertson MP, Wilson JRU (2020) Stronger regional biosecurity is essential to prevent hundreds of harmful biological invasions. Glob Chang Biol 26:2449–2462. https://doi.org/10.1111/gcb.15006

Fernández-Murillo MP, Rico A, Kindlmann P (2015) Exotic plants along roads near La Paz, Bolivia. Weed Res 55:565–573. https://doi.org/10.1111/wre.12174

Fine PVA (2002) The invasibility of tropical forests by exotic plants. J Trop Ecol 18:687–705. https://doi.org/10.1017/S0266467402002456

Forman RTT, Alexander LE (1998) Roads and Their Major Ecological Factors. Annu Rev Ecol Syst 29:207–231

Franzese J, Urrutia J, García RA, et al (2017) Pine invasion impacts on plant diversity in Patagonia: invader size and invaded habitat matter. Biol Invasions 19:1015–1027. https://doi.org/10.1007/s10530-016-1344-6

Fuentes-Lillo E, Lembrechts JJ, Cavieres LA, et al (2021) Anthropogenic factors overrule local abiotic variables in determining non-native plant invasions in mountains. Biol Invasions 23:3671–3686. https://doi.org/10.1007/s10530-021-02602-8

Fuentes-Lillo E, Pauchard A (2019) Invasiones en montañas: ¿Cuánto hemos avanzado en los últimos 10 años y cuáles son los desafíos para los ecosistemas de los Andes? Gayana Botánica 76:141–155. https://doi.org/10.4067/s0717-66432019000200141

Gómez-Ruiz PA, Lindig-Cisneros R, Vargas-Ríos O (2013) Facilitation among plants: A strategy for the ecological restoration of the high-andean forest (Bogotá, D.C.-Colombia). Ecol Eng 57:267–275. https://doi.org/10.1016/j.ecoleng.2013.04.049

Guo Q, Cade BS, Dawson W, et al (2021) Latitudinal patterns of alien plant invasions. J Biogeogr 48:253–262. https://doi.org/10.1111/jbi.13943

Haider S, Kueffer C, Bruelheide H, et al (2018) Mountain roads and non-native species modify elevational patterns of plant diversity. Glob Ecol Biogeogr 27:667–678. https://doi.org/10.1111/geb.12727

Haider S, Lembrechts JJ, McDougall K, et al (2022) Think globally, measure locally: The MIREN standardized protocol for monitoring plant species distributions along elevation gradients. Ecol Evol 12:. https://doi.org/10.1002/ece3.8590

Hernández-Lambraño RE, González-Moreno P, Sánchez-Agudo JÁ (2017) Towards the top: niche expansion of Taraxacum officinale and Ulex europaeus in mountain regions of South America. Austral Ecol 42:577–589. https://doi.org/10.1111/aec.12476

Insel N, Poulsen CJ, Ehlers TA (2010) Influence of the Andes Mountains on South American moisture transport, convection, and precipitation. Clim Dyn 35:1477–1492. https://doi.org/10.1007/s00382-009-0637-1

Lembrechts JJ, Aalto J, Ashcroft MB, et al (2020) SoilTemp: A global database of near-surface temperature. Glob Chang Biol 26:6616–6629. https://doi.org/10.1111/gcb.15123

Lembrechts JJ, Alexander JM, Cavieres LA, et al (2017) Mountain roads shift native and non-native plant species' ranges. Ecography (Cop) 40:353–364. https://doi.org/10.1111/ecog.02200

Lembrechts JJ, Milbau A, Nijs I (2014) Alien roadside species more easily invade alpine than lowland plant communities in a subarctic mountain ecosystem. PLoS One 9:1–10. https://doi.org/10.1371/journal.pone.0089664

Lembrechts JJ, Pauchard A, Lenoir J, et al (2016) Disturbance is the key to plant invasions in cold environments. Proc Natl Acad Sci U S A 113:14061–14066. https://doi.org/10.1073/pnas.1608980113

Lenoir J, Hattab T, Pierre G (2017) Climatic microrefugia under anthropogenic climate change: implications for species redistribution. Ecography (Cop) 40:253–266. https://doi.org/10.1111/ecog.02788

Lenoir J, Svenning JC (2015) Climate-related range shifts - a global multidimensional synthesis and new research directions. Ecography (Cop) 38:15–28. https://doi.org/10.1111/ecog.00967

Liedtke R, Barros A, Essl F, et al (2020) Hiking trails as conduits for the spread of non-native species in mountain areas. Biol Invasions 22:1121–1134. https://doi.org/10.1007/s10530-019-02165-9

Lüdecke D (2018) ggeffects: Tidy Data Frames of Marginal Effects from Regression Models. J Open Source Softw 3:772. https://doi.org/10.21105/joss.00772

Marini L, Bona E, Kunin WE, Gaston KJ (2011) Exploring anthropogenic and natural processes shaping fern species richness along elevational gradients. J Biogeogr 38:78–88. https://doi.org/10.1111/j.1365-2699.2010.02376.x

McDougall KL, Khuroo AA, Loope LL, et al (2011) Plant invasions in mountains: Global lessons for better management. Mt Res Dev 31:380–387. https://doi.org/10.1659/MRD-JOURNAL-D-11-00082.1

McDougall KL, Lembrechts J, Rew LJ, et al (2018) Running off the road: roadside non-native plants invading mountain vegetation. Biol Invasions 20:3461–3473. https://doi.org/10.1007/s10530-018-1787-z

Molina-Montenegro MA, Quiroz CL, Torres-Díaz C, Atala C (2011) Functional differences in response to drought in the invasive Taraxacum officinale from native and introduced alpine habitat ranges. Plant Ecol Divers 4:37–44. https://doi.org/10.1080/17550874.2011.577459

Müllerová J, Vítková M, Vítek O (2011) The impacts of road and walking trails upon adjacent vegetation: Effects of road building materials on species composition in a nutrient poor environment. Sci Total Environ 409:3839–3849. https://doi.org/10.1016/j.scitotenv.2011.06.056

Muñoz AA, Cavieres LA (2008) The presence of a showy invasive plant disrupts pollinator service and reproductive output in native alpine species only at high densities. J Ecol 96:459–467. https://doi.org/10.1111/j.1365-2745.2008.01361.x

New E, To I, Ecology IN, Invasions INS (2007) CONCEPTS & SYNTHESIS. 88:3–17

Norambuena H, Escobar S, Rodriguez F (2000) The Biocontrol of Gorse , Ulex europaeus , in Chile : A Progress Report. Mont Mag West Hist 961:955–961

Oksanen J (2009) Design decisions and implementation details in vegan. Design 2:1–11

Paiaro V, Cabido M, Pucheta E (2011) Altitudinal distribution of native and alien plant species in roadside communities from central Argentina. Austral Ecol 36:176–184. https://doi.org/10.1111/j.1442-9993.2010.02134.x

Pallardy SG (2002) Acli.Pdf. New York 68:270–334

Pauchard A, Alaback PB (2004) Influence of Elevation, Land Use, and Landscape Context on Patterns of Alien Plant Invasions along Roadsides in Protected Areas of South-Central Chile. Conserv Biol 18:238–248. https://doi.org/10.1111/j.1523-1739.2004.00300.x

Pauchard A, Kueffer C, Dietz H, et al (2009) Ain't no mountain high enough: Plant invasions reaching new elevations. Front Ecol Environ 7:479–486. https://doi.org/10.1890/080072

Pauchard A, Milbau A, Albihn A, et al (2016) Non-native and native organisms moving into high elevation and high latitude ecosystems in an era of climate change: new challenges for ecology and conservation. Biol Invasions 18:345–353. https://doi.org/10.1007/s10530-015-1025-x

Pérez-Escobar OA, Zizka A, Bermúdez MA, et al (2022) The Andes through time: evolution and distribution of Andean floras. Trends Plant Sci 27:364–378. https://doi.org/10.1016/j.tplants.2021.09.010

Petitpierre B, McDougall K, Seipel T, et al (2016) Will climate change increase the risk of plant invasions into mountains? Ecol Appl 26:530–544. https://doi.org/10.1890/14-1871

Pyšek P, Hulme PE, Simberloff D, et al (2020) Scientists' warning on invasive alien species. Biol Rev 95:1511–1534. https://doi.org/10.1111/brv.12627

Quiroz CL, Cavieres LA, Pauchard A (2011) Assessing the importance of disturbance, site conditions, and the biotic barrier for dandelion invasion in an Alpine habitat. Biol Invasions 13:2889–2899. https://doi.org/10.1007/s10530-011-9971-4

Raboin ML, Posner JL (2012) Pine or pasture? estimated costs and benefits of land use change in the peruvian andes. Mt Res Dev 32:158–168. https://doi.org/10.1659/MRD-JOURNAL-D-10-00099.1

Rew LJ, McDougall KL, Alexander JM, et al (2020) Moving up and over: redistribution of plants in alpine, Arctic, and Antarctic ecosystems under global change. Arctic, Antarct Alp Res 52:651–665. https://doi.org/10.1080/15230430.2020.1845919

Rivas-Martínez S (2010) Global Bioclimatics. 58

Ruiz D, Moreno HA, Gutiérrez ME, Zapata PA (2008) Changing climate and endangered high mountain ecosystems in Colombia. Sci Total Environ 398:122–132. https://doi.org/10.1016/j.scitotenv.2008.02.038

Sandoya V, Pauchard A, Cavieres LA (2017) Natives and non-natives plants show different responses to elevation and disturbance on the tropical high Andes of Ecuador. Ecol Evol 7:7909–7919. https://doi.org/10.1002/ece3.3270

Sanguinetti J, Buria L, Mamierca L, et al (2014) Manejo de especies exóticas invasoras en Patagonia, Argentina: Priorización, logros y desafíos de integración entre ciencia y gestión identificados desde la Administración de Parques Nacionales. Ecol Austral 183–192

Seipel T, Kueffer C, Rew LJ, et al (2012) Processes at multiple scales affect richness and similarity of non-native plant species in mountains around the world. Glob Ecol Biogeogr 21:236–246. https://doi.org/10.1111/j.1466-8238.2011.00664.x

Speziale KL, Lambertucci SA, Carrete M, Tella JL (2012) Dealing with non-native species: What makes the difference in South America? Biol Invasions 14:1609–1621. https://doi.org/10.1007/s10530-011-0162-0

Teller BJ, Zhang R, Shea K (2016) Seed release in a changing climate: Initiation of movement increases spread of an invasive species under simulated climate warming. Divers Distrib 22:708–716. https://doi.org/10.1111/ddi.12436

Thomas E, van Damme P, Goetghebeur P (2010) Some factors determining species diversity of prepuna and puna vegetations in a Bolivian andes region. Plant Ecol Evol 143:31–42. https://doi.org/10.5091/plecevo.2010.416

Tomiolo S, E. Hulme P, P. Duncan R, A. Harsch M (2016) Influence of climate and regeneration microsites on Pinus contorta invasion into an alpine ecosystem in New Zealand. AIMS Environ Sci 3:525–540. https://doi.org/10.3934/environsci.2016.3.525

Urbina JC, Benavides JC (2015) Simulated Small Scale Disturbances Increase Decomposition Rates and Facilitates Invasive Species Encroachment in a High Elevation Tropical Andean Peatland. Biotropica 47:143–151. https://doi.org/10.1111/btp.12191

Valencia J, Lassaletta L, Velázquez E, et al (2013) Factors Controlling Compositional Changes in a Northern Andean Páramo (La Rusia, Colombia). Biotropica 45:18–26. https://doi.org/10.1111/j.1744-7429.2012.00895.x

Valfré-Giorello TA, Torres RC, Barri FR, Renison D (2019) Control mecánico del árbol no nativo Ligustrum lucidum (Oleaceae): supervivencia, regeneración y costos. Boletín la Soc Argentina Botánica 54:93–104. https://doi.org/10.31055/1851.2372.v54.n1.23588

van Wilgen BW (2012) Evidence, perceptions, and trade-offs associated with invasive alien plant control in the Table Mountain National Park, South Africa. Ecol Soc 17:. https://doi.org/10.5751/ES-04590-170223

Vásquez DLA, Balslev H, Sklenář P (2015) Human impact on tropical-alpine plant diversity in the northern Andes. Biodivers Conserv 24:2673–2683. https://doi.org/10.1007/s10531-015-0954-0

Wang W, Yan J (2021) Shape-Restricted Regression Splines with R Package splines2. J Data Sci 19:498–517. https://doi.org/10.6339/21-jds1020

Wickham H (2008) ggplot2: Elganta graphics for data analysis

Figure 1. Non-native plants that grow associated with anthropogenic disturbances (presence of a road) in the highest elevation areas of the Southern Andean Steppe. a) *Acacia dealbata* growing on the roadside in the Southern Andes (38°41´05S; 71°47´56´´E) at an elevation of 1,479 m.a.s.l, above the tree line of *Araucaria araucana* forest; b) *Verbascum virgatum* growing on the roadside in the South and Central Andes (37°37´35´´S; 71°35´71´´E) at an elevation of 1,401 m.a.s.l, above the tree line, in volcanic soils; c) *Lupinus polyphyllus* growing by the roadside in the subantarctic Andes (46°03´50´´S; 72°00´51´´E) at an elevation of 1014 m.a.s.l; d) *Echium vulgare* growing on the roadside in the South and Central Andes (36°91´25´´S; 71°42´51´´E) at an elevation of 1,527 m.a.s.l.

Figure 2. Grouping of Jaccard similarity measures of the non-native plant communities among the main countries and regions along the Andes mountain range. Páramo= Ecuador and Venezuela; Puna= Bolivia, Southern Andean Steppe= Argentina , Central Chile, South Chile and Subantarctic Chile.

Figure 3. A, B, C. A) Patterns in non-native plant species richness along latitudinal and elevational gradients in the Andes Mountains, separately by biogeographic zone: Páramo (top, Venezuela and Ecuador), Puna (middle, Bolivia), Southern Andean Steppe (bottom, Argentina, central Chile, South Andes, subantarctic Chile). The vertical lines represent the elevation range of the tree line in each of the studied sites. In the páramo, the treeline is situated between 3,400-3,600 m a.s.l. In the Puna, it ranges from 3,700 to 3,900 m a.s.l. Lastly, in the southern Andean steppe, the treeline occurs at elevations between 1,600-1900 m a.s.l. The vertical lines correspond to the elevational range of the tree line for each of the studied sites, . B) The location of each region for which data have been included, colored as in A) presented on a background map of South America showing elevation (m a.s.l.). C) Latitudinal pattern of non-native plants richness in Andean ecosystems 8°N to -55°S. For model coefficients of the associated generalized linear mixed models, see Table 2.