



Anthropogenic factors overrule local abiotic variables in determining non-native plant invasions in mountains

Eduardo Fuentes-Lillo · Jonas J. Lembrechts · Lohengrin A. Cavieres · Alejandra Jiménez · Sylvia Haider · Agustina Barros · Aníbal Pauchard

Received: 23 October 2020 / Accepted: 7 July 2021
© The Author(s), under exclusive licence to Springer Nature Switzerland AG 2021

Abstract The factors that determine patterns of non-native species richness and abundance are context dependent in both time and space. Global change has significantly boosted plant invasions in mountains, therefore, understanding which factors determine the invasion and at what scale they operate are fundamental for decision-making in the conservation of mountain ecosystems. Although much evidence has been gathered on the patterns of non-native species in mountain ecosystems, little is known about what

specific abiotic, biotic, or anthropogenic factors are driven such patterns. Here, we assessed the importance of anthropogenic, biotic, and abiotic factors at two spatial scales as drivers of plant invasions along three roads in south-central Chile. We sampled non-native plant richness and abundance, and each of these explanatory factors, in-situ in 60 transects in disturbed areas and adjacent undisturbed vegetation. Low elevation areas were the most invaded, with patterns of richness and abundance driven mainly by anthropogenic factors, explaining between 20 and 50% of the variance for the three roads. Only for the abundance of non-native species along the road in the Malalcahuello

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10530-021-02602-8>.

E. Fuentes-Lillo (✉) · A. Jiménez · A. Pauchard
Laboratorio de Invasiones Biológicas (LIB), Facultad de Ciencias Forestales, Universidad de Concepción, Concepción, Chile
e-mail: eduafuentes@udec.cl

E. Fuentes-Lillo · J. J. Lembrechts
Research Group of Plants and Ecosystems (PLECO), University of Antwerp, Wilrijk, Belgium

E. Fuentes-Lillo · L. A. Cavieres
Departamento de Botánica, Facultad de Ciencias Naturales Y Oceanográficas, Universidad de Concepción, Concepción, Chile

E. Fuentes-Lillo
School of Education and Social Sciences, Adventist University of Chile, Chillán, Chile

L. A. Cavieres · A. Jiménez · A. Pauchard
Instituto de Ecología Y Biodiversidad (IEB), Santiago, Chile

S. Haider
Institute of Biology / Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle, Germany

S. Haider
German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

A. Barros
Instituto Argentino de Nivología, Glaciología Y Ciencias Ambientales (IANIGLA), CONICET, CCT-Mendoza, Mendoza, Argentina

National Reserve, biotic factors were more important (45% of the variance). At the regional scale, the abundance of non-native species was again explained best by anthropogenic factors (24% of the variance), yet non-native richness was driven most strongly by abiotic factors such as soil nitrogen content and pH (15% of the variance). Our results confirm the conclusions from experimental studies that anthropogenic factors override abiotic factors and are important drivers of non-native species at local and regional scales and that non-native plant invasion in mountains is currently not strongly limited by climate.

Keywords Andes mountains · Invasive species · Non-native species · Human settlement · Protected areas

Introduction

Although the presence of non-native species has become increasingly common in mountain regions, so far, the levels of invasions have shown to be relatively low (Pauchard et al. 2009; McDougall et al. 2011; Marini et al. 2013; Fuentes-Lillo and Pauchard 2019). As in other ecosystems, the invasion process in mountain ecosystems is defined by the interaction between abiotic conditions, biotic interactions, and propagule pressure (Catford et al. 2009). Mountains, however, show interesting specific complexities on the factors that drive and limit invasions and how they vary among regions with different environmental contexts (Alexander et al. 2016; McDougall et al. 2018). In general, anthropogenic factors can increase the success of the invasion since they function as vectors for the transport of propagules and modify the biotic and abiotic conditions that facilitate the establishment of non-native species (Van Der Wal et al. 2008, Catford et al. 2009; Pauchard et al. 2009; Pollnac et al. 2012; Cabra-Rivas et al., 2015, Lembrechts et al. 2017). Most studies of plant invasions in mountains have used elevation as a proxy for a multitude of intertwined variables, such as climate, anthropogenic disturbance and ecosystem types to explain the changing patterns of richness and abundance of non-native species (Pauchard et al. 2009; Seipel et al. 2012). However, few studies have disentangled the mechanistic factors underlying these

patterns, as both observational and experimental studies have shown that these drivers (abiotic, biotic and anthropogenic) are context dependent and vary both in time and on spatial scales (Kumar et al. 2006; Pauchard and Shea 2006; Dray et al. 2012).

Probably the most obvious constraints for plant invasions in mountains are abiotic factors, in particular climate harshness associated to higher elevation (Pauchard et al. 2009). It has been shown that the decrease in the richness of non-native species in the mountains is mainly associated with the large-scale climatic gradients (i.e. temperature and precipitation) determined by elevation (Seipel et al. 2012; Alexander et al. 2016; Haider et al. 2018). At smaller scales, one can see the additional importance of abiotic factors (e.g. soil temperature, soil moisture, nitrogen, pH) as local drivers of the fine-grained richness patterns of non-native species in mountain ecosystems (Buri et al. 2017; Gantchoff et al. 2018; Lembrechts et al. 2018).

Recently, there has been increasing interest in understanding how biotic interactions drive invasive species distribution in mountains. For example, several studies have identified a key role for facilitating interactions in establishing non-native species at the smallest scale (Cavieres et al. 2005, 2007; Badano et al. 2015). Competitive interactions on the other hand are more intense at low elevations. As abiotic conditions become more adverse for growth, facilitation is a key process to explain the presence of non-native species in higher elevation areas (Cavieres et al. 2007; Badano et al. 2015; Alexander et al. 2016). Nevertheless, experimental studies have shown that biotic interactions with the established community can remain negative for non-native plant invaders, even at high elevations (Lembrechts et al. 2016). It has also been observed that more productive communities generate greater resistance to the invasion of non-native species (Pearson et al. 2018). For example, it has been observed in mountain ecosystems in Argentina that the number of non-native species decreases significantly with increasing coverage of native species (Pearson et al. 2018), while in sub-arctic mountain ecosystems where native species richness functions as a filter to explain the decrease in establishment of non-native species, while abiotic factors, mainly temperature explains the presence of non-native species at landscape and regional scales, which is related to the spatial environmental heterogeneity hypothesis, indicating that as environmental

variability (spatial variability) increases, the greater the number of non-native species (Souza et al. 2011; Haider et al. 2018). A deeper understanding of biotic factors is thus needed to explain how biotic interactions (competition and/or facilitation) and the productivity of native ecosystems at multiple scales explain the current patterns of distribution of non-native species in mountains (Wisz et al. 2013).

Propagule pressure and the role of disturbance have been studied in mountain ecosystems using proximity to the road and the presence of human activities as indirect proxies (Seipel et al. 2012). Roads and other corridors have been shown to be key to understanding the presence of non-native species at higher elevations (Alexander et al. 2009; Seipel et al. 2012; Giorgis et al. 2011, 2016; Liedtke et al. 2020). Seed-addition experiments, besides, have identified that an increase in propagule pressure can explain the abundance of non-native species along elevation gradients (Lockwood et al. 2005; McGlone et al. 2011; Pollnac et al. 2012; Lembrechts et al. 2016). Disturbance is known to work through its modification of the climatic conditions, (changes in climatic extremes through the elimination of vegetation and changes in soil conditions such as pH levels, availability of nutrients and soil moisture, due to the presence of roads in ecosystems) favoring the establishment of non-native species (Müllerova et al. 2011, Haider et al. 2010, 2018; McDougall et al. 2018; Thom et al. 2020). At local scales, disturbance also favors the establishment of non-native species through the removal of vegetation and release of resources, mainly in higher elevation areas (Paiaro et al. 2007; Dainese et al. 2017; Pearson et al. 2018).

As global change will generate significant changes in the climatic patterns, and substantial increases in anthropogenic disturbances (Roques 2010; Gou et al. 2018), understanding the factors that determine non-native plant invasions in mountains is of utmost importance to develop efficient conservation policies for protected areas (Slodowicz et al. 2018). Climate change has been shown to lead to increased invasion events, especially at higher elevations (Oke and Thompson 2015; Petitpierre et al. 2016; Shrestha et al. 2018). Additionally, increasing globalization, in mountains, represented by population increases, tourist centers, infrastructure, will have a direct impact on the dispersion and establishment of non-native species (Terzano et al. 2018).

Due to their extremely high climatic and anthropogenic heterogeneity, which allows both observational and experimental studies with a multi-scale approach, mountains are a unique natural laboratory for the study of invasion processes (Pauchard et al. 2009; Alexander et al. 2016; Kueffer et al. 2014). In Chile, mountains provide extremely valuable ecosystem services (e.g. water, recreation), and they represent biodiversity hotspots with high levels of native and endemic species (Lara et al. 2009; Fuentes-Castillo et al. 2019; Fuentes-Lillo and Pauchard 2019). During the last decades, however, human activities associated with tourism, agriculture, mining and forestry have been progressively degrading these ecosystems in Chile (Pauchard and Alaback 2004), and worldwide (Pauchard et al. 2009, 2016).

In this work, we aim to disentangle the importance of the main factors (abiotic, biotic and anthropogenic), that define at local and regional levels the richness and abundance of non-native species along altitudinal gradients in the central-southern Chilean Andes. Propagule pressure was not included in the study due to its high correlation with anthropogenic variables, such as the proximity to human settlements and the distance to road (Pollnac et al. 2012). The study ecosystems are inserted within a matrix of anthropogenic land-uses, with urban centers and agricultural activities in the lowlands and ski and tourist centers at high elevations (Pauchard and Alaback 2004), which means that each elevational gradient that makes up the central-southern Chilean Andes has vegetational, climatic and topographic characteristics that cause the factors that explain the richness and abundance patterns of non-native plants to vary according to each elevational gradient analyzed (Pauchard et al. 2013).

Furthermore, these areas are influenced by natural disturbance processes resulting from volcanic eruptions and natural fire cycles that have given these mountains unique characteristics, both regarding their climate and their floristic composition (González et al. 2010). Thus, the central-southern Chilean Andes are particularly suitable to investigate the role of the different drivers of the invasion process, both from a theoretical point of view and due to the implications for the management and control of non-native species in a disturbed mountain area in an era of global change. Specifically, we aim to answer the following questions: 1) What are the main factors that determine the richness and abundance of non-native species in

the central-southern Andes of Chile? And 2) How do the drivers of richness and abundance of non-native species change from a local (one road) to a regional scale (across all three roads). We hypothesize that at local levels, anthropogenic factors, such as the distance of the road and the distance to human settlements, better explain species richness and abundance patterns for non-native species, while at the regional level abiotic factors like temperature would be more important (Seipel et al. 2012; Lembrechts et al. 2016; Haider et al. 2018). While we anticipate a certain role for biotic factors (i.e., diversity and productivity proxies as a measure of invasibility of the established vegetation), we hypothesize them to be overruled by anthropogenic and abiotic factors, mainly due to the high environmental heterogeneity and high anthropogenic disturbance that predominate in the mountain ecosystems of central-southern Chile, which have historically defined the biodiversity patterns in these ecosystems (Echeverria et al. 2006; Haider et al. 2018).

Methods

Site description

We selected three roads in the Andes mountain range, in the central-south zone of Chile (from 37° S to 39° S): Laguna Laja National Park (LLNP) (37° 38' 45" S, 71° 38' 25" W), Malalcahuello National Reserve (MNR) (38° 43' 49" S, 71° 48' 82" W) and Conguillio National Park (CNP) (39° 41' 17" S, 71° 47' 32" W). The three roads were selected due to the wide environmental gradient they cover, associated with altitudinal gradients ranging from ~ 400 to ~ 1600 m a.s.l. In addition, these roads have year-round vehicular traffic and intense anthropogenic pressure resulting from agricultural activities and tourism. These three roads have similar bioclimatic conditions and composition of native and non-native vegetation (Luebert and Plissock 2017). The roads are located in a xeric bioclimate (Luebert and Plissock 2017). The low elevation areas are dominated by Mediterranean deciduous forests of *Nothofagus obliqua* and *Cryptocarya alba* and temperate deciduous forests of *N. obliqua* and *Persea lingue*. Intermediate elevations are dominated by temperate Andean deciduous forests of *N. alpina* and *Dasyphyllum diacanthoides*. High

elevations are characterized by Andean resinous forests of *Araucaria araucana* and *Festuca scabriuscula* and, in some areas, scrublands of *Discaria chacaya* and *Berberis empetrifolia* (Luebert and Plissock 2017).

Sampling design

To determine the main factors (abiotic, biotic and anthropogenic) that drive non-native species richness and abundance (response variables), we used the standardized survey design proposed by the Mountain Invasion Research Network as described in Seipel et al. (2012). 20 T-shaped transects were installed along each of the three roads. The transects were placed along an elevation gradient ranging from ~ 400 to 1600 m a.s.l. (individual elevation ranges depending on road conditions) in a stratified way, each transect with an altitudinal separation of approximately 100 m. The T-transects consisted each of three 50 m × 2 m plots, with one plot parallel to the road (hereafter called 'roadside') and two plots perpendicular to the road pointing into the adjacent vegetation (an intermediate plot that goes from 2 to 52 m and an interior plot from 52 to 102 m). In each plot all non-native species were recorded and their abundance was measured based on the number of individuals or ramets per plot, assigning a value of 1 (1–10 individuals), 2 (10–100 individuals) or 3 (> 100 individuals) (Seipel et al. 2012). A list of abiotic, biotic and anthropogenic variable was recorded along the roadside and in the adjacent vegetation as detailed below (Table S1). To evaluate the effect of the scale, models were made for each road individually (local scale) and models that include the data of the three roads together (regional scale).

Abiotic variables

To determine the relationship between species richness and abundance of non-native species and abiotic variables, we measured local soil and air temperature, soil humidity and key soil biogeochemical parameters. All variables were measured both in the roadside and in the adjacent vegetation (52 m from the road). Temperature was recorded using iButton sensors (DS1922L, www.maximintegrated.com, measuring every hour for a period of 1 year) at 5 cm depth (soil temperature) and at 1 m height (air temperature). We

calculated growing degree days (GDD soil and air) from these time series as the sum of all daily averages above 5 °C during the growing season (the months of December to February were used, corresponding to the summer season in these ecosystems) (Lembrechts et al. 2016). Soil moisture was measured in each plot at least three times during the growing season (three months, December to February), using a FieldScout TDR 100 soil moisture meter. Finally, in each plot (roadside and adjacent vegetation), 100 g of soil (horizon A) was sampled, consisting of 3 subsamples of soil randomly distributed in each plot (roadside and adjacent vegetation), adding up to approximately 100 g of soil. The soil sampling was carried out during the growing season, and soil was analyzed for soil C / N-ratio, total carbon and nitrogen, nitrate (NO₃⁻), ammonium (NH₄⁺), organic matter (OM) and pH. The analyses were carried out at the Soil, Water and Forest Research laboratory at the Universidad de Concepcion.

Biotic variables

Four variables were recorded in each plot of the T-transects to represent diversity, productivity and invasibility of the native community. Native species richness and abundance were recorded following the same three-point scale as described above for non-native species. Cover of herbs and trees was estimated visually in each plot following a pseudo-log scale from 1 to 8 (1 = up to 1%; 2 = 1–5%; 3 = 6–25%; 4 = 26–50%, 5 = 51–75%, 6 = 76–95%, 7 = 96–100%) (Seipel et al. 2012).

Anthropogenic variables

To assess the influence of anthropogenic disturbances, four variables were recorded in each plot. This included presence/absence agricultural activities (cultivation and livestock), level of (anthropogenic) disturbance, distance to the road, and proximity to human settlements. The level of anthropogenic disturbance was measured on a three-point scale including 0 (no disturbance of vegetation or soil), 1 (moderate disturbance in less than 50% of the plot) and 2 (severe disturbance in more than 50% of the plot). Disturbance consisted of any removal of the vegetation by human factors, like the presence of trails, fire or livestock and cultivation. Distance to the

road was measured in situ in the middle of the plot at the time of establishing the plots using a handheld GPS, these values were fixed for each transect and each road, and correspond to 1 m for the plot parallel to the road, 27 m and 77 m for plots 2 and 3 that are located adjacent to the road. Finally, the proximity to human settlements was measured from each plot (road and adjacent vegetation) to the edge of the closest human settlement, using GPS positions and a geographic information system (GIS; ArcView 3.3) (Tomasetto et al. 2013; Bjørvik et al. 2015). We considered as human settlements any type of building (e.g. villages, farms) that presents a constant flow of people throughout the year. Mountain shelters and buildings for use by ranchers, which are common in these areas, were thus excluded, as they are only irregularly occupied.

Data analysis

All data analyses were run in R version 3.6.1 (R Core Team 2019).

To determine the correlation between each variable within each group (abiotic, biotic and anthropogenic) including the response variables, a Pearson correlation analysis was performed. Using the *ggplot* package, a correlation matrix was constructed, using a threshold of $R^2 > 0.75$ to determine collinearity between the variables (Fig. S1a, b, c). Additionally, all independent variables were plotted as a function of elevation, using the *ggplot* package (if variables were significantly correlated, only the most ecologically relevant variable was included in the following models) (Fig. S2).

To assess the importance of the abiotic, biotic and anthropogenic factors on the non-native species richness and abundance at local (along one road) and regional (across all three roads) scales, we used generalized linear mixed-effects models (GLMMs, using the “*lmer*” function in the package *lme4*). GLMMs were constructed for each road separately, with transect number as a random effect, for the local scale, and with transect nested in road as a random effect for all roads together for the regional scale. All models were adjusted to a Poisson distribution error with logit log. We made separate models for non-native richness and abundance and for each separate group (abiotic, biotic and anthropogenic), using all correlated variables for each group. We selected the best model for each group using the Akaike

Information Criterion (AIC), where the best model is the one with the lowest AIC-value (Venables and Ripley 2002, package MuMIn, Barton 2016). Importantly, elevation was not included in any of the models, because it correlates strongly with the majority of the analyzed variables (e.g. temperature or nitrogen content) so it was only used at the time of plotting for visualization of the most important variables.

Next, to determine the relative importance of each of the three groups as driver of non-native species richness and abundance, models were constructed for each response variable with the three most significant variables that were determined using the group-specific GLMMs above (Table S2). Then, for each response variable (richness and abundance) and for each spatial scale (local and regional), the percentage of variance explained by each group (abiotic, biotic and anthropogenic (Table S2)) was determined using a variance partitioning approach (Lembrechts et al. 2016). By using three variables for each group, we ensure a fair comparison of explained variance across all groups. We calculated for each model the marginal R^2 (fixed effects) and the conditional R^2 (full model) using the *r.squaredGLMM* function of the *MuMIn* package (Table S3) (Barton 2016). To determine the relative importance of each group, a series of models were constructed with (I) only one focus group, (II) all groups except the focus group, and (III) the complete best model with all explanatory variables. We then calculated for each group the differences between the marginal R^2 of the full model and the model without the focal variable and divided by the marginal R^2 value of the full model (Table S3) (Lembrechts et al. 2016).

Results

Along all three roads, non-native species richness decreased with elevation. Non-native species abundance decreased as a function of elevation only for the CNP and MNR roads (the latter with a small increase at high elevations), while for the LLNP it increases towards mid-elevations with a peak near 800 m.a.s.l, followed by a linear decrease with elevation (Fig. 1).

Factors that determine the abundance of non-native species at different scales

Except for the MNP road, anthropogenic factors were the most important driver to explain the abundance of non-native species at the local scale (Table 1, Fig. 4). The abundance of non-native species decreases with increasing distance to human settlements (2 out of 3 models, Fig. 2d, f), increases with the presence of human disturbances (Table S2, Fig. S3 d) and the presence of human activities (Table S2, Fig S3 f). For the MNP road, the most parsimonious model was the biotic model (Table 1, Fig. 4), with the abundance of non-native species decreasing with increasing abundance of native species and herbaceous cover (Table S2, Fig. 2e, Fig S3e). On a regional scale, the abundance of non-native species was explained by anthropogenic factors (Table 1, Fig. 4), where the abundance of non-native species decreases with increasing distance to human settlements, while the abundance of non-native species increases with the presence of agricultural activities (Table S2, Fig. 3c, d).

Factors that determine the richness of non-native species at different scales

Anthropogenic factors were the most important driver to explain the richness of non-native species at local scales (Table 1, Fig. 4). The richness of non-native species decreases with increasing distance to human settlements (3 out of 3 models, Fig. 2a, b, c) and with distance to the road (Table S4, Fig. S3 a, b), while an increase in the richness of non-native species is observed with the presence of agricultural activities (Table S4, Fig. S3 c). On a regional scale, the richness of non-native species is explained by abiotic factors (Table 1, Fig. 4), with an increase in the richness of non-native species as the ammonium content increases and the pH decreases (Table S2, S3, Fig. 3a, b).

Finally, both for the abundance and richness of non-native species for the different spatial scales, there is a significant amount of inexplicable variance (Table 1, Fig. 4).

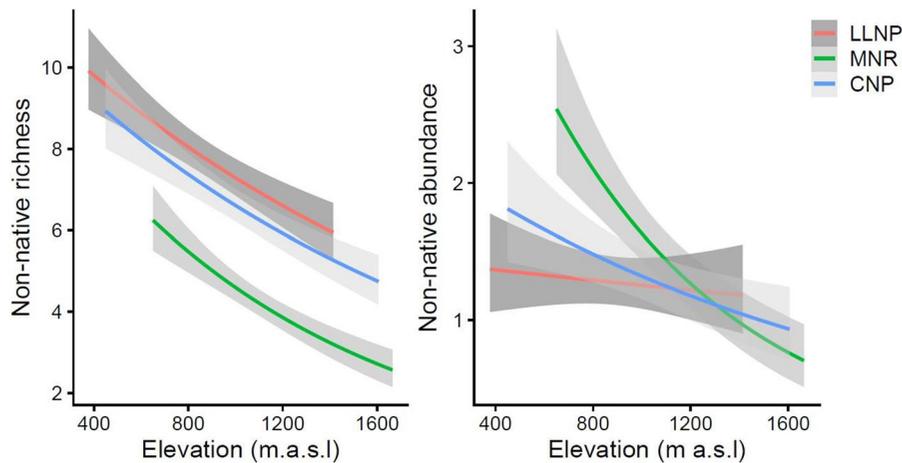


Fig. 1 Elevational patterns of richness and abundance of non-native species along each studied mountain road. Plots include model estimate (line), and 95% confidence intervals (gray

shading). LLNP (Laguna Laja National Park), MNR (Malacahuello National Reserve), CNP (Conguillio National Park). (Color figure online)

Table 1 Values of R^2 , AIC are shown for each scale (local, i.e. separately for each road, and regional) and for each group analyzed (abiotic, biotic and anthropogenic), both for the richness and abundance of non-native species

	Non-native richness		Non-native abundance	
	R^2	AIC	R^2	AIC
<i>LLNP</i>				
Abiotic	0.207	866.3	0.196	859.5
Biotic	0.017	901.1	0.047	885.3
Anthropogenic	0.259	855.4	0.246	847.3
<i>MNP</i>				
Abiotic	0.181	724.6	0.141	952.9
Biotic	0.179	725.0	0.432	882.2
Anthropogenic	0.190	722.8	0.301	907.3
<i>CNP</i>				
Abiotic	0.348	867.7	0.068	906.4
Biotic	0.134	915.0	0.079	904.5
Anthropogenic	0.437	834.5	0.278	865.1
<i>Regional</i>				
Abiotic	0.155	2636.2	0.030	2776.4
Biotic	0.090	2697.2	0.062	2758.2
Anthropogenic	0.019	2662.8	0.238	2656.7

Lower AIC values show the best model for each scale (in bold). *LLNP* (Laguna Laja National Park), *MNR* (Malacahuello National Reserve), *CNP* (Conguillio National Park)

Discussion

As hypothesized, anthropogenic factors were the most important drivers of both the richness and abundance of non-native species at the local scale, with an important role for the proximity to human settlements and the presence of agricultural activities and distance to the road. These factors have been identified as important drivers of plant invasions in other mountain ecosystems across the globe, for example in Argentina (Paiaro et al. 2011), Norway (Lembrechts et al. 2014, 2016; Clavel et al., 2021), Canary Island (Otto et al. 2014), Chile (Pauchard and Alaback 2004), Yellowstone National Park (Pollnac et al. 2012), Ecuador (Sandoya et al. 2017) and Bolivia (Fernández-Murillo et al., 2015). In all these studies, significantly more non-native species were found next to roads compared to more natural habitats away from roads, both at low and high elevations (Seipel et al. 2012; Haider et al. 2018). It is important to note that each road presents different biotic and environmental conditions associated with the local topography and anthropogenic disturbances specific to each road, which explains why the factors that explain the richness and abundance vary according to the spatial scale. This local-scale variation influences and alters regional-scale environmental patterns, this is typical of environmental gradients such as mountain ecosystems (López Angulo et al. 2018). For example, local topography (aspect or slope) can influence local soil

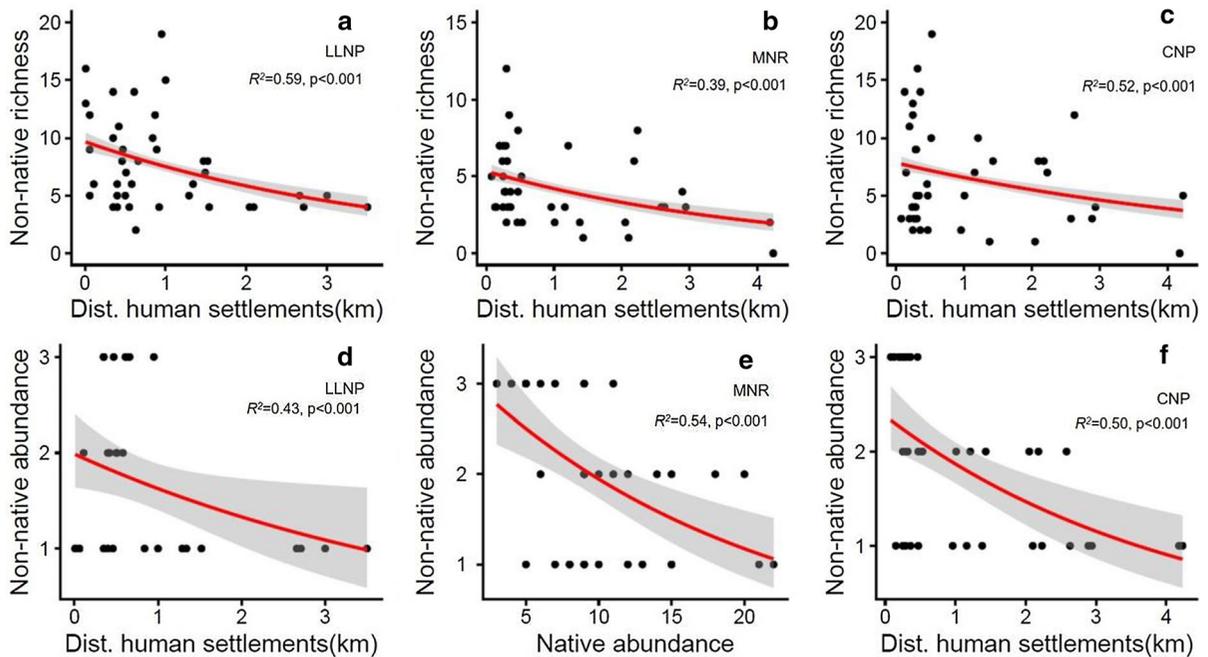


Fig. 2 Graphical representation of the most important variables that make up the best models to explain the richness (a–c) and abundance (d–f) of non-native species at the local scale. Plots include model estimates (red line, from models with a logarithmic correction), and 95% confidence intervals (gray

shading). LLNP (Laguna Laja National Park), MNR (Malcalahuello National Reserve), CNP (Conguillio National Park). For additional variables retained in the final models, see Fig S2. (Color figure online)

quality that increases productivity at local scales, which affects patterns of richness and abundance at regional scales (Eilts et al. 2011).

The importance of roads for explaining patterns of richness and abundance of non-native species represent multiple underlying factors. First of all, roads serve as a vector for the transport of propagules (Pauchard et al. 2009; Taylor et al. 2012; Lembrechts et al. 2014), yet they also modify soil biogeochemical conditions (pH, nitrogen, humidity) (Johnston and Johnston 2004; Lembrechts et al. 2014; Clavel et al., 2021), microclimate (Lembrechts et al. 2016) and native vegetation cover (Pauchard and Alaback 2004). These changes in the microhabitat under the influence of the disturbances associated with the road facilitates non-native species establishment, especially of ruderal species (Lembrechts et al. 2014). In addition to the effects of roads on non-native richness and abundance, as expected, the distance to human settlements was even more important in explaining these patterns. Even its importance few studies on mountains plant invasions have included this factor mainly because it

can be correlated with elevation (Haider et al. 2010; Seipel et al. 2012). However, due to the increased popularity of tourism in mountains including the construction of ski resorts and vacation retreats at a range of elevations, it is important to consider human settlements as a separate factor (Barros et al. 2013, 2020).

As a result of human disturbance from roads, including building and maintenance, changes in soil conditions near roadsides are common (Müllerova et al. 2011) and affect non-native plants as has been shown in studies previous (Vonlanthen et al. 2006; Buri et al. 2017) and this study. Specifically, we found at the regional level that increased ammonium (NH_4^+) and a decrease in pH increased the non-native richness. Ammonium, for example, has been proven to be a good indicator of the richness of non-native species at regional scales (Urbina and Benavides 2015; Pearson et al. 2018). Studies conducted in the central Andes in Argentina have found that significant increases in NO_3^- in the soil are positively correlated with the richness and abundance of non-native species

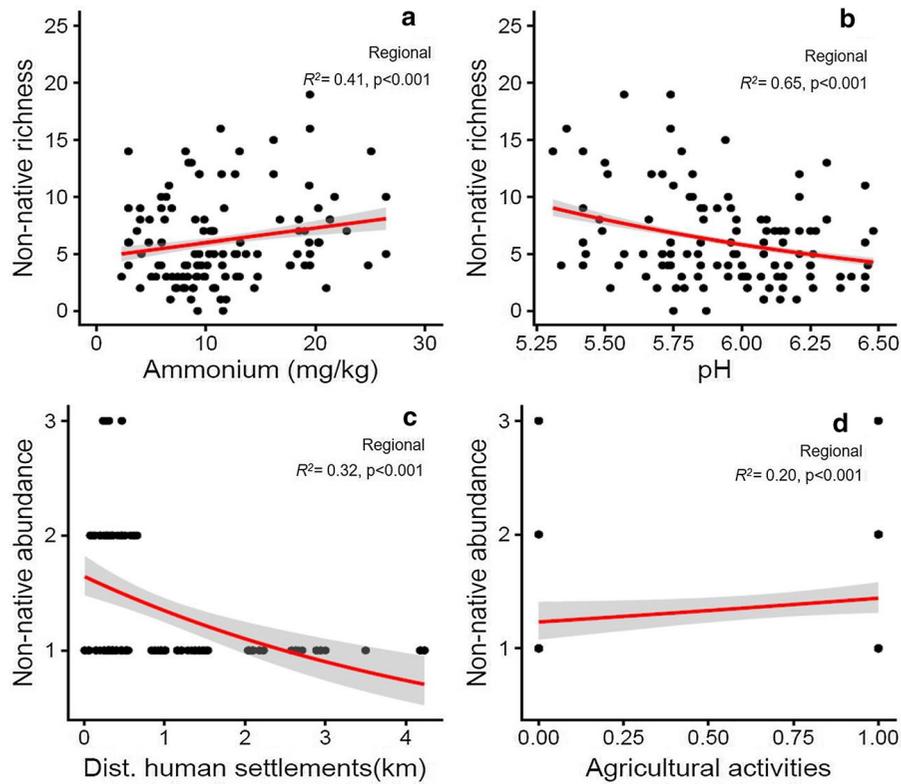


Fig. 3 Graphical representation of the variables that make up the best models of the richness (a-b) and abundance (c-d) of non-native species at the regional scale. Plots include model

estimates (red line, from models with a logarithmic correction), and 95% confidence intervals (gray shading). (Color figure online)

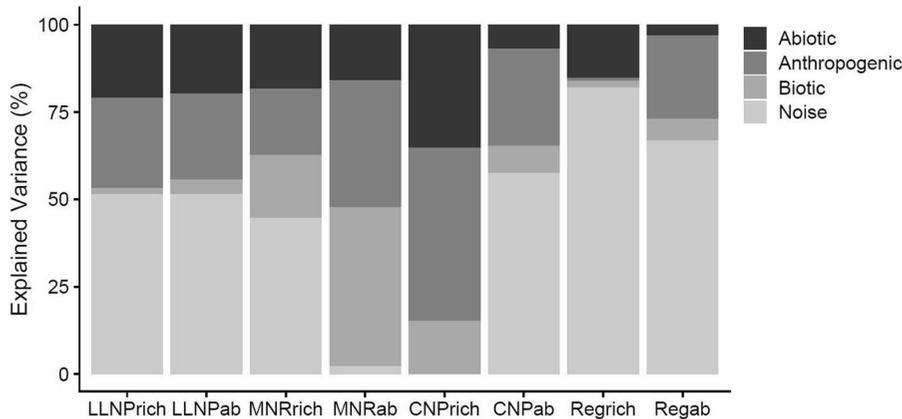


Fig. 4 Total percentage of variance in non-native species richness (rich) and abundance (ab) explained by each factor (abiotic, biotic and anthropogenic) in the best model for each road (local scale), and at the regional scale. Results from a variance partitioning procedure. Noise (percentage of variance

of the data that is not explained by any variable measured in the study) is plotted in light gray. LLNP (Laguna Laja National Park), MNR (Malacahuello National Reserve), CNP (Conguillio National Park). (Color figure online)

(Pearson et al. 2018). The same effect has been found in the Colombian Andes where the addition of nutrients to the soil (mainly nitrogen) facilitated the invasion by the non-native *Pennisetum clandestinum* (Urbina and Benavides et al. 2015). Soil pH has also been shown to be an important parameter to explain the distribution of alpine plant species (Vonlanthen et al. 2006). The pH indeed relates to the concentration of protons, which directly affects plant available minerals (Hossner 2008), with a high pH causing nutrient deficiency in the soil, while low values improve the solubility of toxic metals (Gobat et al. 2004). Therefore, a soil with neutral or slightly acidic pH has the highest nutrient availability (Gobat et al. 2004; Vonlanthen et al. 2006; Hossner 2008; Bury et al. 2017). A study conducted on Bank Peninsula, New Zealand found that soil pH was one of the most important explanatory variables for non-native species richness, out of a series of abiotic, biotic and anthropogenic variables (Tomasetto et al. 2013). Our results confirm that non-native plant richness at the regional scale is determined by abiotic factors (nutrients, temperature, light radiation, pH), where the climatic severity experienced across elevational gradients explains the low richness of non-native plants that manage to establish in higher elevation areas (Pauchard et al. 2009; Seipel et al. 2012).

The critical role of distance to human settlements found in this study may be related to the fact that along most of the roads studied, human settlements are concentrated at low elevations (Fig. S2a), where climatic conditions are more conducive to the growth and development of non-native species (Tomasetto et al. 2013). The lowlands are also the main source of propagules of non-native species (Pauchard and Alaback 2004; Lembrechts et al. 2014) and present high levels of disturbance that eliminate competition and serve as a constant supply of nutrients for the system, significantly favoring the establishment of non-native species (Urbina and Benavides 2015; Lembrechts et al. 2016; Santilli et al. 2018). In sum, distance to human settlements may be an indirect proxy of human footprint and propagule pressure.

We also found a positive effect of the presence of agricultural activities, a variable strongly linked to land use changes along the altitudinal gradient. Anthropogenic land use intensification have been historically concentrated at low elevations (Pauchard and Alaback 2004). Shifts from landscapes dominated

by *Nothofagus sp* forests to grazing pastures and other agricultural uses has favored the establishment and dispersion of non-native species in the region (Pauchard and Alaback 2004), and in many cases, non-native species grasses and herbs have even been deliberately sown to improve forage (Pauchard and Alaback 2004). The importance of these agricultural activities also lies in their modification of microclimatic conditions (by changing from forests to pastures) as well as a constant source of propagules of non-native species (Pauchard and Alaback 2004; Guo et al., 2018; Zellweger et al. 2020). In addition, dispersal processes can be facilitated through the presence of cattle, which functions as a propagation vector for propagules towards higher elevation areas and the forest interior away from roads (Pauchard and Alaback 2004; Seipel et al. 2012; Liedtke et al. 2020). These patterns of land use change, the presence of agricultural activities and the distance to human settlements are the variables that explain the abundance of non-native plants, as they facilitate dispersal and establishment (Marini et al. 2013). It is important to note that at the regional scale, richness is being explained by abiotic factors since climatic severity limits the establishment of non-native plants, while the presence of human activities explains the abundance of non-native plants (Fig. 4). These are mainly associated with the historical removal of native cover that has affected low and medium elevation areas in the mountains of central-southern Chile (Echeverria et al. 2006; Miranda et al. 2015), allowing non-native plants that manage to establish to disperse rapidly due to low biotic resistance and better climatic conditions generated by human disturbances (Lembrechts et al. 2017).

Again, it is important to highlight that anthropogenic disturbances like road building have a large effect on soil conditions like pH and nutrient availability, generally making the soils more alkaline and increasing their nutrient and organic matter content (Müllerova et al. 2011). This relates to the importance of anthropogenic variables as drivers of the abundance of non-native species at regional scales in our study, as has been found in other studies in England (index of human footprint, De Albuquerque et al., 2011), New Zealand (proximity to buildings and roads, Tomasetto et al. 2013) and global mountain ranges (distance to the road, Seipel et al. 2012; Haider et al. 2018; McDougall et al. 2018).

To explain the positive relationships between human disturbance and non-native species richness and abundance, several mechanisms have been proposed. For example, vegetation removal releases a significant amount of resources (nutrients, space etc.), which can be rapidly occupied by non-native species (Barros and Pickering 2014; Barros et al. 2013; Lembrechts et al. 2016). The importance of such vegetation removal has been demonstrated experimentally in mountainous ecosystems of sub-Antarctic Chile and sub-Arctic Norway, where the removal of vegetation was the most important factor throughout the whole invasion process (establishment, growth and flowering) (Lembrechts et al. 2016). Additionally, many of these vegetation removal events interact with dispersal vectors due to the presence of cattle and trails (Liedtke et al., 2020). These factors have specifically been shown to increase the propagule pressure of non-native species such as *Convolvulus arvensis* and *Taraxacum officinale* in Central Andes, Argentina (Barros et al. 2020).

Interestingly, anthropogenic factors were not the main factor along all roads. Indeed, in Malalcahuello National Reserve road, the abundance of native species explained most of the variance in the abundance of non-native species. This road is characterized by densely settled low elevation areas and grasslands dominated by non-native species. But as elevation increases, areas with a high richness of native species can be observed, which would function as a biotic filter for the establishment of non-native species. This pattern coincides with the hypothesis of biotic resistance that indicates that the most diverse communities are more resistant to the invasion of non-native species (Catford et al. 2009; Martin et al. 2009). Additionally, areas with higher herbaceous cover had a lower abundance of non-native species, indicating an important biotic resistance of the native communities towards the population increase of non-native species (De Albuquerque et al., 2011; Phillips-Mao et al. 2014; Lembrechts et al. 2016).

It is important to highlight that abiotic conditions, such as soil and air temperature, were in none of the cases the most important driver at local scales, even though they have been found to be crucial drivers of local invasion in countless other studies, mainly at high elevations (Giraldo-Cañas et al. 2010; Crespo-Pérez et al. 2011; McDougall et al. 2011; Paiaro et al. 2011; Seipel et al. 2012; Tecco et al. 2016; Cuesta

et al. 2017). Our conclusions are however in line with other studies showing that variables such as temperature, precipitation and soil moisture are at local scales usually subjugated by factors such as disturbance and propagule pressure (Pollnac et al. 2012; Tomasetto et al. 2013; Lembrechts et al. 2016; Buri et al. 2017). In fact, the temperature values themselves (expressed as Growing Degree Days in the air and soil) did not vary significantly along the elevation gradient, as local topographical and human-induced heterogeneity overrides the adiabatic lapse rate when measured in-situ (Lembrechts et al. 2017). Additionally, disturbance events create important changes in all these abiotic factors, making disturbance proxies themselves better explanatory variables than the separate abiotic conditions related to climate (Lembrechts et al. 2016).

Finally, it is important to explain that a high percentage (50%) of the variance of the data is not being explained by the factors analyzed in this study, under this context, we can identify at least three factors that may be contributing to explain this percentage of unexplained variance. First, the residence time of non-native species, may explain patterns of declining non-native plant richness and abundance as a function of elevation, assuming that non-native plants have not had sufficient time to colonize and disperse to higher elevation areas (Haider et al. 2010; Alexander et al. 2016). Second, the biogeographic origin, where it has been observed that the richness patterns of non-native plants across the elevational gradient depend on the pre-adaptation to the conditions of the ecosystem to be invaded (Alexander et al. 2011). Observing that plants coming from cold and temperate climate ecosystems are more successful in colonizing higher elevation zones, on the contrary non-native plants coming from temperate ecosystems are more successful in establishing in low elevation zones (Haider et al. 2010; Sandoya et al. 2017). Finally, functional traits (i.e., higher specific leaf area, less thickness and greater nitrogen content) exhibited by some non-native plants may give a competitive advantage over native plants, which could explain the patterns of richness and abundance across elevational gradients found in this study (McDougall et al. 2018; Henn et al. 2019; Kühn et al. 2021).

Management recommendations for non-native species

Our study again highlights the critical role of a wide range of anthropogenic disturbances as drivers of non-native plant invasions in mountains in Chile and across the world, ranging from road building over human settlements to agriculture and tourism. It is therefore key to develop environmental education initiatives about the ecological impact of non-native species for tourists, park ranger, farmer and residents of these vulnerable ecosystems. Based on this, it is also necessary to generate control and management protocols that allow the control of the growth and dispersion of non-native species, and the conservation of undisturbed native vegetation in the peripheral areas of the national reserves and along the roadsides into the national reserves, in order to curb their further expansion into these protected ecosystems. Additionally, limiting agricultural, forestry activities in the national parks is of utmost importance, due to their important effects both on microhabitat conditions and on the spread of propagules (Pauchard and Alaback 2004; Pauchard et al. 2016). As observed, the undisturbed, native flora can work as a biotic barrier to avoid the presence of non-native species. Therefore, generating initiatives to conserve undisturbed areas with native flora also in the lower areas of the gradient and preventing further low elevation land use changes could help to mitigate the establishment of non-native species and their consequent dispersion towards less invaded high elevation areas.

Conclusion

Currently, both observational and experimental research has shown a decrease in non-native species with increasing elevation, mainly associated with the effect of elevation on climatic variables such as temperature. However, few studies looked at the relative importance of underlying factors to this elevational effect, both biotic and anthropogenic and even abiotic (pH, nitrogen etc.) that may help to explain the distribution patterns of non-native species in mountain ecosystems.

Our observational study demonstrated that anthropogenic factors (distance to human settlements and distance to road) override the effect of abiotic factors

on the richness and abundance of non-native species at the local scale. At the regional scale, however, non-native plant species richness is mainly explained by abiotic factors such as nitrogen content and pH, while the abundance of non-native species is again explained by anthropogenic factors.

Based on these results, we can reaffirm the conclusion experimentally obtained by Lembrechts et al. (2016) that anthropogenic factors are the most important to understand the success of non-native species in mountain ecosystems. Importantly, this implies that climatic factors are currently an unlikely factor limiting the distribution of non-native species along altitudinal gradients, as shown for example experimentally for the Swiss Alps (Haider et al. 2011) and in mountain ecosystems of Chile and Norway (Lembrechts et al. 2016). These conclusions reinforce the importance of keeping the expansion of human effects to a minimum (tourism, presence of livestock, infrastructure), both through biosafety protocols or direct control measures on tourism and agricultural activities. Only if such measures are taken, we will be able to control the spread of non-native species in these mountain ecosystems.

Author contributions Research design by EFL, JLL, LC, AJ, SH, AB, AP; Fieldwork by EFL, AJ; Data analysis by EF, JL, SH; Manuscript writing and editing by all authors.

Funding EFL, LC, AJ and AP funded by Fondecyt 1,180,205 and CONICYT PIA AFB170008. EFL was funded by ANID doctoral scholarship 375,957. JLL acknowledges funding by the Research Foundation Flanders (grants OZ7828 and OZ7916) and the University of Antwerp (grant FFB190028). To Alicia Marticorena and the Herbarium CONC who contributed to the taxonomic identification.

Data Availability Not applicable.

Code availability Not applicable.

Declaration

Conflicts of interest Author declared that they have no conflict of interest.

References

Alexander JM, Naylor B, Poll M, Edwards PJ, Dietz H (2009) Plant invasions along mountain roads: the altitudinal

- amplitude of alien Asteraceae forbs in their native and introduced ranges. *Ecography* 32(2):334–344. <https://doi.org/10.1111/j.1600-0587.2008.05605.x>
- Alexander JM, Lembrechts JJ, Cavieres LA, Daehler C, Haider S, Kueffer C, Rew LJ (2016) Plant invasions into mountains and alpine ecosystems: current status and future challenges. *Alp Bot* 126(2):89–103. <https://doi.org/10.1007/s00035-016-0172-8>
- Alexander JM, Kueffer C, Daehler CC, Edwards PJ, Pauchard A, Seipel T, Miren Consortium (2011) Assembly of non-native floras along elevational gradients explained by directional ecological filtering. *Proc National Acad Sci* 108(2): 656–661. <https://doi.org/10.1073/pnas.1013136108>
- Badano EI, Bustamante RO, Villarroel E, Marquet PA, Cavieres LA (2015) Facilitation by nurse plants regulates community invasibility in harsh environments. *J Veg Sci* 26(4):756–767. <https://doi.org/10.1111/jvs.12274>
- 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(1):13–26. <https://doi.org/10.1659/MRD-JOURNAL-D-13-00054.1>
- Barros A, Gonnet J, Pickering C (2013) 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, Aschero V, Mazzolari A, Cavieres LA, Pickering CM (2020) Going off trails: how dispersed visitor use affects alpine vegetation. *J Environ Manage* 267:110546. <https://doi.org/10.1016/j.jenvman.2020.110546>
- Barton K (2016) R package MuMIn: model selection and model averaging based on information criteria (AICc and alike). Vienna, Austria. Available at <https://cran.r-project.org/web/packages/MuMIn/index.html>. Accessed July 2020.
- Bjørvik LM, Dale S, Hermansen GH, Munishi PK, Moe SR (2015) Bird flight initiation distances in relation to distance from human settlements in a Tanzanian floodplain habitat. *J Ornithol* 156(1):239–246. <https://doi.org/10.1007/s10336-014-1121-1>
- Buri A, Cianfrani C, Pinto-Figueroa E, Yashiro E, Spangenberg JE, Adatte T, Pradervand JN (2017) Soil factors improve predictions of plant species distribution in a mountain environment. *Prog Phys Geogr* 41(6):703–722
- Cabra-Rivas I, Saldana A, Castro- Díez P, Gallien L (2015) A multi-scale approach to identify invasion drivers and invaders' future dynamics. *Biol Invasions* 18:411–426. <https://doi.org/10.1007/s10530-015-1015-z>
- Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Divers Distrib* 15(1):22–40. <https://doi.org/10.1111/j.1472-4642.2008.00521.x>
- Cavieres LA, Quiroz CL, Molina-Montenegro MA, Muñoz AA, Pauchard A (2005) Nurse effect of the native cushion plant *Azorella monantha* on the invasive non-native *Taraxacum officinale* in the high-andes of central Chile. *Perspect Plant Ecol Evol Syst* 7(3):217–226. <https://doi.org/10.1016/j.ppees.2005.09.002>
- Cavieres LA, Badano EI, Sierra-Almeida A, Molina-Montenegro MA (2007) Microclimatic modifications of cushion plants and their consequences for seedling survival of native and non-native herbaceous species in the high Andes of central Chile. *Arct Antarct Alp Res* 39(2):229–236. [https://doi.org/10.1657/1523-0430\(2007\)39\[229:MMOCPA\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2007)39[229:MMOCPA]2.0.CO;2)
- Clavel J, Lembrechts J, Alexander J, Haider S, Lenoir J, Milbau A, Verbruggen E (2021) The role of arbuscular mycorrhizal fungi in nonnative plant invasion along mountain roads. *New Phytol* 230(3):1156–1168. <https://doi.org/10.1111/nph.16954>
- Crespo-Pérez V, Rebaudo F, Silvain JF, Dangles O (2011) Modeling invasive species spread in complex landscapes: the case of potato moth in ecuador. *Landscape Ecol* 26(10):1447–1461. <https://doi.org/10.1007/s10980-011-9649-4>
- Cuesta F, Muriel P, Llambí LD, Halloy S, Aguirre N, Beck S, Gámez LE (2017) Latitudinal and altitudinal patterns of plant community diversity on mountain summits across the tropical Andes. *Ecography* 40(12):1381–1394. <https://doi.org/10.1111/ecog.02567>
- Dainese M, Aikio S, Hulme PE, Bertolli A, Prosser F, Marini L (2017) Human disturbance and upward expansion of plants in a warming climate. *Nat Clim Chang* 7(8):577–580. <https://doi.org/10.1038/nclimate3337>
- De Albuquerque FS, Castro-Díez P, Rueda M, Hawkins BA, Rodríguez MA (2011) Relationships of climate, residence time, and biogeographical origin with the range sizes and species richness patterns of exotic plants in Great Britain. *Plant Ecol* 212(11):1901. <https://doi.org/10.1007/s11258-011-9962-7>
- Dray S, Péliissier R, Couteron P, Fortin MJ, Legendre P, Peres-Neto PR, Dufour AB (2012) Community ecology in the age of multivariate multiscale spatial analysis. *Ecol Monogr* 82(3):257–275. <https://doi.org/10.1890/11-1183.1>
- Echeverría C, Coomes D, Salas J, Rey-Benayas JM, Lara A, Newton A (2006) Rapid deforestation and fragmentation of Chilean temperate forests. *Biol Conserv* 134(4):481–494. <https://doi.org/10.1016/j.biocon.2006.01.017>
- Eilts JA, Mittelbach GG, Reynolds HL, Gross KL (2011) Resource heterogeneity, soil fertility, and species diversity: effects of clonal species on plant communities. *Am Nat* 177(5):574–588. <https://doi.org/10.1086/659633>
- Fernández-Murillo MP, Rico A, Kindlmann P (2015) Exotic plants along roads near La Paz Bolivia. *Weed Res* 55(6):565–573. <https://doi.org/10.1111/wre.12174>
- Fuentes-Castillo T, Scherson RA, Marquet PA, Fajardo J, Corcoran D, Román MJ, Pliscoff P (2019) Modelling the current and future biodiversity distribution in the Chilean Mediterranean hotspot. The role of protected areas network in a warmer future. *Divers Distrib* 25(12):1897–1909. <https://doi.org/10.1111/ddi.12988>
- 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 Bot* 76(2):141–155. <https://doi.org/10.4067/S0717-66432019000200141>
- Gantchoff MG, Wilton CM, Belant JL (2018) Factors influencing exotic species richness in Argentina's national parks. *PeerJ* 6:e5514. <https://doi.org/10.7717/peerj.5514>
- Giorgis MA, Tecco PA, Cingolani AM, Renison D, Marcora P, Paiaro V (2011) Factors associated with woody alien species distribution in a newly invaded mountain system of

- central Argentina. *Biol Invasions* 13(6):1423–1434. <https://doi.org/10.1007/s10530-010-9900-y>
- Giorgis MA, Cingolani AM, Tecco PA, Cabido M, Poca M, Von Wehrden H (2016) Testing alien plant distribution and habitat invasibility in mountain ecosystems: growth form matters. *Biol Invasions* 18(7):2017–2028. <https://doi.org/10.1007/s10530-016-1148-8>
- Giraldo-Canas D (2010) Distribution and invasion of C3 and C4 grasses (Poaceae) along an altitudinal gradient in the Andes of Colombia. *Caldasia* 32(1):65–86
- Gobat JM, Aragno M, Matthey W (2004) The living soil: fundamentals of soil science and soil biology. Science Publishers, New York
- Gonzalez ME, Veblen TT, Sibold JS (2010) Influence of fire severity on stand development of *Araucaria araucana*–*Nothofagus pumilio* stands in the Andean cordillera of south-central Chile. *Austral Ecol* 35(6):597–615. <https://doi.org/10.1111/j.1442-9993.2009.02064.x>
- Guo Q, Fei S, Shen Z, Iannone BV, Knott J, Chown SL (2018) A global analysis of elevational distribution of non-native versus native plants. *J Biogeogr* 45(4):793–803. <https://doi.org/10.1111/jbi.13145>
- Haider S, Alexander J, Dietz H, Trepl L, Edwards PJ, Kueffer C (2010) The role of bioclimatic origin, residence time and habitat context in shaping non-native plant distributions along an altitudinal gradient. *Biol Invasions* 12(12):4003–4018. <https://doi.org/10.1007/s00442-019-04498-7>
- Haider S, Alexander JM, Kueffer C (2011) Elevational distribution limits of non-native species: combining observational and experimental evidence. *Plant Ecol Divers* 4(4):363–371. <https://doi.org/10.1080/17550874.2011.637973>
- Haider S, Kueffer C, Bruelheide H, Seipel T, Alexander JM, Rew LJ et al (2018) Mountain roads and non-native species modify elevational patterns of plant diversity. *Glob Ecol Biogeogr* 27(6):667–678. <https://doi.org/10.1007/s10530-010-9815-7>
- Henn JJ, Yelenik S, Damschen EI (2019) Environmental gradients influence differences in leaf functional traits between native and non-native plants. *Oecologia* 191(2):397–409. <https://doi.org/10.1007/s00442-019-04498-7>
- Hossner L (2008) Field pH. In: Chesworth W (ed) *Encyclopedia of Soil Science*. Springer, Dordrecht
- Johnston FM, Johnston SW (2004) Impacts of road disturbance on soil properties and on exotic plant occurrence in sub-alpine areas of the Australian Alps. *Arct Antarct Alp Res* 36(2):201–207. [https://doi.org/10.1657/1523-0430\(2004\)036\[0201:IODOS\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2004)036[0201:IODOS]2.0.CO;2)
- Kueffer C, Daehler C, Dietz H, McDougall K, Parks C, Pauchard A et al (2014) The mountain invasion research network (MIREN). Linking local and global scales for addressing an ecological consequence of global change. *Gaia-Ecol Perspect Sci Soc* 23(3):263–265
- Kühn P, Ratier-Backes A, Römermann C, Bruelheide H, Haider S (2021) Contrasting patterns of intraspecific trait variability in native and non-native plant species along an elevational gradient on Tenerife Canary Islands. *Annals Botany* 127(4):565–576. <https://doi.org/10.1093/aob/mcaa067>
- Kumar S, Stohlgren TJ, Chong GW (2006) Spatial heterogeneity influences native and nonnative plant species richness. *Ecology* 87(12):3186–3199. [https://doi.org/10.1890/0012-9658\(2006\)87\[3186:SHINAN\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[3186:SHINAN]2.0.CO;2)
- Lara A, Little C, Urrutia R, McPhee J, Álvarez-Garretón C, Oyarzún C, Arismendi I (2009) Assessment of ecosystem services as an opportunity for the conservation and management of native forests in Chile. *For Ecol Manage* 258(4):415–424. <https://doi.org/10.1016/j.foreco.2009.01.004>
- 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*. <https://doi.org/10.1371/journal.pone.0089664>
- Lembrechts JJ, Pauchard A, Lenoir J, Nuñez MA, Geron C, Ven A et al (2016) Disturbance is the key to plant invasions in cold environments. *Proc Natl Acad Sci* 113(49):14061–14066. <https://doi.org/10.1073/pnas.1608980113>
- Lembrechts JJ, Alexander JM, Cavieres LA, Haider S, Lenoir J, Kueffer C et al (2017) Mountain roads shift native and non-native plant species' ranges. *Ecography* 40(3):353–364. <https://doi.org/10.1111/ecog.02200>
- Lembrechts JJ, Lenoir J, Nuñez MA, Pauchard A, Geron C, Bussé G et al (2018) Microclimate variability in alpine ecosystems as stepping stones for non-native plant establishment above their current elevational limit. *Ecography* 41(6):900–909. <https://doi.org/10.1111/ecog.03263>
- Liedtke R, Barros A, Essl F, Lembrechts JJ, Wedegärtner RE, Pauchard A, Dullinger S (2020) Hiking trails as conduits for the spread of non-native species in mountain areas. *Biol Invasions* 22(3):1121–1134. <https://doi.org/10.1007/s10530-019-02165-9>
- Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. *Trends Ecol Evol* 20(5):223–228. <https://doi.org/10.1016/j.tree.2005.02.004>
- López-Angulo J, Pescador DS, Sánchez AM, Mihoč MA, Cavieres LA, Escudero A (2018) Determinants of high mountain plant diversity in the Chilean Andes: from regional to local spatial scales. *PLoS ONE* 13(7):e0200216. <https://doi.org/10.1371/journal.pone.0200216.s002>
- Luebert F, Pliscoff P (2017) *Sinopsis bioclimática y vegetacional de Chile: Segunda Edición*. Santiago, Chile: Editorial Universitaria
- Marini L, Bertolli A, Bona E, Federici G, Martini F, Prosser F, Bommarco R (2013) Beta-diversity patterns elucidate mechanisms of alien plant invasion in mountains. *Glob Ecol Biogeogr* 22(4):450–460. <https://doi.org/10.1111/geb.12006>
- Martin PH, Canham CD, Marks PL (2009) Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. *Front Ecol Environ* 7(3):142–149. <https://doi.org/10.1890/070096>
- McDougall KL, Alexander JM, Haider S, Pauchard A, Walsh NG et al (2011) Alien flora of mountains: global comparisons for the development of local preventive measures against plant invasions. *Divers Distrib* 17(1):103–111. <https://doi.org/10.1111/j.1472-4642.2010.00713.x>

- McDougall KL, Lembrechts J, Rew LJ, Haider S, Cavieres LA, Kueffer C et al (2018) Running off the road: roadside non-native plants invading mountain vegetation. *Biol Invasions* 20(12):3461–3473. <https://doi.org/10.1007/s10530-018-1787-z>
- McGlone CM, Sieg CH, Kolb TE (2011) Invasion resistance and persistence: established plants win, even with disturbance and high propagule pressure. *Biol Invasions* 13(2):291–304. <https://doi.org/10.1007/s10530-010-9806-8>
- Miranda A, Altamirano A, Cayuela L, Pincheira F, Lara A (2015) Different times, same story: native forest loss and landscape homogenization in three physiographical areas of south-central of Chile. *Appl Geogr* 60:20–28. <https://doi.org/10.1016/j.apgeog.2015.02.016>
- Müllerová J, Vítková M, Vitek 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(19):3839–3849. <https://doi.org/10.1016/j.scitotenv.2011.06.056>
- Oke OA, Thompson KA (2015) Distribution models for mountain plant species: the value of elevation. *Ecol Model* 301:72–77. <https://doi.org/10.1016/j.ecolmodel.2015.01.019>
- Otto R, Arteaga MA, Delgado JD, Arévalo JR, Blandino C, Fernández-Palacios JM (2014) Road edge effect and elevation patterns of native and alien plants on an oceanic island (Tenerife, Canary Islands). *Folia Geobot* 49(1):65–82. <https://doi.org/10.1007/s12224-013-9159-z>
- Paiaro V, Mangeaud A, Pucheta E (2007) Alien seedling recruitment as a response to altitude and soil disturbance in the mountain grasslands of central Argentina. *Plant Ecol* 193(2):279–291. <https://doi.org/10.1007/s11258-007-9265-1>
- Paiaro V, Cabido M, Pucheta E (2011) Altitudinal distribution of native and alien plant species in roadside communities from central Argentina. *Austral Ecol* 36(2):176–184. <https://doi.org/10.1111/j.1442-9993.2010.02134.x>
- 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(1):238–248. <https://doi.org/10.1111/j.1523-1739.2004.00300.x>
- Pauchard A, Shea K (2006) Integrating the study of non-native plant invasions across spatial scales. *Biol Invasions* 8(3):399–413. <https://doi.org/10.1007/s10530-005-6419-8>
- Pauchard A, Kueffer C, Dietz H, Daehler CC, Alexander J, Edwards P et al (2009) Ain't no mountain high enough: plant invasions reaching new elevations. *Front Ecol Environ* 7(9):479–486. <https://doi.org/10.1890/080072>
- Pauchard A, Fuentes N, Jiménez A, Bustamante R, Marticorena A (2013) Alien plants homogenise protected areas: evidence from the landscape and regional scales in south central Chile. In: Pyšek P, Richardson DM, Genovesi P, Foxcroft LC (eds) *Plant invasions in protected areas*. Springer, Dordrecht, pp 191–208
- Pauchard A, Milbau A, Albiñá A, Alexander J, Burgess T, Daehler C 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(2):345–353. <https://doi.org/10.1007/s10530-015-1025-x>
- Pearson DE, Ortega YK, Villarreal D, Lekberg Y, Cock MC, Eren Ö, Hierro JL (2018) The fluctuating resource hypothesis explains invasibility, but not exotic advantage following disturbance. *Ecology* 99(6):1296–1305. <https://doi.org/10.1002/ecy.2235>
- Petitpierre B, McDougall K, Seipel T, Broennimann O, Guisan A et al (2016) Will climate change increase the risk of plant invasions into mountains? *Ecol Appl* 26(2):530–544. <https://doi.org/10.1890/14-1871>
- Phillips-Mao L, Larson DL, Jordan NR (2014) Effects of native herbs and light on garlic mustard (*Alliaria petiolata*) invasion. *Invasive Plant Sci Manage* 7(2):257–268. <https://doi.org/10.1614/IPSM-D-13-00003.1>
- Pollnac F, Seipel T, Repath C et al (2012) Plant invasion at landscape and local scales along roadways in the mountainous region of the greater yellowstone ecosystem. *Biol Invasions* 14(8):1753–1763. <https://doi.org/10.1007/s10530-012-0188-y>
- Roques A (2010) Alien forest insects in a warmer world and a globalised economy: impacts of changes in trade, tourism and climate on forest biosecurity. *NZ J For Sci* 40(Suppl):S77–S94
- 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(19):7909–7919. <https://doi.org/10.1002/ece3.3270>
- Santilli L, Castro SA, Figueroa JA et al (2018) Exotic species predominates in the urban woody flora of central Chile. *Gayana Botanica* 75(2):568–588. <https://doi.org/10.4067/S0717-66432018000200568>
- Seipel T, Kueffer C, Rew LJ, Daehler CC, Pauchard A 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(2):236–246. <https://doi.org/10.1111/j.1466-8238.2011.00664.x>
- Shrestha UB, Sharma KP, Devkota A, Siwakoti M, Shrestha BB (2018) Potential impact of climate change on the distribution of six invasive alien plants in Nepal. *Ecol Ind* 95:99–107. <https://doi.org/10.1016/j.ecolind.2018.07.009>
- Slodowicz D, Descombes P, Kikodze D, Broennimann O et al (2018) Areas of high conservation value at risk by plant invaders in Georgia under climate change. *Ecol Evol* 8(9):4431–4442. <https://doi.org/10.1002/ece3.4005>
- Souza L, Bunn WA, Simberloff D, Lawton RM, Sanders NJ (2011) Biotic and abiotic influences on native and exotic richness relationship across spatial scales: favourable environments for native species are highly invulnerable. *Funct Ecol* 25(5):1106–1112. <https://doi.org/10.1111/j.1365-2435.2011.01857.x>
- Taylor S, Kumar L, Reid N, Kriticos DJ (2012) Climate change and the potential distribution of an invasive shrub *Lantana camara* L. *PloS one*. <https://doi.org/10.1371/journal.pone.0035565>
- Team RC (2019) R: A language and environment for statistical computing. Vienna, Austria. Available from: <http://www.RProject.org/>
- Tecco PA, Pais-Bosch AI, Funes G et al (2016) Mountain invasions on the way: are there climatic constraints for the expansion of alien woody species along an elevation

- gradient in Argentina? *J Plant Ecol* 9(4):380–392. <https://doi.org/10.1093/jpe/rtv064>
- Terzano D, Kotzé I, Marais C, Cianciullo S et al (2018) Environmental and anthropogenic determinants of the spread of alien plant species: insights from South Africa's quaternary catchments. *Plant Ecol* 219(3):277–297. <https://doi.org/10.1007/s11258-018-0795-5>
- Thom D, Sommerfeld A, Sebold J, Hagge J, Müller J, Seidl R (2020) Effects of disturbance patterns and deadwood on the microclimate in European beech forests. *Agric For Meteorol* 291:108066. <https://doi.org/10.1016/j.agrformet.2020.108066>
- Tomasetto F, Duncan RP, Hulme PE (2013) Environmental gradients shift the direction of the relationship between native and alien plant species richness. *Divers Distrib* 19(1):49–59. <https://doi.org/10.1111/j.1472-4642.2012.00939.x>
- 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(2):143–151. <https://doi.org/10.1111/btp.12191>
- Van der wal R, Truscott AM, Pearce I, Cole L, Harris M, Wanless S (2008) Multiple anthropogenic changes cause biodiversity loss through plant invasion. *Glob Change Biol*, 14 (6): 1428–1436. <https://doi.org/10.1111/j.1365-2486.2008.01576.x>
- Venables WN, Ripley BD (2002) Random and mixed effects. In: Ripley BD (ed) *Modern applied statistics with S*, Springer, New York, pp 271–300
- Vonlanthen CM, Kammer PM, Eugster W et al (2006) Alpine vascular plant species richness: the importance of daily maximum temperature and pH. *Plant Ecol* 184(1):13–25. <https://doi.org/10.1007/s11258-005-9048-5>
- Wisz MS, Pottier J, Kissling WD, Pellissier L et al (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biol Rev* 88(1):15–30. <https://doi.org/10.1111/j.1469-185X.2012.00235.x>
- Zellweger F, De Frenne P, Lenoir J, Vangansbeke P, Verheyen K, Bernhardt-Römermann M, Coomes D (2020) Forest microclimate dynamics drive plant responses to warming. *Science* 368(6492):772–775. <https://doi.org/10.1126/science.aba6880>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.