

This item is the archived peer-reviewed author-version of:

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

Reference:

Fuentes Lillo Eduardo, Lembrechts Jonas, Cavieres Lohengrin A., Jimenez Alejandra, Haider Sylvia, Barros Agustina, Pauchard Anibal.- Anthropogenic factors overrule local abiotic variables in determining non-native plant invasions in mountains
Biological invasions - ISSN 1387-3547 - Dordrecht, Springer, 23:12(2021), p. 3671-3686
Full text (Publisher's DOI): <https://doi.org/10.1007/S10530-021-02602-8>
To cite this reference: <https://hdl.handle.net/10067/1804150151162165141>

1 **Anthropogenic factors overrule local abiotic variables in determining non-native plant**
2 **invasions in mountains**
3

4 Eduardo Fuentes-Lillo^{1,2,3}, Jonas J. Lembrechts², Lohengrin A. Cavieres^{3,4}, Alejandra Jiménez^{1,4}, Sylvia
5 Haider^{6,7}, Agustina Barros⁵, Aníbal Pauchard^{1,4}
6

7 ¹Laboratorio de Invasiones Biológicas (LIB), Facultad de Ciencias Forestales, Universidad de
8 Concepción, Concepción, Chile.

9 ²Research Group on Plants and Ecosystems, University of Antwerp.

10 ³Departamento de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Universidad de
11 Concepción, Concepción, Chile.

12 ⁴Instituto de Ecología y Biodiversidad (IEB), Santiago, Chile.

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

15 ⁶ Institute of Biology / Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg,
16 Halle, Germany

17 ⁷ German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany
18

19 Corresponding author : eduafuentes@udec.cl
20

21 **Acknowledgments (including Funding)**

22 EFL, LC, AJ and AP funded by Fondecyt 1180205 and CONICYT PIA AFB170008. EFL was funded by ANID
23 doctoral scholarship 375957. JJJL acknowledges funding by the Research Foundation Flanders
24 (grants OZ7828 and OZ7916) and the University of Antwerp (grant FFB190028). To Alicia Marticorena and
25 the Herbarium CONC who contributed to the taxonomic identification.
26

27 **Conflicts of interest/Competing interests: Not applicable**

28 **Availability of data and material (data transparency): Not applicable**

29 **Code availability (software application or custom code): Not applicable**

30 **Authors' contributions**

31 Research design by EFL, JJJL, LC, AJ, SH, AB, AP; Fieldwork by EFL, AJ; Data analysis by EF, JL, SH;
32 Manuscript writing and editing by all authors.
33
34

35 **Abstract** The factors that determine patterns of non-native species richness and abundance are context
36 dependent in both time and space. Global change has significantly boosted plant invasions in mountains,
37 therefore, understanding which factors determine the invasion and at what scale they operate are fundamental
38 for decision-making in the conservation of mountain ecosystems. Although much evidence has been gathered
39 on the patterns of non-native species in mountain ecosystems, little is known about what specific abiotic, biotic,
40 or anthropogenic factors drive such patterns. Here, we assessed the importance of anthropogenic, biotic,
41 and abiotic factors at two spatial scales as drivers of plant invasions along three roads in south-central Chile.
42 We sampled non-native plant richness and abundance, and each of these explanatory factors, in-situ in 60
43 transects in disturbed areas and adjacent undisturbed vegetation. Low elevation areas were the most invaded,
44 with patterns of richness and abundance driven mainly by anthropogenic factors, explaining between 20 and
45 50% of the variance for the three roads. Only for the abundance of non-native species along the road in the
46 Malalcahuello National Reserve, biotic factors were more important (45% of the variance). At the regional
47 scale, the abundance of non-native species was again explained best by anthropogenic factors (24% of the
48 variance), yet non-native richness was driven most strongly by abiotic factors such as soil nitrogen content and
49 pH (15% of the variance). Our results confirm the conclusions from experimental studies that anthropogenic

50 factors override abiotic factors and are important drivers of non-native species at local and regional scales and
51 that non-native plant invasion in mountains is currently not strongly limited by climate.

52

53 **Keywords: Andes mountains, invasive species, non-native species, human settlement, protected areas.**

54

55

56

57

58

59

60

61

62 **Introduction**

63
64 Although the presence of non-native species has become increasingly common in mountain regions, so far, the
65 levels of invasions have shown to be relatively low (Pauchard et al. 2009; McDougall et al. 2011; Marini et al.
66 2013; Fuentes-Lillo and Pauchard 2019). As in other ecosystems, the invasion process in mountain ecosystems
67 is defined by the interaction between abiotic conditions, biotic interactions, and propagule pressure (Catford et
68 al. 2009). Mountains, however, show interesting specific complexities on the factors that drive and limit
69 invasions and how they vary between regions with different environmental contexts (Alexander et al. 2016;
70 McDougall et al. 2018). In particular, anthropogenic factors can increase the success of the invasion since they
71 function as vectors for the transport of propagules and modify the biotic and abiotic conditions that facilitate
72 the establishment of non-native species (Catford et al. 2009; Pauchard et al. 2009; Pollnac et al. 2012;
73 Lembrechts et al. 2017). Most studies of plant invasions in mountains have used elevation as a proxy for a
74 multitude of intertwined variables, such as climate, anthropogenic disturbance and ecosystem types to explain
75 the changing patterns of richness and abundance of non-native species (Pauchard et al. 2009; Seipel et al. 2012).
76 However, few studies have disentangled the mechanistic factors underlying these patterns, as both observational
77 and experimental studies have shown that these drivers (abiotic, biotic and anthropogenic) are context
78 dependent and vary both in time and on spatial scales (Kumar et al. 2006; Pauchard and Shea 2006; Dray et al.
79 2012).

80
81 Probably the most obvious constraints for plant invasions in mountains are abiotic factors, in particular
82 climate harshness associated to higher elevation (Pauchard et al. 2009). It has been shown that the decrease in
83 the richness of non-native species in the mountains is mainly associated with the large-scale climatic gradients
84 (i.e. temperature and precipitation) determined by elevation (Seipel et al. 2012; Alexander et al. 2016; Haider
85 et al. 2018). At smaller scales, one can see the additional importance of abiotic factors (e.g. soil temperature,
86 soil moisture, nitrogen, pH) as local drivers of the fine-grained richness patterns of non-native species in
87 mountain ecosystems (Buri et al. 2017; Gantchoff et al. 2018; Lembrechts et al. 2018).

88
89 Recently, there has been increasing interest in understanding how biotic interactions drive invasive
90 species distribution in mountains. For example, several studies have identified a key role for facilitating
91 interactions in establishing non-native species at the smallest scale (Cavieres et al. 2005,2007; Badano et al.
92 2015). Competitive interactions on the other hand are more intense at low elevations. As abiotic conditions
93 become more adverse for growth, facilitation is a key process to explain the presence of non-native species in
94 higher elevation areas (Cavieres et al. 2007; Badano et al. 2015; Alexander et al. 2016). Nevertheless,
95 experimental studies have shown that biotic interactions with the established community can remain negative
96 for non-native plant invaders, even at high elevations (Lembrechts et al. 2016). It has also been observed that
97 more productive communities generate greater resistance to the invasion of non-native species. For example, it
98 has been observed in mountain ecosystems in Argentina that the number of non-native species decreases
99 significantly with increasing coverage of native species (Pearson et al. 2018). A deeper understanding of biotic
100 factors is thus needed to explain how biotic interactions (competition and/or facilitation) with the established
101 community at multiple scales explain the current patterns of distribution of non-native species in mountains
102 (Wisz et al. 2013).

103
104 Propagule pressure and the role of disturbance have been studied in mountain ecosystems using
105 proximity to the road and the presence of human activities as indirect proxies (Seipel et al. 2012). Roads and
106 other corridors have been shown to be key to understanding the presence of non-native species at higher
107 elevations (Alexander et al. 2009; Seipel et al. 2012; Giorgis et al. 2011, 2016; Liedtke et al. 2020). Seed-
108 addition experiments, on the other hand, have identified that an increase in propagule pressure can explain the
109 abundance of non-native species along elevation gradients (Lockwood et al. 2005; McGlone et al. 2011; Pollnac
110 et al. 2011; Lembrechts et al. 2016). Disturbance is known to work through its modification of the climatic

111 conditions, favoring the establishment of non-native species (Haider et al. 2010, 2018; McDougall et al. 2018).
112 At local scales, disturbance also favors the establishment of non-native species through the removal of
113 vegetation and release of resources, mainly in higher elevation areas (Paiaro et al. 2007; Dainese et al. 2017;
114 Pearson et al. 2018).

115
116 As global change will generate significant changes in the climatic patterns, and substantial increases
117 in anthropogenic disturbances (Roques 2010; Gou et al. 2018), understanding the factors that determine non-
118 native plant invasions in mountains is of utmost importance to develop efficient conservation policies for
119 protected areas (Slodowicz et al. 2017). Climate change has been shown to lead to increased invasion events,
120 especially at higher elevations. (Oke and Thompson 2015; Petitpierre et al. 2016; Shrestha et al. 2018).
121 Additionally, increasing globalization, in mountains represented by population increases, tourist centers,
122 infrastructure, will have a direct impact on the dispersion and establishment of non-native species (Terzano et
123 al. 2018).

124
125 Due to their extremely high climatic and anthropogenic heterogeneity, which allows both observational
126 and experimental studies with a multi-scale approach, mountains are a unique natural laboratory for the study
127 of invasion processes (Pauchard et al. 2009; Alexander et al. 2016; Kueffer et al. 2014). In Chile, mountains
128 provide extremely valuable ecosystem services (e.g. water, recreation), and they represent biodiversity hotspots
129 with high levels of native and endemic species (Lara et al. 2009; Fuentes-Castillo et al. 2019; Fuentes-Lillo and
130 Pauchard 2019). During the last decades, however, human activities associated with tourism, agriculture,
131 mining and forestry have been progressively degrading these ecosystems in Chile (Pauchard and Alaback 2004),
132 and worldwide (Pauchard et al 2009, 2015).

133
134 In this work, we aim to disentangle the importance of the main factors (abiotic, biotic and
135 anthropogenic), that define at local and regional levels the richness and abundance of non-native species along
136 altitudinal gradients in the central-southern Chilean Andes. Propagule pressure was not included in the study
137 due to its high correlation with anthropogenic variables, such as the proximity to human settlements and the
138 distance to road (Pollnac et al. 2011). These ecosystems are inserted within a matrix of anthropogenic land-
139 uses, with urban centers and agricultural activities in the lowlands and ski and tourist centers at high elevations
140 (Pauchard and Alaback 2004). Furthermore, these areas are influenced by natural disturbance processes
141 resulting from volcanic eruptions and natural fire cycles that have given these mountains unique characteristics,
142 both regarding their climate and their floristic composition (González et al. 2010). Thus, the central-southern
143 Chilean Andes are particularly suitable to investigate the role of the different drivers of the invasion process,
144 both from a theoretical point of view and due to the implications for the management and control of non-native
145 species in a disturbed mountain area in an era of global change. Specifically, we aim to answer the following
146 questions: 1) What are the main factors that determine the richness and abundance of non-native species in the
147 central-southern Andes of Chile? And 2) How do the drivers of richness and abundance of non-native species
148 change from a local (one road) to a regional scale (across all three roads). We hypothesize that at local levels,
149 anthropogenic factors such as the distance of the road and the distance to human settlements, explain species
150 richness and abundance patterns for non-native species, while at the regional level abiotic factors like
151 temperature would be more important. While we anticipate a certain role for biotic factors (i.e. diversity and
152 productivity proxies as a measure of invasibility of the established vegetation), we hypothesize them to be
153 overruled by anthropogenic and abiotic factors.

154 155 **Methods**

156 157 158 **Site description**

159 We selected three roads in the Andes mountain range, in the central-south zone of Chile (from 37 ° S to 39 °
160 S): Laguna Laja National Park (LLNP) (37° 38' 45''S, 71° 38' 25''W), Malacahuello National Reserve (MNR)
161 (38° 43' 49''S, 71° 48' 82''W) and Conguillio National Park (CNP) (39° 41' 17''S, 71° 47' 32''W). The three
162 roads were selected due to the wide environmental gradient they cover, associated with altitudinal gradients
163 ranging from ~400 to ~1600 m a.s.l. In addition, these roads have year-round vehicular traffic and intense
164 anthropogenic pressure resulting from agricultural activities and tourism. These three roads have similar
165 bioclimatic conditions and composition of native and non-native vegetation (Luebert and Plissock 2017). The
166 roads are located in a xeric bioclimate (Luebert and Plissock 2017). The low elevation areas are dominated by
167 Mediterranean deciduous forests of *Nothofagus obliqua* and *Cryptocaria alba* and temperate deciduous forests
168 of *N. obliqua* and *Persea lingue*. Intermediate elevations are dominated by temperate Andean deciduous forests
169 of *N. alpina* and *Dasyphyllum diacanthoides*. High elevations are characterized by Andean resinous forests of
170 *Araucaria araucana* and *Festuca scabriuscula* and, in some area's, scrublands of *Discaria chacaye* and
171 *Berberis empetrifolia* (Luebert and Plissock 2017).

172

173 **Sampling design**

174 To determine the main factors (abiotic, biotic and anthropogenic) that drive non-native species richness and
175 abundance (response variables), we used the standardized survey design proposed by the Mountain Invasion
176 Research Network as described in Seipel et al. (2012). 20 T-shaped transects were installed along each of the
177 three roads. The transects were placed along an elevation gradient ranging from ~400 to 1600 m a.s.l. (individual
178 elevation ranges depending on road conditions) in a stratified way, each transect with an altitudinal separation
179 of approximately 100 m. The T-transects consisted each of three 50 m x 2 m plots, with one plot parallel to the
180 road (hereafter called 'roadside') and two plots perpendicular to the road pointing into the adjacent vegetation
181 (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
182 species were recorded and their abundance was measured based on the number of individuals or ramets per
183 plot, assigning a value of 1 (1-10 individuals), 2 (10-100 individuals) or 3 (>100 individuals) (Seipel et al.
184 2012). A list of abiotic, biotic and anthropogenic variable was recorded along the roadside and in the adjacent
185 vegetation as detailed below (Table S1). To evaluate the effect of the scale, models were made for each road
186 individually (local scale) and models that include the data of the three roads together (regional scale).

187

188 **Abiotic variables**

189 To determine the relationship between species richness and abundance of non-native species and abiotic
190 variables, we measured local soil and air temperature, soil humidity and key soil biogeochemical parameters.
191 All variables were measured both in the roadside and in the adjacent vegetation (52 m from the road).
192 Temperature was recorded using iButton sensors (DS1922L, www.maximintegrated.com, measuring every
193 hour for a period of 1 year) at 5 cm depth (soil temperature) and at 1 m height (air temperature). We calculated
194 growing degree days (GDD soil and air) from these time series as the sum of all daily averages above 5°C
195 during the growing season (the months of December to February were used, corresponding to the summer
196 season in these ecosystems) (Lembrechts et al. 2016). Soil moisture was measured in each plot at least three
197 times during the growing season (three months, December to February), using a FieldScout TDR 100 soil
198 moisture meter. Finally, in each plot (roadside and adjacent vegetation), 100 g of soil (horizon A) was sampled,
199 consisting of 3 subsamples of soil randomly distributed in each plot (roadside and adjacent vegetation), adding
200 up to approximately 100 g of soil. The soil sampling was carried out during the growing season, and soil was
201 analyzed for soil C / N-ratio, total carbon and nitrogen, nitrate (NO₃⁻), ammonium (NH₄⁺), organic matter (OM)
202 and pH. The analyzes were carried out at the Soil, Water and Forest Research laboratory at the Universidad de
203 Concepcion.

204

205 **Biotic variables**

206 Four variables were recorded in each plot of the T-transects to represent diversity, productivity and invasibility
207 of the native community. Native species richness and abundance were recorded following the same three-point

208 scale as described above for non-native species. Cover of herbs and trees was estimated visually in each plot
209 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 =
210 76-95%, 7 = 96-100%) (Seipel et al. 2012).

211

212 **Anthropogenic variables**

213 To assess the influence of anthropogenic disturbances, four variables were recorded in each plot. This included
214 presence/absence agricultural activities (cultivation and livestock), level of (anthropogenic) disturbance,
215 distance to the road, and proximity to human settlements. The level of anthropogenic disturbance was measured
216 on a three-point scale including 0 (no disturbance of vegetation or soil), 1 (moderate disturbance in less than 50
217 % of the plot) and 2 (severe disturbance in more than 50 % of the plot). Disturbance consisted of any removal
218 of the vegetation by human factors, like the presence of trails, fire or livestock and cultivation. Distance to the
219 road was measured in situ in the middle of the plot at the time of establishing the plots using a handheld GPS,
220 these values were fixed for each transect and each road, and correspond to 1 m for the plot parallel to the road,
221 27 m and 77 m for plots 2 and 3 that are located adjacent to the road. Finally, the proximity to human settlements
222 was measured from each plot (road and adjacent vegetation) to the edge of the closest human settlement, using
223 GPS positions and a geographic information system (GIS; ArcView 3.3) (Tomasseto et al. 2013; Bjørvik et al.
224 2015). We considered as human settlements any type of building (e.g. villages, farms) that presents a constant
225 flow of people throughout the year. Mountain shelters and buildings for use by ranchers, which are common in
226 these areas, were thus excluded, as they are only irregularly occupied.

227

228 **Data analysis**

229

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

231

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

238

239 To assess the importance of the abiotic, biotic and anthropogenic factors on the non-native species
240 richness and abundance at local (along one road) and regional (across all three roads) scales, we used
241 generalized linear mixed-effects models (GLMMs, using the “*lmer*” function in the package *lme4*). GLMMs
242 were constructed for each road separately, with transect number as a random effect, for the local scale, and with
243 transect nested in road as a random effect for all roads together for the regional scale. All models were adjusted
244 to a Poisson distribution error with logit log. We made separate models for non-native richness and abundance
245 and for each separate group (abiotic, biotic and anthropogenic), using all correlated variables for each group.
246 We selected the best model for each group using the Akaike Information Criterion (AIC), where the best model
247 is the one with the lowest AIC-value (Venables and Ripley 2002, package MuMIn, Barton 2016). Importantly,
248 elevation was not included in any of the models, because it correlates strongly with the majority of the analyzed
249 variables (e.g. temperature or nitrogen content) so it was only used at the time of plotting for visualization of
250 the most important variables.

251

252 Next, to determine the relative importance of each of the three groups as driver of non-native species
253 richness and abundance, models were constructed for each response variable with the three most significant
254 variables that were determined using the group-specific GLMMs above (Table S2). Then, for each response
255 variable (richness and abundance) and for each spatial scale (local and regional), the percentage of variance
256 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 non-native species richness and abundance at the local scale.

Except in one road, anthropogenic factors were the most important drivers of both richness and abundance of non-native species at the local scale (Table 1, Fig. 4). Non-native species richness and abundance decreased with increasing distance to human settlements (6 out of 6 models), and distance to the road (4 out of 6) (Table S2, S4, Fig. 2a, b, c, d, f), and increased in the presence of agricultural activities (2 out of 6) (Table S2, Fig. S3c, f), roadsides (5 out of 6) (Table S2, Fig. S3a, b), and human disturbance (1 out of 6) (Table S2, Fig. S3d). Only in the case of the abundance of non-native species along MNR, the most parsimonious model was the biotic model, with the abundance of non-native species decreasing with increasing abundance of native species and herbaceous cover (Table S2, Fig. 2e, Fig S3e). Importantly, while both the richness and abundance of non-native species were mostly explained by anthropogenic variables, there was a significant amount of unexplained variance (Table 1, Fig. 4).

Factors that determine the richness and abundance of non-native at regional scale

Regional non-native species abundance was best explained by anthropogenic factors, with lower non-native abundance with increasing distance from human settlements, yet higher abundance in the presence of agricultural activities (Table S2, Fig. 3c, d). However, regional non-native richness was best explained by abiotic conditions, with increasing richness with increasing amounts of ammonium, and decreasing pH (Table S2, S3, Fig. 3a, b). Models at the regional scale explained ca. 30 % of the total variance (Table S3, Fig.4).

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. 2020), Canary Island (Otto et al. 2014), Chile (Pauchard and Alaback 2004), Yellowstone National Park (Pollnac et al. 2010), Ecuador (Sandoya et al. 2017) and Bolivia (Fernandez-Murillo et al. 2016). 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).

306 The importance of roads for explaining patterns of richness and abundance of non-native species
307 represent multiple underlying factors. First of all, roads serve as a vector for the transport of propagules
308 (Pauchard et al. 2009; Taylor et al. 2012; Lembrechts et al. 2014), yet they also modify soil biogeochemical
309 conditions (pH, nitrogen, humidity) (Johnston and Johnston 2004, Lembrechts et al. 2014; Clavel et al. 2020),
310 microclimate (Lembrechts et al. 2016) and native vegetation cover (Pauchard and Alaback 2004). These
311 changes in the microhabitat under the influence of the disturbances associated with the road facilitates non-
312 native species establishment, especially of ruderal species (Lembrechts et al. 2014). In addition to the effects
313 of roads on non-native richness and abundance, as expected, the distance to human settlements was even more
314 important in explaining these patterns. Even its importance few studies on mountains plant invasions have
315 included this factor mainly because it can be correlated with elevation (Haider et al. 2010; Seipel et al. 2012).
316 However due to the increased popularity of tourism in mountains including the construction of ski resorts and
317 vacation retreats at a range of elevations, it is important to consider human settlements as a separate factor
318 (Barros et al. 2013, 2020).

319
320 As a result of human disturbance from roads, including building and maintenance, changes in soil
321 conditions near roadsides are common (Müllerova et al. 2011) and affect non-native plants as has been shown
322 in previous (Buri et al. 2017, Vonlanthen et al. 2006, other refs) and this study. In our study we found at the
323 regional level that increased ammonium (NH_4^+) and a decrease in pH affected non-native richness. NH_4^+ , for
324 example, has been proven to be a good indicator of the richness of non-native species at regional scales (Urbina
325 and Benavides 2015; Pearson et al. 2017). Studies conducted in the central Andes in Argentina have found that
326 significant increases in NO_3^- in the soil are positively correlated with the richness and abundance of non-native
327 species (Pearson et al. 2017). The same effect has been found in the Colombian Andes where the addition of
328 nutrients to the soil (mainly nitrogen) facilitated the invasion by the non-native *Pennisetum clandestinum*
329 (Urbina and Benavides et al. 2015). Soil pH has also been shown to be an important parameter to explain the
330 distribution of alpine plant species (Vonlanthen et al. 2006). The pH indeed relates to the concentration of
331 protons, which directly affects plant available minerals (Hossner 2008), with a high pH causing nutrient
332 deficiency in the soil, while low values improve the solubility of toxic metals (Gobat et al. 2004). Therefore, a
333 soil with neutral or slightly acidic pH has the highest nutrient availability (Gobat et al 2004; Vonlanthen et al.
334 2006; Hossner 2008; Bury et al. 2017). A study conducted on Bank Peninsula, New Zealand found that soil pH
335 was one of the most important explanatory variables for non-native species richness, out of a series of abiotic,
336 biotic and anthropogenic variables (Tomasetto et al. 2013).

337
338 The critical role of distance to human settlements found in this study may be related to the fact that
339 along most of the roads studied, human settlements are concentrated at low elevations (Fig. S2a), where climatic
340 conditions are more conducive to the growth and development of non-native species (Tomasetto et al. 2013).
341 The lowlands are also the main source of propagules of non-native species (Pauchard and Alaback 2004;
342 Lembrechts et al. 2014) and present high levels of disturbance that eliminate competition and serve as a constant
343 supply of nutrients for the system, significantly favoring the establishment of non-native species (Urbina and
344 Benavides 2015; Lembrechts et al. 2016; Santilli et al. 2018). In sum, distance to human settlements may be an
345 indirect proxy of human footprint and propagule pressure.

346
347 We also found a positive effect of the presence of agricultural activities, a variable strongly linked to
348 land use changes along the altitudinal gradient. Anthropogenic land use intensification have been historically
349 concentrated at low elevations (Pauchard and Alaback 2004). Shifts from landscapes dominated by *Nothofagus*
350 *sp* forests to grazing pastures and other agricultural uses has favored the establishment and dispersion of non-
351 native species in the region (Pauchard and Alaback 2004), and in many cases, non-native species grasses and
352 herbs have even been deliberately sown to improve forage (Pauchard and Alaback 2004). The importance of
353 these agricultural activities also lies in their modification of microclimatic conditions (by changing from forests
354 to pastures) as well as a constant source of propagules of non-native species (Pauchard and Alaback 2004; Guo

355 et al 2017; Zellweger et al. 2020). In addition, dispersal processes can be facilitated through the presence of
356 cattle, which functions as a propagation vector for propagules towards higher elevation areas and the forest
357 interior away from roads (Pauchard and Alaback 2004; Seipel et al. 2012; Liedtke et al. 2019).

358
359 Again, it is important to highlight that anthropogenic disturbances like road building have a large effect
360 on soil conditions like pH and nutrient availability, generally making the soils more alkaline and increasing
361 their nutrient and organic matter content (Müllerova et al. 2011). This relates to the importance of anthropogenic
362 variables as drivers of the abundance of non-native species at regional scales in our study, as has been found in
363 other studies in England (index of human footprint, Albuquerque et al. 2010), New Zealand (proximity to
364 buildings and roads, Tomasetto et al. 2013) and global mountain ranges (distance to the road, Seipel et al. 2012;
365 Haider et al. 2018; McDougall et al. 2018).

366
367 To explain the positive relationships between human disturbance and non-native species richness and
368 abundance, several mechanisms have been proposed. For example, vegetation removal releases a significant
369 amount of resources (nutrients, space etc.), which can be rapidly occupied by non-native species (Barros and
370 Pickering 2014; Barros et al. 2013; Lembrechts et al. 2016). The importance of such vegetation removal has
371 been demonstrated experimentally in mountainous ecosystems of sub-Antarctic Chile and sub-Arctic Norway,
372 where the removal of vegetation was the most important factor throughout the whole invasion process
373 (establishment, growth and flowering) (Lembrechts et al. 2016). Additionally, many of these vegetation
374 removal events interact with dispersal vectors due to the presence of cattle and trails (Liedtke et al. 2019). These
375 factors have specifically been shown to increase the propagule pressure of non-native species such as
376 *Convolvulus arvensis* and *Taraxacum officinale* in Central Andes, Argentina (Barros et al. 2020).

377
378 Interestingly, anthropogenic factors were not the main factor along all roads. Indeed, in Malalcahuello
379 National Reserve road, the abundance of native species explained most of the variance in the abundance of non-
380 native species. This road is characterized by densely settled low elevation areas and grasslands dominated by
381 non-native species. But as elevation increases, areas with a high richness of native species can be observed,
382 which would function as a biotic filter for the establishment of non-native species. This pattern coincides with
383 the hypothesis of biotic resistance that indicates that the most diverse communities are more resistant to the
384 invasion of non-native species (Catford et al. 2009; Martin et al. 2009). Additionally, areas with higher
385 herbaceous cover had a lower abundance of non-native species, indicating an important biotic resistance of the
386 native communities towards the population increase of non-native species (Albuquerque et al. 2010; Phillips-
387 Mao et al. 2014; Lembrechts et al. 2016).

388
389 It is important to highlight that abiotic conditions, such as soil and air temperature, were in none of the
390 cases the most important driver at local scales, even though they have been found to be crucial drivers of local
391 invasion in countless other studies, mainly at high elevations (Giraldo-Cañas et al. 2010; Crespo-Pérez et al.
392 2011; McDougall et al. 2011; Paiaro et al. 2011; Seipel et al. 2012; Tecco et al. 2016; Taylor et al. 2016; Cuesta
393 et al. 2017). Our conclusions are however in line with other studies showing that variables such as temperature,
394 precipitation and soil moisture are at local scales usually subjugated by factors such as disturbance and
395 propagule pressure (Pollnac et al. 2010; Tomasetto et al. 2013; Lembrechts et al. 2016; Buri et al. 2017). In
396 fact, the temperature values themselves (expressed as Growing Degree Days in the air and soil) did not vary
397 significantly along the elevation gradient, as local topographical and human-induced heterogeneity overrides
398 the adiabatic lapse rate when measured in-situ (Lembrechts et al. 2017). Additionally, disturbance events create
399 important changes in all these abiotic factors, making disturbance proxies themselves better explanatory
400 variables than the separate abiotic conditions related to climate (Lembrechts et al. 2016).

401
402
403

404 **Management recommendations for non-native species**

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

419

420 **Conclusion**

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

426 Our observational study demonstrated that anthropogenic factors (distance to human settlements and
427 distance to road) override the effect of abiotic factors on the richness and abundance of non-native species at
428 the local scale. At the regional scale, however, non-native plant species richness is mainly explained by abiotic
429 factors such as nitrogen content and pH, while the abundance of non-native species is again explained by
430 anthropogenic factors.

431 Based on these results, we can reaffirm the conclusion experimentally obtained by Lembrechts et al.
432 (2016) that anthropogenic factors are the most important to understand the success of non-native species in
433 mountain ecosystems. Importantly, this implies that climatic factors are currently an unlikely factor limiting the
434 distribution of non-native species along altitudinal gradients, as shown for example experimentally for the Swiss
435 Alps (Haider et al. 2011) and in mountain ecosystems of Chile and Norway (Lembrechts et al. 2016). These
436 conclusions reinforce the importance of keeping the expansion of human effects to a minimum (tourism,
437 presence of livestock, infrastructure), both through biosafety protocols or direct control measures on tourism
438 and agricultural activities. Only if such measures are taken, we will be able to control the spread of non-native
439 species in these mountain ecosystems.

440

441 **References**

442

443 Alexander JM, Lembrechts JJ, Cavieres LA, Daehler C, Haider S, Kueffer C, Rew LJ (2016) Plant invasions into
444 mountains and alpine ecosystems: current status and future challenges. *Alpine Botany*, 126(2), 89-103.
445 <https://doi.org/10.1007/s00035-016-0172-8>

446

447 Arroyo MTK, Marticorena C, Matthei O, Cavieres L (2000) Plant invasions in Chile: present patterns and future
448 predictions. *Invasive species in a changing world*, 385-421.

449

450 Barros A, Pickering CM (2014) Non-native plant invasion in relation to tourism use of Aconcagua Park, Argentina,
451 the highest protected area in the Southern Hemisphere. *Mountain Research and Development*, 34(1), 13-26.
452 <https://doi.org/10.1659/MRD-JOURNAL-D-13-00054.1>

453

454 Barros A, Gonnet J, Pickering C (2013) Impacts of informal trails on vegetation and soils in the highest protected
455 area in the Southern Hemisphere. *Journal of environmental management*, 127, 50-60.
456 <https://doi.org/10.1016/j.jenvman.2013.04.030>
457

458 Barros A, Aschero V, Mazzolari A, Cavieres LA, Pickering CM (2020) Going off trails: How dispersed visitor use
459 affects alpine vegetation. *Journal of Environmental Management*, 267, 110546.
460 <https://doi.org/10.1016/j.jenvman.2020.110546>
461

462 Barton K (2016) R package MuMIn: model selection and model averaging based on information criteria (AICc and
463 alike).
464

465 Buri A, Cianfrani C, Pinto-Figueroa E, Yashiro E, Spangenberg JE, Adatte T, Pradervand JN (2017) Soil factors
466 improve predictions of plant species distribution in a mountain environment. *Progress in Physical*
467 *Geography*, 41(6), 703-722. <https://doi.org/10.1177%2F0309133317738162>
468

469 Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into
470 a single theoretical framework. *Diversity and distributions*, 15(1), 22-40. [https://doi.org/10.1111/j.1472-](https://doi.org/10.1111/j.1472-4642.2008.00521.x)
471 [4642.2008.00521.x](https://doi.org/10.1111/j.1472-4642.2008.00521.x)
472

473 Cavieres LA, Badano EI, Sierra-Almeida A, Molina-Montenegro MA (2007) Microclimatic modifications of
474 cushion plants and their consequences for seedling survival of native and non-native herbaceous species in the
475 high Andes of central Chile. *Arctic, Antarctic, and Alpine Research*, 39(2), 229-236.
476 [https://doi/full/10.1657/1523-0430\(2007\)39\[229:MMOCPA\]2.0.CO;2](https://doi/full/10.1657/1523-0430(2007)39[229:MMOCPA]2.0.CO;2)
477

478 Cavieres LA, Quiroz CL, Molina-Montenegro MA, Muñoz AA, Pauchard A (2005) Nurse effect of the native
479 cushion plant *Azorella monantha* on the invasive non-native *Taraxacum officinale* in the high-Andes of central
480 Chile. *Perspectives in Plant Ecology, Evolution and Systematics*, 7(3), 217-226.
481 <https://doi.org/10.1016/j.ppees.2005.09.002>
482

483 Choler P, Michalet R, Callaway RM (2001) Facilitation and competition on gradients in alpine plant
484 communities. *Ecology*, 82(12), 3295-3308. [https://doi.org/10.1890/0012-](https://doi.org/10.1890/0012-9658(2001)082[3295:FACOGI]2.0.CO;2)
485 [9658\(2001\)082\[3295:FACOGI\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[3295:FACOGI]2.0.CO;2)
486

487 Crespo-Pérez V, Rebaudo F, Silvain JF, Dangles O (2011) Modeling invasive species spread in complex
488 landscapes: the case of potato moth in Ecuador. *Landscape ecology*, 26(10), 1447-1461.
489 <https://doi.org/10.1007/s10980-011-9649-4>
490

491 Cuesta F, Muriel P, Llambí LD, Halloy S, Aguirre N, Beck S, Gámez LE (2017) Latitudinal and altitudinal patterns
492 of plant community diversity on mountain summits across the tropical Andes. *Ecography*, 40(12), 1381-1394.
493 <https://doi.org/10.1111/ecog.02567>
494

495 De Albuquerque FS, Castro-Díez P, Rueda M, Hawkins BA, Rodríguez MA (2011) Relationships of climate,
496 residence time, and biogeographical origin with the range sizes and species richness patterns of exotic plants in
497 Great Britain. *Plant Ecology*, 212(11), 1901. <https://doi.org/10.1007/s11258-011-9962-7>
498

499 Dray S, Péliissier R, Couteron P, Fortin MJ, Legendre P, Peres-Neto PR, Dufour AB (2012) Community ecology
500 in the age of multivariate multiscale spatial analysis. *Ecological Monographs*, 82(3), 257-275.
501 <https://doi.org/10.1890/11-1183.1>
502

503 Fernández-Murillo MP, Rico A, Kindlmann P (2015) Exotic plants along roads near La Paz, Bolivia. *Weed*
504 *Research*, 55(6), 565-573. <https://doi.org/10.1111/wre.12174>
505

506 Figueroa JA, Castro SA, Marquet PA, Jaksic FM (2004) Invasión de plantas exóticas en la región mediterránea de
507 Chile: causas, historia e impactos. *Revista chilena de historia natural*, 77(3), 465-483.
508 <http://dx.doi.org/10.4067/S0716-078X2004000300006>
509

510 Fuentes-Lillo E, Pauchard A (2019) Invasiones en montañas: ¿ Cuánto hemos avanzado en los últimos 10 años y
511 cuáles son los desafíos para los ecosistemas de los Andes?. *Gayana Bot*, 76(2), 141-155.
512 <http://dx.doi.org/10.4067/S0717-66432019000200141>
513

514 Fuentes N, Pauchard A, Sánchez P, Esquivel J, Marticorena A (2013) A new comprehensive database of alien plant
515 species in Chile based on herbarium records. *Biological Invasions*, 15(4), 847-858.
516 <https://doi.org/10.1007/s10530-012-0334-6>
517

518 Giraldo-Canas D (2010) Distribution and invasion of C3 and C4 grasses (Poaceae) along an altitudinal gradient in
519 the Andes of Colombia. *Caldasia*, 32(1), 65-86. <https://www.jstor.org/stable/23642004>
520

521 Gobat JM, Aragno M, Matthey W (2004) The living soil: fundamentals of soil science and soil biology. Science
522 Publishers.
523

524 Gonzalez ME, Veblen TT, Sibold JS (2010) Influence of fire severity on stand development of Araucaria araucana–
525 Nothofagus pumilio stands in the Andean cordillera of south-central Chile. *Austral Ecology*, 35(6), 597-615.
526 <https://doi.org/10.1111/j.1442-9993.2009.02064.x>
527

528 Guo Q, Fei S, Shen Z, Iannone BV, Knott J, Chown SL (2018) A global analysis of elevational distribution of non-
529 native versus native plants. *Journal of biogeography*, 45(4), 793-803. <https://doi.org/10.1111/jbi.13145>
530

531 Haider S, Alexander J, Dietz H, Trepl L, Edwards PJ, Kueffer C (2010) The role of bioclimatic origin, residence
532 time and habitat context in shaping non-native plant distributions along an altitudinal gradient. *Biological*
533 *Invasions*, 12(12), 4003-4018.
534

535 Haider S, Kueffer C, Bruelheide H, Seipel T, Alexander JM, Rew LJ et al (2018) Mountain roads and non-native
536 species modify elevational patterns of plant diversity. *Global ecology and biogeography*, 27(6), 667-678.
537 <http://dx.doi.org/10.1007/s10530-010-9815-7>
538

539 Hossner L (2008) Field pH. In *Encyclopedia of Soil Science* (pp. 271-272). Springer Dordrecht.
540

541 Hughes C, Eastwood R (2006) Island radiation on a continental scale: exceptional rates of plant diversification
542 after uplift of the Andes. *Proceedings of the National Academy of Sciences*, 103(27), 10334-10339.
543 <https://doi.org/10.1073/pnas.0601928103>
544

545 Kueffer C, Daehler C, Dietz H, McDougall K, Parks C, Pauchard A et al (2014) The Mountain Invasion Research
546 Network (MIREN). Linking local and global scales for addressing an ecological consequence of global
547 change. *Gaia-Ecological Perspectives for Science and Society*, 23(3), 263-265.
548 <https://doi.org/10.14512/gaia.23.3.11>
549

550 Kumar S, Stohlgren TJ, Chong GW (2006) Spatial heterogeneity influences native and nonnative plant species
551 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)
552

553 Lembrechts JJ, Alexander JM, Cavieres LA, Haider S, Lenoir J, Kueffer C et al (2017) Mountain roads shift native
554 and non-native plant species' ranges. *Ecography*, 40(3), 353-364. <https://doi.org/10.1111/ecog.02200>
555

556 Lembrechts JJ, Lenoir J, Nuñez MA, Pauchard A, Geron C, Bussé G et al (2018). Microclimate variability in alpine
557 ecosystems as stepping stones for non-native plant establishment above their current elevational
558 limit. *Ecography*, 41(6), 900-909. <https://doi.org/10.1111/ecog.03263>
559

560 Lembrechts JJ, Milbau A, Nijs I (2014) Alien roadside species more easily invade alpine than lowland plant
561 communities in a subarctic mountain ecosystem. *PLoS One*, 9(2).
562 <https://doi.org/10.1371/journal.pone.0089664>
563

564 Lembrechts JJ, Pauchard A, Lenoir J, Nuñez MA, Geron C, Ven A et al (2016) Disturbance is the key to plant
565 invasions in cold environments. *Proceedings of the National Academy of Sciences*, 113(49), 14061-14066.
566 <https://doi.org/10.1073/pnas.1608980113>
567

568 Liedtke R, Barros A, Essl F, Lembrechts JJ, Wedegärtner RE, Pauchard A, Dullinger S (2020) Hiking trails as
569 conduits for the spread of non-native species in mountain areas. *Biological Invasions*, 22(3), 1121-1134.
570 <https://doi.org/10.1007/s10530-019-02165-9>
571

572 Luebert F, Plischoff P (2017) Sinopsis bioclimática y vegetacional de Chile: Segunda Edición.
573

574 Marini L, Bertolli A, Bona E, Federici G, Martini F, Prosser F, Bommarco R (2013) Beta-diversity patterns
575 elucidate mechanisms of alien plant invasion in mountains. *Global Ecology and Biogeography*, 22(4), 450-460.
576 <https://doi.org/10.1111/geb.12006>
577

578 Martin PH, Canham CD, Marks PL (2009) Why forests appear resistant to exotic plant invasions: intentional
579 introductions, stand dynamics, and the role of shade tolerance. *Frontiers in Ecology and the Environment*, 7(3),
580 142-149. <https://doi.org/10.1890/070096>
581

582 McDougall KL, Alexander JM, Haider S, Pauchard A, Walsh NG et al (2011) Alien flora of mountains: global
583 comparisons for the development of local preventive measures against plant invasions. *Diversity and*
584 *Distributions*, 17(1), 103-111. <https://doi.org/10.1111/j.1472-4642.2010.00713.x>
585

586 McDougall KL, Lembrechts J, Rew LJ, Haider S, Cavieres LA, Kueffer C et al (2018) Running off the road:
587 roadside non-native plants invading mountain vegetation. *Biological invasions*, 20(12), 3461-3473.
588 <http://dx.doi.org/10.1007/s10530-018-1787-z>
589

590 Müllerová J, Vítková M, Vítek O (2011) The impacts of road and walking trails upon adjacent vegetation: Effects
591 of road building materials on species composition in a nutrient poor environment. *Science of the total*
592 *environment*, 409(19), 3839-3849. <https://doi.org/10.1016/j.scitotenv.2011.06.056>
593

594 Oke OA, Thompson KA (2015) Distribution models for mountain plant species: the value of elevation. *Ecological*
595 *Modelling*, 301, 72-77. <https://doi.org/10.1016/j.ecolmodel.2015.01.019>
596

597 Otto R, Arteaga MA, Delgado JD, Arévalo JR, Blandino C, Fernández-Palacios JM (2014) Road edge effect and
598 elevation patterns of native and alien plants on an oceanic island (Tenerife, Canary Islands). *Folia*
599 *Geobotanica*, 49(1), 65-82. <https://doi.org/10.1007/s12224-013-9159-z>
600

601 Paiaro V, Cabido M, Pucheta E (2011) Altitudinal distribution of native and alien plant species in roadside
602 communities from central Argentina. *Austral Ecology*, 36(2), 176-184. [https://doi.org/10.1111/j.1442-](https://doi.org/10.1111/j.1442-9993.2010.02134.x)
603 [9993.2010.02134.x](https://doi.org/10.1111/j.1442-9993.2010.02134.x)
604

605 Pauchard A, Alaback PB (2004) Influence of elevation, land use, and landscape context on patterns of alien plant
606 invasions along roadsides in protected areas of South-Central Chile. *Conservation Biology*, 18(1), 238-248.
607 <https://doi.org/10.1111/j.1523-1739.2004.00300.x>
608

609 Pauchard A, Shea K (2006) Integrating the study of non-native plant invasions across spatial scales. *Biological*
610 *invasions*, 8(3), 399-413. <https://doi.org/10.1007/s10530-005-6419-8>
611

612 Pauchard A, Kueffer C, Dietz H, Daehler CC, Alexander J, Edwards P et al (2009) Ain't no mountain high enough:
613 plant invasions reaching new elevations. *Frontiers in Ecology and the Environment*, 7(9), 479-486.
614 <https://doi.org/10.1890/080072>
615

616 Pauchard A, Milbau A, Albiñá A, Alexander J, Burgess T, Daehler C et al (2016) Non-native and native organisms
617 moving into high elevation and high latitude ecosystems in an era of climate change: new challenges for ecology
618 and conservation. *Biological invasions*, 18(2), 345-353. <https://dx.doi.org/10.1007/s10530-015-1025-x>
619

620 Pearson DE, Ortega YK, Villarreal D, Lekberg Y, Cock MC, Eren Ö, Hierro JL (2018) The fluctuating resource
621 hypothesis explains invasibility, but not exotic advantage following disturbance. *Ecology*, 99(6), 1296-1305.
622 <https://doi.org/10.1002/ecy.2235>
623

624 Petitpierre B, McDougall K, Seipel T, Broennimann O, Guisan A et al (2016) Will climate change increase the risk
625 of plant invasions into mountains?. *Ecological Applications*, 26(2), 530-544. <https://doi.org/10.1890/14-1871>
626

627 Phillips-Mao L, Larson DL, Jordan NR (2014) Effects of native herbs and light on garlic mustard (*Alliaria petiolata*)
628 invasion. *Invasive Plant Science and Management*, 7(2), 257-268. <https://doi.org/10.1614/IPSM-D-13-00003.1>
629

630 Pollnac F, Seipel T, Repath C et al (2012) Plant invasion at landscape and local scales along roadways in the
631 mountainous region of the Greater Yellowstone Ecosystem. *Biological Invasions*, 14(8), 1753-1763.
632 <http://dx.doi.org/10.1007/s10530-012-0188-y>
633

634 Quiroz CL, Cavieres LA, Pauchard A (2011) Assessing the importance of disturbance, site conditions, and the
635 biotic barrier for dandelion invasion in an Alpine habitat. *Biological invasions*, 13(12), 2889-2899.
636 <https://doi.org/10.1007/s10530-011-9971-4>
637

638 Rodriguez R, Marticorena C, Alarcón D, Baeza C et al (2018) Catálogo de las plantas vasculares de Chile. *Gayana*.
639 *Botánica*, 75(1), 1-430. <http://dx.doi.org/10.4067/S0717-66432018000100001>
640

641 Roques A (2010) Alien forest insects in a warmer world and a globalised economy: impacts of changes in trade,
642 tourism and climate on forest biosecurity. *New Zealand Journal of Forestry Science*, 40(Suppl), S77-S94.
643

644 Sandoya V, Pauchard A, Cavieres LA (2017). Natives and non-natives plants show different responses to elevation
645 and disturbance on the tropical high Andes of Ecuador. *Ecology and evolution*, 7(19), 7909-7919.
646 <https://doi.org/10.1002/ece3.3270>
647

648 Santilli L, Castro SA, Figueroa JA et al (2018) Exotic species predominates in the urban woody flora of central
649 Chile. *Gayana. Botánica*, 75(2), 568-588. <http://dx.doi.org/10.4067/S0717-66432018000200568>
650

651 Seipel T, Kueffer C, Rew, LJ, Daehler CC, Pauchard A et al (2012) Processes at multiple scales affect richness and
652 similarity of non-native plant species in mountains around the world. *Global Ecology and Biogeography*, 21(2),
653 236-246. <https://doi.org/10.1111/j.1466-8238.2011.00664.x>
654

655 Shrestha UB, Sharma KP, Devkota A, Siwakoti M, Shrestha BB (2018) Potential impact of climate change on the
656 distribution of six invasive alien plants in Nepal. *Ecological Indicators*, 95, 99-107.
657 <https://doi.org/10.1016/j.ecolind.2018.07.009>
658

659 Slodowicz D, Descombes P, Kikodze D, Broennimann O et al (2018) Areas of high conservation value at risk by
660 plant invaders in Georgia under climate change. *Ecology and evolution*, 8(9), 4431-4442.
661 <https://doi.org/10.1002/ece3.4005>
662

663 Taylor S, Kumar L, Reid N, Kriticos DJ (2012) Climate change and the potential distribution of an invasive shrub,
664 *Lantana camara* L. *PloS one*, 7(4). <https://doi.org/10.1371/journal.pone.0035565>
665

666 Team RC (2013) R: A language and environment for statistical computing.
667

668 Tecco PA, Pais-Bosch AI, Funes G et al (2016) Mountain invasions on the way: are there climatic constraints for
669 the expansion of alien woody species along an elevation gradient in Argentina?. *Journal of Plant Ecology*, 9(4),
670 380-392. <https://doi.org/10.1093/jpe/rtv064>
671

672 Terzano D, Kotzé I, Marais C, Cianciullo S et al (2018) Environmental and anthropogenic determinants of the
673 spread of alien plant species: insights from South Africa's quaternary catchments. *Plant ecology*, 219(3), 277-
674 297. <https://doi.org/10.1007/s11258-018-0795-5>
675

676 Tomasetto F, Duncan RP, Hulme PE (2013) Environmental gradients shift the direction of the relationship between
677 native and alien plant species richness. *Diversity and Distributions*, 19(1), 49-59.
678 <https://doi.org/10.1111/j.1472-4642.2012.00939.x>
679
680 Urbina JC, Benavides JC (2015) Simulated small scale disturbances increase decomposition rates and facilitates
681 invasive species encroachment in a high elevation tropical Andean peatland. *Biotropica*, 47(2), 143-151.
682 <https://doi.org/10.1111/btp.12191>
683
684 Venables WN, Ripley BD (2002) Random and mixed effects. In *Modern applied statistics with S* (pp. 271-300).
685 Springer, New York, NY. https://doi.org/10.1007/978-0-387-21706-2_10
686
687 Vonlanthen CM, Kammer PM, Eugster, W et al (2006) Alpine vascular plant species richness: the importance of
688 daily maximum temperature and pH. *Plant Ecology*, 184(1), 13-25. [https://doi.org/10.1007/s11258-005-9048-](https://doi.org/10.1007/s11258-005-9048-5)
689 [5](https://doi.org/10.1111/j.1469-185X.2012.00235.x)
690
691 Wisz MS, Pottier J, Kissling WD, Pellissier L et al (2013) The role of biotic interactions in shaping distributions
692 and realised assemblages of species: implications for species distribution modelling. *Biological reviews*, 88(1),
693 15-30. <https://doi.org/10.1111/j.1469-185X.2012.00235.x>
694
695
696

697 **Table 1** Values of R^2 , AIC are shown for each scale (local, i.e. separately for each road, and regional) and for
698 each group analyzed (abiotic, biotic and anthropogenic), both for the richness and abundance of non-native
699 species. Lower AIC values show the best model for each scale. LLNP (Laguna Laja National Park), MNR
700 (Malcalhuello National Reserve), CNP (Conguillio National Park)

| | Non-native Richness | | Non-native Abundance | |
|-----------------|---------------------|---------------|----------------------|---------------|
| | R^2 | AIC | R^2 | AIC |
| LLNP | | | | |
| 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 |
| MNP | | | | |
| 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 |
| CNP | | | | |
| 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 |
| Regional | | | | |
| 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 |

721
722
723
724
725
726
727