Non-Native Herbivores Promote Plant Invasions Away From Mountain Roads in the Andes

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Title: Non-native herbivores promote plant invasions away from mountain roads in the Andes

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26 **Abstract**

27 While the role of environmental filters, usually described by elevation as proxy, and anthropogenic
28 disturbance as drivers of non-native plant diversity and abundance in mountains have been
29 extensively studied, the impact of herbivores are less explored. Livestock grazing can facilitate the
30 introduction of non-native species by seed dispersal and reduce biotic resistance due to
31 consumption and trampling of native plants, even in the highest protected areas in the Andes. We
32 here explored the effects of elevation, livestock and distance to the road on non-native and native
33 plant distributions. Our results confirm the largely negative relationship of non-native plant richness
34 and cover with elevation, with a peak in richness and cover at low to intermediate elevations.
35 Similarly, we show a strong decline in non-native richness with increasing distance to the road,
36 especially at low elevations, accompanied by a strong negative effect of roads on native species
37 richness. Most importantly, however, we show that the presence of non-native herbivores greatly
38 increases the cover of non-native species away from the roadside, identifying herbivore disturbance
39 as a potential catalyst of non-native plant invasion into natural vegetation of high-Andean protected
40 areas. Our results confirm the often-shown role of disturbance as driver of plant invasions in
41 mountains, yet highlight the interactive effects of disturbance by roads and herbivory: roads funnel
42 non-native species towards higher elevations, while non-native herbivores can promote non-native
43 plant success away from the roadside and into the natural vegetation. Hence, regulating soil and
44 non-native herbivory disturbance is important for minimizing plant invasions at high elevation in
45 the Arid Andes.

46 **Keywords:** livestock, aliens, plant invasions, elevational gradient, Andean plant communities.

47

48 **Introduction**

49 Plant invasions in mountains are an increasing threat to biodiversity conservation as climate
50 changes and anthropogenic disturbance increases (Pauchard et al., 2009; McDougall et al., 2011;
51 Seipel et al., 2012; Petitpierre et al., 2016). There have been recent efforts to assess distribution and
52 abundance of non-native plants in mountain areas around the world including in Europe (Alexander
53 et al., 2009), Asia (McDougall et al., 2011), North America (Parks et al., 2005), Australia
54 (McDougall et al., 2005), New Zealand (Jesson et al., 2000), and the Andes in South America
55 (Pauchard & Alaback, 2004; Cavieres et al., 2005, 2007; Badano et al., 2007; Jiménez et al., 2008;

56 Fuentes-Lillo & Pauchard, 2019). Most of these studies highlighted that disturbance and
57 environmental filtering due to increasing abiotic stress with elevation both play a critical role
58 controlling non-native plant diversity in mountains (Alexander et al., 2011; Alexander et al., 2016).

59 Roads are a common disturbance factor in mountains and are known to facilitate the
60 expansion of non-native plants to higher elevations (Alexander et al., 2011) and lead to biotic
61 homogenization (Haider et al., 2020). Roads can affect various local abiotic and biotic factors
62 including soil structure and chemistry (Mullerova et al., 2011), removal of native vegetation during
63 its construction and maintenance (Gelbard & Belnap, 2003), and changes in microclimatic
64 conditions (Lembrechts et al., 2016). Roads can also facilitate non-native species introductions
65 through the unintentional dispersal of seeds by vehicles (Ansong & Pickering, 2013a). As a result,
66 mountain roads often host a higher diversity of non-native species than the surrounding landscape,
67 yet with a progressive decline in non-native diversity with increasing elevation (Alexander et al.,
68 2011). With their often disruptive effects on native species communities and positive effects on
69 non-natives, mountain roads can truly funnel non-native species into mountain environments.
70 Nevertheless, invasion of non-native plant species away from mountain roads has been shown to be
71 fairly limited up till now, among others due to the invasion resistance of undisturbed mountain
72 vegetation (Lembrechts et al., 2016, McDougall et al., 2018). As a result, the set of traits needed for
73 non-native plant species to follow roads to high elevations is different from the one needed to
74 invade undisturbed mountain vegetation (McDougall et al., 2018).

75 Domestic livestock is an important disturbance factor and can promote the introduction and
76 establishment of non-native species acting as seed dispersal agents and through trampling and
77 grazing disturbance (Loydi & Zalba, 2009; Ansong & Pickering, 2013b). These disturbances can
78 reduce biotic resistance due to consumption and trampling, potentially facilitating the introduction
79 and expansion of disturbance-resistant species, including many non-native species, even in the
80 highest protected areas in the Andes (Barros & Pickering, 2014; Barros et al., 2020). As such,
81 domestic livestock could potentially break the stalemate that limits plant invasion away from
82 roadsides by reducing the resistance of the native vegetation and changing abiotic conditions in
83 favor of the roadside invaders. Additionally, “alien alliances” have commonly been observed,
84 where non-native herbivores promote non-native plants from their home range (Parker et al., 2006).

85 Despite the recognized importance of environmental filtering on determining diversity of
86 both natives and non-natives in mountains (McCain & Grytnes, 2010), plant richness patterns of
87 natives vs non-natives can differ substantially. A recent global synthesis along elevation gradients
88 highlighted that distribution patterns are not ubiquitously consistent, with differences across regions
89 and between plots at roadsides and undisturbed further plots (Haider et al., 2018). For the Andes
90 region, explicit comparisons of plant species richness along elevation gradients have shown that the
91 most common pattern for non-natives and natives was a hump shaped curve, both in the roadside
92 and the interior vegetation (Haider et al., 2018). However, in plots at the roadsides a monotonically
93 decrease for native richness was detected in temperate and tropical forests in Argentina and
94 Colombia (Sandoya et al., 2017; Haider et al., 2018). Roads' effect on plant richness patterns in the
95 Arid Andes of Argentina have not yet been explored. In this region, although native plant
96 communities are characterized by species adapted to extreme climate conditions at high elevations,
97 non-native species are still present, potentially driven by human disturbances and livestock (Barros
98 & Pickering, 2014; Barros et al., 2020).

99 Studying the combined effects of elevation, road disturbance and domestic livestock (and/or
100 other non-native herbivores) on non-native plant distributions is thus critical to understand the
101 interactive effects of these multiple disturbances, especially in regions where non-native herbivores
102 are the main disturbance agents and a potential threat for plant invasions (Barros et al., 2014; Barros
103 et al., 2020; Liedtke et al., 2020). Understanding how both disturbance types separately and
104 together affect native communities and promote non-native plant invasions can assist in the
105 development of mitigation actions as well as preventing further plant invasions in higher elevation
106 ecosystems. It can also contribute to disentangle the importance of theories about environmental
107 filtering (elevation), biotic resistance (herbivores) and soil disturbances (i.e. roads) and their
108 interactions (Catford et al., 2009).

109 We here aim to understand the effects of disturbance related to road and non-native
110 herbivores on plant diversity and invasions in the Arid Andes of Argentina. Specifically, we ask: (1)
111 How non-native and native plant richness are affected by elevation, road disturbance and non-native
112 herbivores? and 2) How non-native cover is affected by non-native herbivores in conjunction with
113 road disturbance along elevation? For the first question, we hypothesized that native and non-native
114 plant richness differ in their distribution pattern along elevation. We predict that many non-native

species would be more restricted in elevation than native species due to a lower adaptation to local environmental stress and the lowland provenance of most non-native species. We also expect that distance to the road and herbivores, as a surrogate of disturbance, would also affect positively non-native richness by increased bare soil and propagule pressure. Instead, native richness would be negatively affected by these disturbance factors. For the second question, we expect that in conjunction with environmental filtering imposed by elevation, distance to the road and the abundance of non-native herbivores would also be important factors explaining non-native cover.

Methods:

Site description

The study was conducted during summer 2016-2017 in the central zone of the Arid Andes of Argentina, in the province of Mendoza from -32° S to -33° S, in the Cordillera Frontal and Precordillera mountain ranges. We selected three mountain roads in protected areas: Villavicencio Natural Reserve (-32° 31' 31" S, - 69° 0' 33" W), Cordon del Plata Provincial Park (-33° 0' 14" S, 69° 17' 50" W), and Portillo-Piuquenes Natural Reserve (- 33° 35' 51" S, - 69° 0' 33" W) (Fig. 1). The three roads were selected due to their similarity in flora and bioclimatic conditions, and for the wide elevational gradient that they cover, ranging from 1755 to ~3919 m a.s.l. The gravel roads are open to traffic year-round, except at higher elevations (>2800 m a.s.l) during winter, where they can be temporarily closed due to snow cover.

Overall, the climate in the region is cold and dry, with strong variations in temperature and precipitation due to the broad elevational range and complex topography (Méndez, 2004). Low elevation areas are characterized by greater aridity and higher temperatures whereas higher elevation areas are cooler and wetter (Méndez, 2004). Precipitation mainly falls in autumn and winter, with precipitation totals ranging from 398 mm in Cordon del Plata to 120 mm in Villavicencio. On average, annual mean temperature ranges from 18°C in summer to 6° C in winter, with minimum temperatures during winter season below 0° C in these mountain roads (Cara et al., unpublished).

Soils in general are little developed and exhibit great spatial heterogeneity in depth and granulometric composition (Méndez, 2004; Méndez et al., 2006). Between 2400-3200 m a.s.l soils

are seasonally frozen, with permafrost occurring at higher elevations (Roig et al., 2007). The region forms part of the Andean biogeographic region (Morrone, 2006), and features a low (1700-2400 m a.s.l), intermediate (2500-3200) and high Andean vegetation belt (3200-4000 m a.s.l). The surveys were conducted mostly in steppe vegetation. The low and intermediate belts are characterized by shrublands (dominated by species such as *Adesmia pinifolia*, *A. aegiceras*, *Colliguaja integerrima*, *Junellia juniperina*) and herbaceous steppes (e.g. *Pappostipa chrysophylla*, *Senecio subulatus*, *Acaena pinnatifida*). The high Andean belt, where vegetation is more sparse, is dominated by cushion shrubs (e.g. *Azorella monantha*, *A. subterranea*) and some perennial herbaceous plants (e.g. *S. trifidus*, *Poa holciformis*) (Méndez et al., 2006, Kiesling et al., In Press). Previous floristic surveys have recorded over 500 native plant species in the region (Méndez et al., 2006; Méndez, 2009).

The provincial parks surrounding these mountain roads have limited past human use, and currently have very little human infrastructure except for a few mountain lodges. The main anthropogenic pressure results from regular touristic activities (sightseeing & mountain sports, use of mountain lodges), and livestock grazing, including horses and cows (Barros & Pickering, 2015). Other non-native wild grazers include the European hare (*Lepus europaeus*). The only large native grazing mammal is the camelid *Lama guanicoe* (guanaco) (Barros et al., 2014). Small and medium native rodents are also common, including species of caviomorphs such as the genus *Galea*, and several genera of sigmodontinae rodents such as *Phyllotis*, *Euneomys*, *Abrothrix*, among others (Novillo & Ojeda, 2014)

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165 *Field sampling design and data collection*

Standardized vegetation surveys following the survey design of the international Mountain Invasion Research Network (MIREN, Haider et al., 2021) were performed along the 3 mountain roads between spring 2016 and summer 2017. Each road was divided into 19 equally spaced elevation bands along the gradient, resulting in 20 sample sites (hereafter called ‘transects’) per road. Each transect had a "T" shape, consisting of three 50 x 2 m plots, one along the edge of the road (plot 1) and two others perpendicular to the road and leading away from the edge of the road (plot 2 and 3).

172 We recorded the cover percentage of all angiosperms and gymnosperms in each plot in each
173 transect, using visual estimation. Total vegetation cover was estimated by the sum of each species
174 cover. Additionally, abundance of feces of ungulate and medium mammals and their identity and
175 status (non-native or native) were noted. Non-native herbivores included horses and mules, cows,
176 goats, and lagomorphs (European rabbits (*Oryctolagus cuniculus*) and European hare (*Lepus*
177 *europaeus*)). Native mammals included rodents and the wild camelid *Lama guanicoe*.

178 Plant species were identified, verified and finally stored in the Ruiz Leal Herbarium MERL
179 (IADIZA, Argentina). Plant species identification and classification as native or non-native was
180 based on the Darwinion Institute Flora database (www.floraargentina.edu.ar) following criteria by
181 Zuloaga et al. (2008). Data was collected, compiled and standardized following the protocol of the
182 MIREN consortium network and submitted to the MIREN database (Haider et al., 2021).

183

184 *Data Analyses*

185 All the analyses were performed in R (R Core, 2018). We analyzed if native and non-native plant
186 richness changed with elevation, abundance of non-native herbivores, and distance to the road
187 (PLOT 1=near road, PLOT 2=middle, PLOT 3= interior) by fitting mixed generalized linear models
188 (GLMMs) assuming a Poisson (log link). We used the same explanatory variables to analyze non-
189 native cover assuming a binomial (logit link) distribution. For GLMMs, we used `glmer()` function in
190 the `lme4` package (Bates et al., 2015). In all the models, road was used as a random factor due to our
191 field design for data collection. Continuous predictor variables were centered and scaled in order to
192 standardize predictions so that the units of the regression coefficients are the same. In order to
193 explore predictive importance of fixed and random effects on plant richness and cover we applied
194 `r.squaredGLMM()` function from `MuMIn` package (Barton, 2020) and calculated marginal and
195 conditional R^2 , this is the variance explained by fixed effects and the variance explained by both
196 fixed and random effects, respectively (Nakagawa & Schielzeth, 2013). To analyze the variance
197 explained in GLMMs by unique or shared predictors we used `partR2()` function in `partR2` package
198 (Stoffel et al., 2021), this is calculated by monitoring the reduction in the fixed effect variance when
199 a specified predictor is removed from the model, in relation to the total estimated variance.

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201 We analyzed plant richness separately for native and non-native species. In order to
 202 select the best relationship of richness and explanatory variables we compared models with or
 203 without quadratic elevation term, and models with and without the interaction of elevation and
 204 distance to the road, with and without the interaction between non-native herbivore abundance and
 205 distance to the road. We compared with Likelihood Ratio Tests the adjustment of models with and
 206 without interaction terms and to determine whether to keep or not interactive effects. Non-native
 207 plant cover was tested using as response variable the ratio of non-native cover: total plant cover to
 208 consider the expected low cover in harsh habitats in the high Andes, and to show the relative non-
 209 native plant dominance in the total vegetation cover.

210

211 **Results:**

212 *(1) General results*

213 A total of 360 plant species were recorded along the 3 surveyed mountain roads, of which 41 (11%)
 214 were non-native. Both native and non-native plant species richness decreased with elevation (Table
 215 1, Table S1, Fig. 1). In 88% of the plots, at least one non-native plant species was detected.
 216 Roadside plots hosted more than twice (2.33 times) the number of non-native species than the
 217 interior plots. The most common non-native species were from temperate European origin (Figs.
 218 S1, S2) and occupied an elevation range greater than 1000 m, with some of them distributed
 219 throughout the whole elevation gradient, including many common global invaders such as
 220 *Taraxacum officinale* and *Cerastium arvense*.

221 We recorded a total of 1639 animal droppings, of which 81% were from non-native
 222 herbivores, mainly horses or mules (41%), hares (20%) and cows (17%). Dung feces recorded from
 223 native herbivores were from guanacos (11 %) and micromammals (8%). At two of the roads,
 224 Manzano and Vallecitos, non-native herbivores (mainly cows and horses) were most abundant on
 225 the intermediate plots while along the third road they were more abundant (mainly European hare)
 226 in the roadside. The abundance of native and non-native herbivores were negatively correlated
 227 (Spearman correlation, $S = 1139500$, $p = 0.02$, $\rho = -0.17$), hence only non-native herbivore counts
 228 were included in the following analyses.

229 *(2) Native and non-native plant species richness*

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Both native and non-native plant species richness decreased with elevation, but road distance had contrasting effects. Indeed, native species richness was on average 24% lower in the roadside than in interior plots, while non-native richness was 50% greater at roadsides. Non-native herbivores were not important in explaining native and non-native species richness patterns (Table S1). In GLMMs variance associated to the random factor (road identity) was more important for native richness (~20%) than for non-native richness (~4%, see Table S1a, b).

Importantly, while native species richness decreased monotonously (Fig 2a), non-native richness was best described by a hump-shaped pattern – with a peak in richness below the mid-elevation point at around 2000-2200 m a.s.l. (Fig. 2b). The interaction between distance to the road and elevation was important to describe native richness, but it was irrelevant for non-native richness. Increasing distance to the road resulted in a regular decline in non-native richness. However, native richness was almost constant along the elevational gradient near the roadside, but decreased linearly in vegetation far away from the road. When analyzing variance partitioning for fixed effects in GLMMs, elevation explained most of non-native richness variance (71%) and distance to the road explained the rest of variance (7%). For native richness, the interaction of elevation and distance to the road explained 38% of the variance.

(3) *Non-native plant cover*

Non-native plant cover was explained by the interactions of elevation with road distance, and non-native herbivores with road distance. The variance associated to the random factor (road identity) was very low (1%). Elevation negatively affected non-native cover, yet it decreased smoother at roadsides compared to interior plots (Table S2, Fig 3a). Overall, non-native cover was always greater in roadsides than in interior plots (~ 12 % higher, Fig. 3a). Non-native plant cover was positively affected by the abundance of non-native herbivores, but only at middle and interior plots. These plots showed an increase in non-native cover with increasing herbivory from around 10 to 25% (Table S2, Fig. 3b). The variance was mainly explained by the interaction of elevation with road distance (16%), and a lower percentage (2%) was explained by the interaction of road distance with non-native herbivores.

257

Discussion

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Our study confirms the findings from a growing body of literature showing the negative correlation of non-native plant species with distance to the road and elevation (Alexander et al., 2011; Seipel et al., 2012; Lembrechts et al., 2014; Haider et al., 2018), yet goes further up by incorporating the role of non-native herbivores. Indeed, we found a positive effect of non-native herbivores on non-native cover in plots away from the road, highlighting their role in facilitating plant invasions into natural environments after their establishment in roadsides. These findings support previous research stating the importance of interacting effects, such as combined disturbance and climate, determining non-native plant invasions (Eschtruth & Battles, 2009; Geppert et al., 2021). Roads also positively affected non-native plant species richness, yet had a pervasive effect on native plants. These results emphasize the important role of recurrent disturbance from roads in creating novel communities dominated by non-native species in the extreme environment that characterize the high Andes.

Environmental filtering and road disturbance

Our results support previous research stating the importance of environmental filtering and disturbance in determining species richness patterns and non-native cover along elevation gradients (Alexander et al., 2011; Marini et al., 2012). The patterns found for non-native richness followed the most common patterns observed globally, with a curved hump-shape for non-natives and a linear decline with elevation for natives (Rahbek, 2005; McCain & Grytnes, 2010). This also supports previous research conducted in tropical and temperate parts of the Andes (Sandoya et al., 2017; Haider et al., 2018). The hump-shaped curve observed for non-natives can be attributed to the climatic harshness experienced at the two ends of the gradient in the Arid Andes, including higher aridity at low elevations and low temperatures at high elevations. Other studies have also observed that aridity can be a limiting factor for non-native plants success at lower elevations (Arevalo et al. 2005; Haider et al., 2010; Jakobs et al., 2010). At higher elevations, the combination of lower propagule pressure and lower temperatures may have limited non-native plant establishment, allowing only a subset of lowland species to occur at these elevations (Haider et al., 2010; Alexander et al., 2011; Marini et al., 2013; Averett et al., 2016; Haider et al., 2018). For native species, there was a lack of association between native richness and elevation in the roadside plots, probably explained by recurrent disturbance from roads.

Roadside environments are characterized by high rates of disturbance and reduced competition, often favoring non-native plants with more acquisitive strategies over native plants

with more conservative strategies (Spellerberg, 1998; Tecco et al., 2010; Haider et al., 2018). Non-natives recorded in our study area were mainly ruderal plants with broad tolerance to recurrent disturbance, also growing in other Andean regions and known as common global invaders (Fuentes-Lillo & Pauchard, 2019). Species were characterized by acquisitive strategies, mainly annuals or short-lived perennials herbs, with high relative growth rate, high seed reproduction and high Specific Leaf Area and low Leaf Dry Matter Content (Mazzolari et al., 2018). In contrast, native species, as observed in other mountain regions, tend to have more specific morphological and functional adaptations along the elevational gradient but with lower tolerance to recurrent human disturbance (Alexander et al., 2011). These are usually conservative species characterized by woody perennial forms, slow growth rate, reduced foliar area and high Leaf Dry Matter Content (Mazzolari et al., 2018). Hence the greater non-native richness at roadsides than interior plots, probably reflects the importance of their functional traits affecting their performance in roadside habitats. Other factors contributing to this pattern could be the higher propagule pressure on roads (Pauchard & Alaback, 2004), that can be associated to seed dispersal by vehicles and imported soil materials that increases seed banks of non-native species at roadside edges (Gelbard & Belnap, 2003; Ansong & Pickering, 2013a)

305 **The role of non-native herbivory on non-native plant invasions**

In addition to the role of road disturbance, non-native herbivores can contribute to non-native plant success in mountains. We found that non-native herbivores, using dung abundance as a proxy, interacted with distance to the road, promoting plant invasions at further distances from the road edge. The impact of non-native herbivores on non-native plant invasion has been widely documented before (Maron & Vilà, 2001; Parker & Hay, 2005; Bobadilla et al., 2020; Geppert et al., 2021). Habitat modification due to trampling disturbance from domestic livestock, for example, can damage vegetation and expose soils favouring non-native plants more tolerant to disturbances (Barros et al., 2014; Farrell & Fehmi, 2018); selective browsing and grazing on natives over non-native species can indirectly promote their abundance (Mack, 1989; Parker et al., 2006). Other mechanisms that could be promoting non-native seed establishment beyond roads are seeds dispersal through the fur, cots and in the dung of animals, with many of the most frequent non-natives recorded in our study (e.g. *Taraxacum officinale*, *Verbascum thapsus*, *Rosa rubiginosa*) known to be dispersed through livestock (Ansong & Pickering, 2013b; Dacar et al., 2019).

Other factors related to herbivory that could be contributing to non-native invasion, is the relatively high abundance of non-native herbivores compared to natives. Non-native herbivores (mainly horses and cows) were the most dominant (81%) and the only native grazing large mammal, the guanaco, only accounted for 11% in our study area. Native and non-native herbivores were also negatively correlated, with decreasing abundance of natives at greater abundance of non-natives. The lower abundance of large native herbivores, the guanaco, could be due to several reasons, including historical hunting pressure (Schroeder et al., 2013), differences in habitat selection (Ovejero et al. 2011; Esteban et al., 2012) and animal avoidance of areas with human pressure such as vehicle roads and settlements (Donadio & Buskirk, 2006; Acebes et al., 2012). Previous research has shown that alteration of herbivore communities, including loss or reduction of native herbivores, can reduce biotic resistance to plant invasions because native herbivores tend to limit the abundance of non-native plants while non-native herbivores tend to promote their abundance (Parker et al., 2006). This is linked to the invasional meltdown hypothesis that associates biological invasions with facilitation processes between non-native species (Relva et al., 2010; Simberloff & Von Holle, 1999).

Unfortunately, the nature of our study does not allow us to identify the underlying mechanisms that explain the positive relationship between non-native herbivory and plant invasions. To better understand how herbivory, including native and non-native grazers, affect non-native plant success in this system, further observational and experimental studies are required, including assessing feeding preferences of non-natives vs. native grazers e.g. (Relva et al., 2010; Morrison & Hay, 2011; Averill et al., 2016) as well as disentangling the direct effects (seed dispersal, trampling or consumption) and indirect effects (mutualistic interactions) of non-native herbivores on native and introduced plants (Villalobos & Zalba, 2010; Root et al., 2020).

342

343 **Conclusion**

Our study confirmed previous research assessing non-native and native plant distribution patterns along elevation gradients, observing similar patterns in the Arid Andes as those found globally, with largely declining richness of native and non-native plant species with increasing elevation. Our results also highlighted the importance of recurrent disturbance from roads in harsh environments,

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such as the Arid Andes, with strong negative impacts on native species richness in roadsides compared to areas further from the road, especially at lower elevations, yet significant increases in non-native species richness. Additionally, we found a positive effect of non-native herbivores on non-native plant success, highlighting their potential role as “alien allies” spreading non-native plants away from the roadside. The fact that non-native herbivory can promote invasions further from the roads and even at high elevations suggests that this disturbance potentially has a much broader area of impact than roadside disturbance itself. Consequently, implementing management guidelines aimed to minimize disturbance from roads and grazing of non-native herbivores is a key action for active restoration and to limit plant invasions in Andean mountains.

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DECLARATIONS

Conflict of interest The authors declare no conflict of interest.

Authors’ contributions: V. Aschero, A.A. Barros, A. Pauchard and J.J. Lembrechts designed the study; V.Aschero, A. Mazzolari, A.A. Barros, M.A. Alvarez, F. Cuevas, A. Novillo, M. Pérez Sosa, and L. Bonjour carried out the field work; L. Bonjour, M.A. Alvarez, V. Aschero, and A.A. Barros, identified the plant species; V.Aschero, A. A. Barros, analyzed the data and wrote the first draft of the article. All authors contributed to manuscript writing, editing the discussion, and critical review of the article.

Data availability

376 Data collected according to the MIREN road survey protocol. Details about data-sharing agreement
377 is available on the network’s website (www.mountaininvasions.org) and provided if requested to
378 VA vaschero@mendoza-conicet.gob.ar or AB anaagustinabarros@gmail.com.

379

380 **TABLES AND FIGURE CAPTIONS**

381 **Table 1.** Average number of species and percentage of vegetation cover (mean $\pm$ standard error)
382 estimated at different elevations (m a.s.l) per plot (100 m²). The data were collected following the
383 international MIREN standard T-transect vegetation survey.

Elevation	Range m a.s.l (min-max)	Native richness	Non-native richness	Native cover (%)	Non-native cover (%)
Low (n=21)	1754-2557	20 $\pm$ 5	5 $\pm$ 2	51.5 $\pm$ 31.8	23.0 $\pm$ 22.7
Middle (n=21)	2635-3272	19 $\pm$ 6	3 $\pm$ 2	58.7 $\pm$ 33.3	15.3 $\pm$ 16.3
High (n=18)	3300-3919	16 $\pm$ 7	1 $\pm$ 1	50.7 $\pm$ 32.3	5.8 $\pm$ 8.3

384

385 **FIGURE CAPTIONS**

386 **Fig. 1** Map of the study area located in the Arid Central Andes in Argentina (-33° 0' 14" S, 69° 17'
387 50" W). Red polygons represent protected areas and black lines the roads surveyed.

388 **Fig. 2** Predicted (lines) and observed (points) of (a) native and (b) non-native species richness along
389 the elevation gradient and at different distances from vehicular roads (Plot 1=roadside, 2= middle
390 and 3=interior) in the Arid Central Andes of Argentina. Because the explanatory variable had
391 different range, elevation was standardized using the *scale()* function in R.

392 **Fig. 3** Non-native plant cover response predicted by binomial GLMMs using (a) elevation and (b)
393 non-native herbivores as explanatory variables (color lines; Plot 1=roadside, 2= middle and
394 3=interior).

395

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Figures

Figure 1

Map of the study area located in the Arid Central Andes in Argentina ($-33^{\circ} 0' 14''$ S, $69^{\circ} 17' 50''$ W). Red polygons represent protected areas and black lines the roads surveyed.

Figure 2

Predicted (lines) and observed (points) of (a) native and (b) non-native species richness along the elevation gradient and at different distances from vehicular roads (Plot 1=roadside, 2= middle and 3=interior) in the Arid Central Andes of Argentina. Because the explanatory variable had different range, elevation was standardized using the scale() function in R.

Figure 3

Non-native plant cover response predicted by binomial GLMMs using (a) elevation and (b) non-native herbivores as explanatory variables (color lines; Plot 1=roadside, 2= middle and 3=interior).

Supplementary Files

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