

# Hiking and Livestock Favor Non-Native Plants in The High Andes

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## Research Article

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# Abstract

Hikers and livestock using mountain trails damage native vegetation and act as seed vectors, thus favouring the spread of non-native plants. We evaluated the effect of trails and livestock abundance on the success of non-native plants in the arid central Andes of Argentina. We surveyed six trails, covering elevations between 2400 m and 3570 m a.s.l. and recorded non-native and native vegetation using transects distributed along the elevational gradient and spanning distances up to 22 m from the trail. We assessed how non-native occurrence, richness and cover varied with distance from the trail, intensity of use by livestock, native plant community composition and elevation. We found that trails favoured non-native occurrence, but did not influence richness and cover, while livestock favoured non-native occurrence, richness and cover. Non-native richness and cover decreased with elevation and varied with native community composition. In addition, non-native richness was positively correlated with native shrub cover suggesting possible facilitative interactions. Our results show that despite strong environmental filtering that decreases non-native abundance with elevation, non-natives occur up to the upper limits of vegetation, and that trails and livestock favour their spread in the mountains.

# Introduction

Mountain ecosystems harbor high biodiversity with high endemism and can act as biodiversity refuges, especially during periods of rapid climate change. Mountain environments also offer ecosystem services such as water provision, recreation, and tourism (Grêt-Regamey et al. 2012; Perrigo et al. 2020). Biological invasions, a component of global change, threaten mountain biodiversity and the services it provides (Kowarik and von der Lippe 2007). Non-native plant species are widespread in mountain regions worldwide, with almost 200 species recorded in alpine regions (Alexander et al. 2016). Non-native plants may modify plant-pollinator interactions and reproductive success of native species (Aizen et al. 2008; Muñoz and Cavieres 2008; Bruckman and Campbell 2016; Goodell and Parker 2017), resident community composition (Gaertner et al. 2011; Bravo-Monasterio et al. 2016; Haider et al. 2018), trophic interactions (Valtonen et al. 2006; Pearson 2008), the hydrological cycle (Le Maitre et al. 2015), nutrient cycling, soil biology (Souza-Alonso et al. 2015; Fernandez et al. 2017; Le Roux et al. 2018), and ecosystem services (Vilà et al. 2011). Hence, the prospect of future climate change, growing tourism, and productive activities in mountains increase their vulnerability to plant invasions (Alexander et al. 2016).

Many of the non-native plants occurring in mountain areas are found in the vicinity of infrastructure that concentrate human traffic such as vehicular roads and tourist trails (Pickering and Mount 2010; Seipel et al. 2012; Barros and Pickering 2014). Roads can facilitate the introduction of non-native species into mountains as they combine high propagule pressure with recurrent disturbances (Pauchard and Alaback 2004; Lembrechts et al. 2017; McDougall et al. 2018). The combination of these two factors, which enhance ecosystem invasibility, can also occur on tourist trails as disturbance from trail construction and trampling by hikers reduces native vegetation height and cover, and degrades soils through erosion and compaction (Lucas-Borja et al. 2011; Barros et al. 2013, 2020; Ballantyne and Pickering 2015; Barros and Pickering 2017; Pickering and Norman 2017). Those impacts can decrease plant competition, increase

resource availability for non-native establishment, and alter species distribution ranges along elevational gradients (Davis et al. 2000). In addition, hikers may act as seed vectors through their clothing and equipment, carrying seeds from lower elevation areas, increasing propagule pressure (Pickering & Mount, 2010).

Livestock represents another important driver of plant invasions (Ansong and Pickering 2013), promoting the establishment of non-native plants even into high elevations (Barros and Pickering 2014; Liedtke et al. 2020). In the arid Andes of Argentina, for example, livestock such as horses and mules are widely used to transport baggage and equipment for mountaineers and hikers towards the high peaks (Barros et al. 2013). Through trampling and grazing, livestock also degrades soil and vegetation, while dispersing seeds in their fur and dung, increasing ecosystem susceptibility to invasion (Loydi and Zalba 2009; Ansong and Pickering 2013; Barros et al. 2013)

In addition to disturbance by visitors and livestock, climatic conditions and resident community composition can also affect plant invasions (Pauchard et al. 2009; Pollnac and Rew 2014). In mountains, climatic conditions vary strongly with elevation over narrow spatial scales; increased elevation is usually associated with lower temperatures, more persistent snow cover, and greater frequency of frost and exposure to UVB rays (Körner 2007), all of which may limit the spread of most non-native species towards higher elevations (Pauchard et al. 2009; Alexander et al. 2011). Native species composition may also change with elevation, thus influencing species interactions and community assembly, further regulating invasion success (von Holle 2013; Pollnac and Rew 2014; Averett et al. 2016). Community invasibility can vary with species diversity, with more diverse communities likely to be less prone to invasion (e.g. Maron and Marler 2007; Byun et al. 2013; Pollnac and Rew 2014). Their susceptibility to invasion can also be affected by the dominant species or vegetation structure; for example, forests have been reported to make invasions more difficult in mountain environments (Pauchard and Alaback 2004; Averett et al. 2016; Liedtke et al. 2020), while some shrubs may facilitate invasion (Badano et al. 2007; Cavieres et al. 2008; Llambí et al. 2018; Cavieres 2021).

While there is evidence that both hikers and livestock favour non-natives in the mountains (Barros and Pickering 2014; Barros et al. 2020; Liedtke et al. 2020), their effect along elevational gradients remains unclear. Given that trails extend to high elevations and into more pristine environments and there is already evidence showing that non-native plants are expanding their range (Pauchard et al. 2009; Pyšek et al. 2011), we need to understand these processes for the management and conservation of mountain environments. Here we assess the effect of mountain trails used by hikers and livestock abundance on the success of non-native plants along elevational gradients. We hypothesized that mountain trails favour non-native plants, as they concentrate human flow and therefore involve greater disturbance and propagule pressure. In that regard, we predicted greater non-native success (higher occurrence, richness and cover) near trail edges and trailheads, as such distances represent a proxy of a gradient of propagule pressure and disturbance. We also hypothesized that livestock can affect non-natives because they are propagule dispersers and disturbance generators; we expected that with higher intensity of livestock use, non-native success would increase. We include resident community composition as a factor potentially

influencing non-native success. We predict that success will vary with resident community composition and that plant communities with higher native shrub cover will favour non-native plant success as a result of facilitative interactions in climatically stressful environments. Finally, we also hypothesize that non-native success is influenced by elevation and expect that as elevation increases, non-native success will decrease as a consequence of increasing climatic stress.

## Methods

### Study area

We conducted this study on six trails located in the Central Andes Mountains, in Mendoza, Argentina (Fig. 1). These trails lie mostly in protected areas, and are the main entrance routes to the local Provincial Parks for tourists and climbers. We surveyed three trails in Cordón del Plata Provincial Park (1755 km<sup>2</sup>, 69° 26' W, 32° 58' S): Lomas Blancas, Piedra Grande and Morro Negro; and three trails in Aconcagua Provincial Park (657 km<sup>2</sup>, 69° 26' W, 32° 58' S) and surrounding areas: Quebrada de Vacas, Quebrada de Horcones, and Quebrada de Vargas. These trails are informal, not professionally designed, and are used by both hikers and domestic livestock. Many sections of the trails had multiple secondary trails generating impacts beyond the main trail (Barros et al. 2013, 2020). We covered an elevation gradient between 2400 and 3570 m a.s.l. (See Supplementary Material, Table S1 for further details). These areas constitute an internationally popular tourism and recreation destination due to the stunning landscapes with peaks over 5000 m, including mount Plata (5968 m a.s.l.) and Aconcagua (6962 m a.s.l.) (Barros et al. 2013). For example, in the 2018–2019 season (November to April), ca. 9000 people visited Aconcagua Park and 6000 Cordón del Plata Park (Secretaría de Ambiente y Ordenamiento Territorial, 2020). These areas also support livestock (mainly mules, horses, and cows) for human subsistence and transportation of mountain equipment.

The protected areas were created with the aim of conserving glaciers, rivers, Andean ecosystems, and archeological sites (Barros et al. 2013). The region has a great diversity of microclimates, determined by a complex topography, which generates different vegetation physiognomies (Méndez 2004; Morello et al. 2012). The climate is cold and dry, with precipitation concentrated mainly in the winter, between May and August (Morello et al. 2012). The average annual precipitation in Cordón del Plata Park is 398 mm (1979–2015), whereas Aconcagua Park is drier, with an annual precipitation of 100 mm (2003–2013) (Barros and Pickering 2014; Trombotto et al. 2020). The soils are, in general, little developed and exhibit substantial spatial heterogeneity in depth and granulometric composition (Méndez, 2004; Méndez et al., 2006). The vegetation consists of scrubland communities (including *Adesmia pinifolia*, *Nassauvia axillaris*, and *Berberis empetrifolia*) shrubby steppes (*Adesmia subterranea* and *Azorella monantha*, among others) and herbaceous steppes (*Acaena pinnatifida* and *Phacelia secunda*, among others). Between 3800 and 4200 m a.s.l. the vegetation cover is sparse and dominated by slow growing perennial herbs (e.g. *Chaetanthera pulvinata*, *Nassauvia pinnigera* and *Nototriche transandina* in Aconcagua, and *Colobanthus subulatus*, *Nassauvia cumingii*, and *Senecio crithmoides* in Cordón del Plata). With more than 500 native plant species identified, the Cordón del Plata Park has greater plant diversity than

Aconcagua, where over 120 vascular plant species have been recorded (Méndez 2004, 2007; Méndez et al. 2006).

## Sampling

We carried out the field surveys in the summer season (January-March) of 2018 and 2019. Selected sites were intensively used for mountaineering activities and had a broad elevational range, with an average difference in elevation of 650 m a.s.l. between the start and the end of the trail. The sampling followed the T-trail survey protocol developed by the Mountain Invasion Research Network (MIREN) (Liedtke et al. 2020). We surveyed twenty transects along each trail, located approximately every ca. 35 m of elevation starting at the trailhead, avoiding areas with secondary trails. Each transect consisted of three 2 m x 10 m plots arranged in a T-shape, for a total of 120 transects (360 plots) (Fig. 2). In each plot, we identified and estimated the cover of all vascular plant species, both native and non-native. To estimate the level of livestock activity (cows, horses and mules), we estimated dung density on each plot (Ender et al. 2017). We collected plant specimens that could not be identified in the field and subsequently identified them with herbarium specimens and taxonomic keys in the Ruiz Leal Herbarium of the Argentine Institute for Dryland Research (IADIZA, CONICET Science and Technology Center, Mendoza). We classified species according to their origin and life forms using the database from the Darwinion Botanical Institute (Instituto de Botánica Darwinion 2018). We recorded the trail track, elevation and transect location with a GPS device and later processed them with QGIS and R software to determine the distance of each transect to the start of the trail.

## Analyses

We conducted all analyses with R version 3.6.1 (R Core Team 2019). To evaluate non-native plant success along mountain trails spanning the elevation gradient, we considered three response variables for non-native plants: occurrence (presence/absence of any non-native species), richness (number of non-native species present), and cover (the summed cover of all non-native species per plot). We applied Zero-altered Generalized Linear Mixed Models (two-part models) using the *glmmTMB* function (Brooks et al. 2017). In these models, presence-absence data are modeled with a binomial probability distribution with a logit link function (models the probability that a zero value is observed), while the non-zero observations are modeled with a truncated Poisson model for species richness with a log link function and a Beta distribution with a logit link function for cover (Zuur et al. 2009; Damgaard and Irvine 2019). Two-part models are appropriate for studies of non-native species invasions, as they usually have an overabundance of zeros in sites lacking non-natives (Damgaard and Irvine 2019). In our survey, 32% of the plots lacked non-natives (Supplementary Material, Fig. S1). In addition, these models allowed us to answer two questions in the same statistical structure: what determines the occurrence of non-native species and, in plots where non-natives were present, what determines their richness and cover. We eliminated non-significant predictors and compared the fit of the two models with a likelihood ratio test (LRT).

To assess the effect of trails on non-native plants success we included six explanatory variables in the models, 1) distance of each plot from the edge of the trail (plot number within the T-transect: plot 1 - adjacent to trail edge, plot 2 - intermediate plot, plot 3 - plot furthest from the trail edge); 2) the distance from the trailhead, considering both distances as proxy measures of a gradient of disturbance and propagule pressure; 3) dung density as a measure of livestock use intensity; 4) elevation (m a.s.l.). Finally, we consider two variables related to the composition of the resident community: 5) the coordinates of each plot resulting from a non-metric multidimensional scaling (NMDS1 and NMDS2), and 6) shrub cover (sum of all shrub covers per plot). We performed the non-metric multidimensional analysis considering the proportional cover of native species using the *metaMDS* function of the package *vegan* (Oksanen et al. 2019) in R ( $k = 2$ ,  $trymax = 20$ ,  $distance = \text{Bray-Curtis}$ ). We checked that these variables were not too strongly correlated with each other based on Pearson's correlation coefficient, using the *ggpairs* function of the *GGally* package (Schloerke et al. 2020). Based on the criteria proposed by Dormann et al. (2013), we considered them to be too correlated if they had a Pearson's coefficient greater than 0.71, which was the case for none of these six variables.

We also considered as additional variables precipitation (Supplementary Material, Fig. S2) and mean temperature (Supplementary Material, Fig. S3) data based on the period 1979–2013 obtained from the CHELSA global climate database (Karger et al. 2016, 2017) and downscaled to 1.2 arc second resolution, with a tile size of roughly 90 m<sup>2</sup> at this latitude, using Geographically Weighed Regressions based on elevation, slope, northness, eastness, distance from the ocean, and potential solar radiation derived from the SRTM high-resolution Digital Elevation Model (NASA Shuttle Radar Topography Mission. SRTM 2013) following the procedure outlined in (Lenoir et al. 2017; Lembrechts et al. 2019). We assessed the correlation of these variables with the rest of the predictor variables and also relate these variables to the ordination obtained from the multidimensional scaling analysis (NMDS) using the *envfit* function of the *vegan* package. Temperature was highly and negatively correlated with elevation (corr. -0.76) and precipitation was positively correlated with the NMDS1 axis (corr. 0.75). We therefore included elevation instead of temperature in the models, as it resulted in a lower AIC and as the elevational gradient may represent other unmeasured covariates that may influence establishment and propagation of non-native plants (e.g. atmospheric pressure, vapour pressure, solar radiation (Körner 2007)). Similarly, we decided to include the NMDS1 and NMDS2 axes in the models instead of precipitation as it improved the AIC and these values would be representative of the community composition and the climatic gradient among which they change (Supplementary Material, Table S6 and S7).

We scaled the metric predictors (distance from trailhead, dung density, elevation, NMDS1, NMDS2, shrub cover, temperature, and precipitation) to a mean of zero and a standard deviation of one to make regression coefficients directly comparable. We included trail identity as a random factor in the models. To plot the partial effects of the fixed-effect predictor variables we use the *Effect* package (Fox and Weisberg 2018).

## Results

We recorded 41 non-native and 183 native plant species, while sixteen taxa could not be identified to the species level. The most abundant families among the non-natives were Brassicaceae, Asteraceae, Fabaceae and Poaceae (Supplementary material, Table S2, S3), while the most abundant non-native species were *Taraxacum officinale*, *Cerastium arvense*, *Trifolium repens*, *Convolvulus arvensis*, and *Rumex acetosella*, all of them herbaceous. Only two non-native species were shrubs, *Rosa rubiginosa* and *Tamarix ramosissima*. Considering all native and non-native species surveyed, *T. officinale*, *C. arvense* and *T. repens* were among the ten most abundant species in terms of cover. Most non-native species were recorded at different elevations along the gradient, only 32% were observed at only one specific elevation (Fig. 3). *C. arvensis*, and *T. officinale* were present along the entire elevational gradient (Fig. 3). Seven non-native species had not been recorded previously in our study area (Supplementary material, Table S3) (Méndez 2009; Barros and Pickering 2014; Aschero et al. 2017).

In the non-metric multidimensional scaling analysis we observed an ordering of the surveyed plots based on similarity in native species composition, separating the Cordón del Plata sites from the Aconcagua sites. In the Cordón del Plata the plots are well grouped per trail, while in Aconcagua the three trails are more intermingled (Fig. 4). The first NMDS axis was slightly positively associated with precipitation but negatively associated with temperature and, conversely, the NMDS2 axis was negatively associated with precipitation and positively associated with temperature (Table 1).

We found that non-native occurrence, decreased significantly with increasing distance to the trail edge and distance to the trailhead (Fig. 5 a, b; Supplementary material, Table S4). However, both trail related factors did not significantly influence non-native richness and cover. Livestock dung density, a proxy for habitat use by domestic herbivores, favoured the occurrence, richness and cover of non-natives (Fig. 5 c, d, e; Supplementary material, Table S4, S5). Resident community composition, represented by the NMDS1 axis, had a significant effect on the occurrence and richness of non-natives, showing an increase with increasing NMDS1 axis value. The highest values of the NMDS1 axis correspond to the Cordón del Plata, therefore, our results show that there were more non-natives in this area than in Aconcagua. The NMDS1 axis had no influence on the coverage (Fig. 5 f, g; Supplementary material, Table S4). NMDS2 axis, representing mostly within-protected area variation in species composition, had no significant effect on the response variables analyzed. Shrub cover favoured non-native richness but had no significant effect on occurrence and cover (Fig. 5 h; Supplementary material, Table S4). Finally, elevation correlated negatively with richness and cover, but did not influence non-native occurrence (Fig. 5 i, j; Supplementary material, Table S4 y S5).

Distance to the trailhead had the largest effect on the occurrence of non-natives, followed by NMDS1, dung density and distance to the trail. Elevation and NMDS1 had the greatest effects on species richness while shrub cover and dung density had the least effect (Supplementary material, Table S4). Elevation was the variable with the largest magnitude effect on non-native cover (Supplementary material, Table S5).

## Discussion

We found that recreational trails in the arid Andes of Mendoza play a key role in determining the occurrence of non-native species. This effect may be due to both increased disturbances and increased propagule pressure associated with the concentration of human and animal flow. We found a greater non-native occurrence closer to the trailheads, which lie next to roads with high vehicle traffic. Road edges represent important propagule sources for non-natives in mountain environments (Pauchard and Alaback 2004; Lembrechts et al. 2017; Haider et al. 2018). Therefore, the decreased non-native occurrence with increasing distance to the trailhead may be due to increasing distance to roads, which may act as propagule sources. We also observed a higher non-native occurrence at the trail edges compared to the interior plots. The latter result suggests that disturbance is a prerequisite for nonnative establishment in mountain ecosystems, due to reduced competition with native plants and resource release (Davis et al. 2000; Pauchard et al. 2009). These findings agree with previous observational and experimental research suggesting that disturbance is a key factor determining non-native plant establishment and success (Rose and Hermanutz 2004; Pauchard et al. 2009; Barros and Pickering 2014; Lembrechts et al. 2016; Barros et al. 2020; Liedtke et al. 2020; Geppert et al. 2021). Moreover, because hikers may carry seeds in their equipment and clothing (Pickering and Mount 2010), the higher occurrence of non-native plants near trails may reflect a greater propagule pressure on trails. However, we cannot assess the relative importance of the disturbances and increased propagule pressure in the occurrence based on our observational data.

Although trails influenced non-native occurrence, contrary to our expectation they did not affect non-native richness and abundance. This result contrasts with the study by Liedtke et al. (2020) in northern Patagonian forests trails using the same study design, which found that distance to the trail did affect these vegetation attributes. These contrasting results could be partly due to the type of ecosystem assessed and the recreational use patterns of hiking and livestock grazing. Contrary to the Andean Patagonian forests, the Arid Andes of central Argentina are characterized by treeless vegetation dominated by sparse, low vegetation that favors dispersed use by visitors and animals, and informal secondary trail creation (Leung 2012; Barros and Pickering 2017; Barros et al. 2020). Dispersed use by both animals and visitors could extend disturbance and seed dispersal beyond trail boundaries, which may explain why we found no significant differences in non-native richness and cover by distance from the trail.

We found that livestock affected the occurrence, richness and cover of non-native plants. Livestock can favor plant invasions through different mechanisms, transporting seeds through their fur, cots, and dung (Ansong and Pickering 2013), and generating favorable microhabitats for non-natives, including higher soil nutrients and soil moisture on pile dungs (Loydi and Zalba 2009; Quinn et al. 2010). In fact, many of the abundant non-native species of our surveys have been shown to germinate in horse dung, including *Taraxacum officinale*, *Trifolium repens*, *Convolvulus arvensis*, *Poa annua*, and *P. pratensis* (Supplementary material, Table S3) (Ansong and Pickering 2013; Dacar et al. 2019). On the other hand, grazing disturbance alters soils and affects plant community composition and structure, favoring non-native species (Vavra et al. 2007; Törn et al. 2010; Ansong and Pickering 2013). Hence, livestock disturbance can result in a positive feedback loop between the seeds they dispersed on the ground,

nutrient input from the dung and trampling disturbance (Wells and Lauenroth 2007), all of which favor non-native plant establishment, richness and cover. Quantifying the magnitude of the effect of the potential roles of livestock (propagule disperser, disturbance agent by trampling and grazing) on occurrence, richness and abundance, as well as possible synergistic effects with anthropogenic trampling, could provide valuable information for habitat management but requires a specific experimental approach.

In our study area, the occurrence and richness of non-native species varied according to the composition of the native vegetation, as reported in other studies (e.g. Milbau et al. 2013; Pollnac and Rew 2014; Alexander et al. 2016). Our analyses indicated that the richness and occurrence of non-natives increased with higher NMDS1 values. The NMDS1 axis separated the points for Cordón del Plata and Aconcagua Park into two groups with higher NMDS1 values for Cordón del Plata, and this axis correlated positively with higher precipitation values. These results indicated that the plant communities of the Cordón del Plata, with higher precipitation, have greater richness and coverage of non-native species than those of Aconcagua. In addition, we detected a positive effect between native shrub cover and non-native species richness, suggesting a facilitative interaction as has been reported in other studies in the Arid Andes and other stressful environments (Bruno et al. 2003; Cavieres et al. 2005; Badano et al. 2007; von Holle 2013; Lucero et al. 2019). For example, one of the most abundant native shrubs in our study region, *Azorella monantha*, has been reported to facilitate non-native species in the Andes of Chile, as this species provides suitable microhabitats (e.g. smoother temperatures variations, higher nutrient availability, greater soil moisture), that favor the establishment of non-native species (Cavieres et al. 2005, 2007). These positive interactions could result in greater vulnerability to plant invasion in the arid Andes compared to mountains with forest cover that may act as potential barriers for their establishment, as it has been observed in other regions (Averett et al. 2016; McDougall et al. 2018; Liedtke et al. 2020). Hence, further observational and experimental studies along stress gradients are required to expand our knowledge about native non-native plant interactions as well as to identify what communities are more sensitive to plant invasions.

Finally, while non-native occurrence remained unchanged with elevation, non-native richness and cover decreased significantly. This result is largely in line with those of other studies in the Andes and other mountain regions of the world (Barros and Pickering 2014; Alexander et al. 2016; Averett et al. 2016; Yang et al. 2018; Liedtke et al. 2020). In our study region, elevation constitutes a strong environmental filter, associated with decreasing temperature and increased solar radiation, winds and permafrost in soils (Trombotto et al. 1997; Körner 2007; Roig et al. 2007). The gradual increase in environmental stress with elevation may reduce non-native cover and richness at high elevation. However, although we found a general trend towards decreased occurrence of most non-native species with elevation, two species, *Taraxacum officinale* and *Cerastium arvense*, occurred up to the highest elevation surveyed; these species have a wide ecological tolerance due to their great phenotypic plasticity (Quiroga et al. 2002; Molina-Montenegro et al. 2012) and are among the globally most invasive non-native plant species in mountains (Seipel et al. 2012). *T. officinale* shows plastic leaf morphology and physiological traits in response to variations in light availability; for example, in alpine environments leaves have wider angles which may

provide a greater protection against increased light intensity. This strategy may help maintain high physiological performance in alpine environments, facilitating their invasions in these environments (Molina-Montenegro et al. 2012). In turn, *C. arvense* tends to produce larger flowers in alpine environments compared to lowland areas, likely because larger, more attractive flowers compensate for the reduced activity and abundance of pollinators at higher elevations (Quiroga et al. 2002). Future studies should attempt to further disentangle the adaptive strategies of species not constrained by the environmental filters operating in our study area.

## Conclusion

We found that non-native plants in the arid Central Andes occur along the entire elevational gradient up to the upper limits of vegetation; thus even high elevation areas with harsh climatic conditions experience plant invasions. We also found that disturbance by hikers and livestock play a key role in non-native plant invasions in the region. Disentangling the influences of hikers and non-native herbivores on plant invasions contributes not only to understanding the invasion process but also to develop management actions to minimize the expansion of non-natives plants into relatively undisturbed mountain environments. As potential management actions, we suggest delimiting formal trails and campsites and to provide information to visitors to reduce trampling impacts outside formal trails. In addition, limiting livestock on these sites of high conservation value should be a key strategy as they increase the richness and cover of non-native plants.

Under the current scenario of climate change and increased human pressure on mountains, it is imperative to implement collaborative research using standardized protocols such as those from the Mountain Invasion Research Network (MIREN) (Liedtke et al. 2020; Haider et al. 2021) and Global Observation Research Initiative in Alpine Environments (GLORIA) to understand the processes governing plant invasions and species redistributions at local and global scales.

## Declarations

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**Availability of data and material:** the datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

**Authors' contributions:** María Alisa Alvarez, Ana Agustina Barros, Diego Pedro Vázquez, Jonas J. Lembrechts, and Valeria Aschero designed the study; María Alisa Alvarez, Ana Agustina Barros, and Lorena de Jesús Bonjour carried out the field work and identified the plant species; Ronja E. M. Wedegärtner obtained the climatic data; María Alisa Alvarez, Ana Agustina Barros, Diego Pedro Vázquez,

and Valeria Aschero analysed the data and wrote the article. All authors contributed to the discussion and critical review of the article.

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## Tables

Table 1  
 Model fit results to evaluate the effect of environmental variables in the NMDS ordination.

VECTORS	NMDS1	NMDS2	r <sup>2</sup>	Pr(> r)
Precipitation	0.33214	-0.94323	0.1827	0.001***
Mean temperature	-0.59458	0.80404	0.1618	0.001***
Max temperature	-0.49517	0.86879	0.1837	0.001***
Min temperature	-0.55003	0.83514	0.1670	0.001***
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1. Permutation: free. Number of permutations: 999				

## Figures



Figure 1

Location of surveyed trails. Blue, yellow and green polygons indicate Protected Areas. Coloured lines indicate the surveyed trails and black dots indicate the location of the transects (Image credit: Hugo Debandi)



Figure 2

Schematic of the survey methodology

Lim ● max ● min

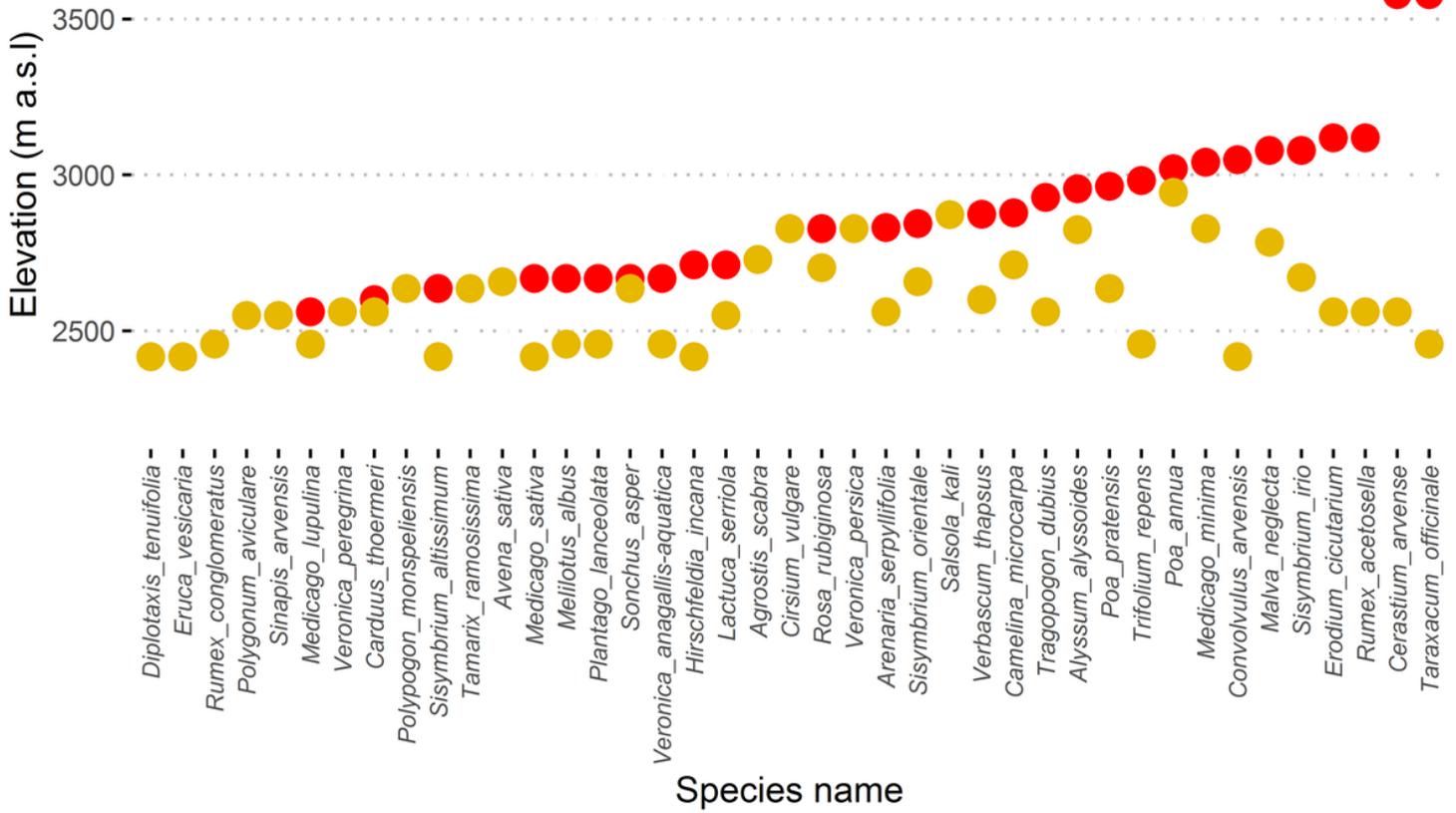
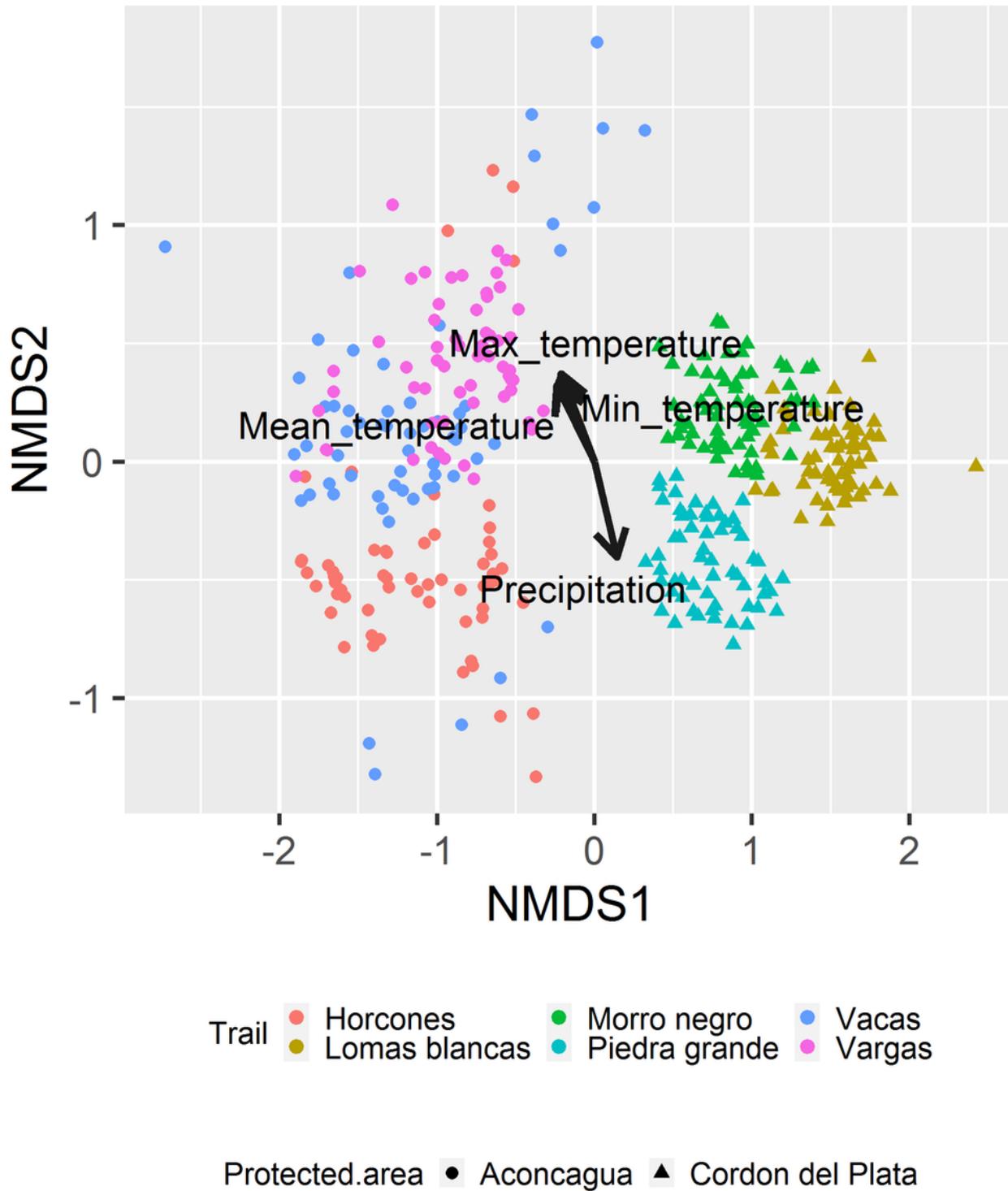


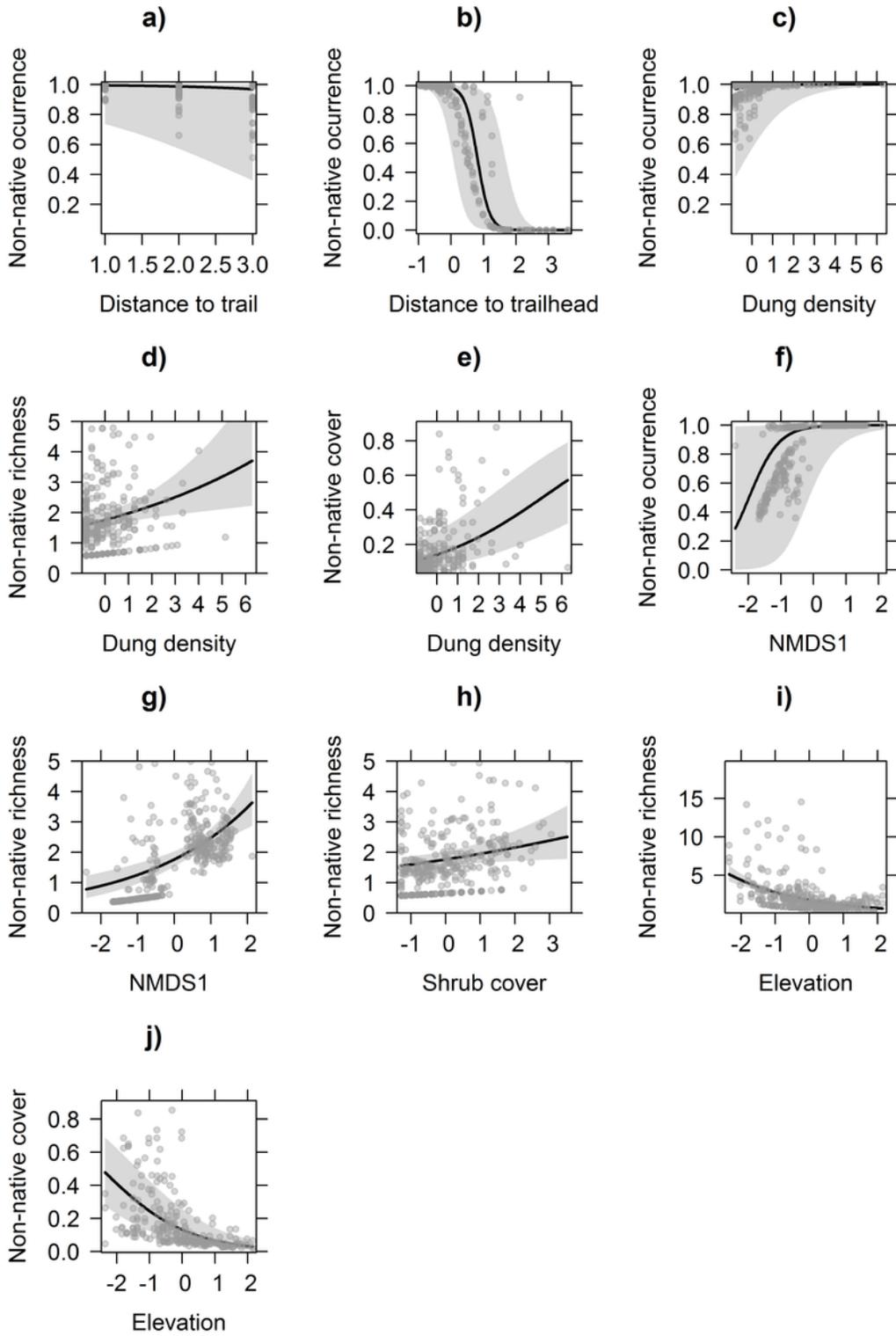
Figure 3

Minimum (yellow circle) and maximum elevation (red circle) of detection of the non-native species recorded in the survey, ordered by maximum elevation of detection. When only a yellow circle is shown, the species was detected at a single elevation only



**Figure 4**

Non-metric multidimensional scaling analysis based on the coverage of native species surveyed in 360 plots distributed along the 6 trails. The environmental variables considered significantly explained the ordination. The arrow points to the direction of the most rapid change in the environmental variable (direction of the gradient)



**Figure 5**

Partial effect plots of fixed effect predictor variables (scaled to a mean of zero and standard deviation of one) for non-natives occurrence, richness and cover. Points represent the sampled plots, shaded areas around regression lines their 95% confidence intervals. Position of points on the y-axis is equal to the partial fit (position on the regression line) plus the corresponding residual

## Supplementary Files

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