Hiking and livestock favor non-native plants in the high Andes

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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 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 leads to decreasing non-native abundance with increasing elevation, non-natives occur up to the upper limits of vegetation, and that trails and livestock favour non-native spread in these mountains.

Second Abstract in native language.

Resumen  Las personas y el ganado que utilizan los senderos de montaña dan añan la vegetación nativa

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y actúan como vectores de semillas, favoreciendo la propagación de plantas exóticas. Evaluamos el efecto de los senderos y la abundancia del ganado sobre el éxito de las plantas exóticas en los Andes áridos centrales de Argentina. Relevamos seis senderos, abarcando elevaciones entre 2400 m y 3570 m s.n.m. Registramos la vegetación exótica y nativa mediante transectas distribuidas a lo largo del gradiente de elevación y abarcando distancias de hasta 22 m desde el sendero. Evaluamos cómo varía la ocurrencia, la riqueza y la cobertura de exóticas con la distancia al sendero, la intensidad de uso por el ganado, la composición de la comunidad de plantas nativas y la elevación. Encontramos que los senderos favorecieron la ocurrencia de exóticas, pero no influyeron en la riqueza y cobertura, y que el ganado favoreció tanto la ocurrencia como la riqueza y la cobertura de exóticas. La riqueza y la cobertura de exóticas disminuyeron con la elevación y variaron en función de la composición de la comunidad nativa. Además, la riqueza de exóticas se correlacionó positivamente con la cobertura de arbustos nativos, sugiriendo posibles interacciones de facilitación. Nuestros resultados muestran que a pesar del fuerte filtrado ambiental que lleva a una disminución de la abundancia de exóticas con la elevación, éstas ocurren hasta los límites superiores de la vegetación, y que los senderos y el ganado favorecen su propagación.

**Keywords** Mountains · Non-native plants · Trails · Anthropogenic disturbance · Elevational gradient

**Introduction**

Mountain ecosystems harbor high biodiversity with high endemism and can act as biodiversity refuges, especially during periods of rapid climate change, while 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 (Guertner 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). These impacts from non-native plants on mountain ecosystems are expected to increase due to global change, so it is imperative to understand the processes that favor their spread (Pauchard et al. 2009).

Many of the non-native plants occurring in mountain areas are found in the vicinity of infrastructure that concentrates human traffic such as vehicular roads and tourist hiking trails (Pickering and Mount 2010; Seipel et al. 2012; Barros and Pickering 2014; Liedtke et al. 2020; Fuentes-Lillo et al. 2021). Roads can facilitate the introduction of non-native species into mountains as they combine high propagule pressure with recurrent disturbances (Pauchard and Alaback 2004; Fernández-Murillo et al. 2015; Lembrecchts et al. 2017; Sandoya 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). Disturbances that involve damage or destruction of part of the resident vegetation may favor the establishment of non-native plants by reducing competition and freeing up additional resources (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 and 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 favor 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 favor 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. In addition, we hypothesized that biotic factors, including the composition of the resident community and native shrub cover also affect non-native success. We predicted that non-native success will vary with the composition of the resident community. We also expected non-native success to be affected by native shrub cover, with higher shrub cover favoring non-native plant success as a result of facilitative interactions in climatically stressful environments. Finally, we hypothesized that non-native success is influenced by elevation, and expected that as elevation increases, non-native success decreases as a consequence of increasing climatic stress.

**Methods**

**Study area**

We conducted this study in 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 km², 69° 26’ W, 32° 58’ S): Lomas Blancas, Piedra Grande and Morro Negro; and three trails in Aconcagua Provincial Park (657 km², 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 (including *Adesmia subterranea* and *Azorella monantha*) and herbaceous steppes (including *Acaena pinnatifida* and *Phacelia secunda*). Between 3800 and 4200 m a.s.l. the vegetation cover is sparse and dominated by slow growing perennial herbs (e.g.

Fig. 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)
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Chaetanthera pulvinata, Nassauvia pinnigera and Nototriche transandina in Aconcagua, and Colobanthus subulatus, Nassauvia cumingii, and Senecio crithmoides in Cordón del Plata. Shrub species are present along the entire elevation gradient surveyed; however, there is a shift of shrub species from erect to cushion shrubs with increasing elevation (i.e., at low elevations, Adesmia pinifolia and Berberis empetrifolia with average heights of 1.5 m and at high elevations, A. subterranea, Azorella monantha with average heights of 5 cm; Kiesling et al. 2021). 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 in each plot by counting the dung piles; dung counts represent a reliable yet quick method to estimate the activity level of herbivorous mammals in their habitats (Barnes 2001).

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 glmnTM 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 logit 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.

Fig. 2 Schematic of the survey methodology
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 the success of non-native plants, 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 considered 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 = 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. 2021). Based on the criteria proposed by Dormann et al. (2013), we considered them to be too correlated if the absolute value of Pearson’s coefficient was greater than 0.7, which was not the case for any of these six variables.

As additional climatic variables, we also included precipitation (Supplementary Material, Fig. S2) and minimum, maximum and mean temperature data (Supplementary Material, Fig. S3) based on the period 1979–2013 obtained from the CHIELSA global climate database (Karger et al. 2016, 2017) and downscaled to 1.2 arc second resolution, with a tile size of roughly 90 m$^2$ 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) and Lembrechts et al. (2019). We assessed the correlation between these variables and 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. Minimum, maximum and mean temperatures were highly and negatively correlated with elevation (corr. −0.79; −0.76; 0.82 respectively) 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, Tables S7 and S8).

To assess whether distance to the trail edge and to the trailhead represent a gradient of disturbance by livestock, we assessed whether dung density varied as a function of these distances. To this end, we fitted a GLMM with the glmmTMB function using a Poisson distribution with a log link function, using trail identity as a random factor.

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, Tables 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). The most abundant native species were *Poa holciformis*, *Bromus catharticus*, *Nassauvia axillaris*, *Poa ligularis* and *Berberis empetrifolia*. Both native richness (mean 12.95 sd 7.4 in T-transect plot 1, and mean 12.8 sd 7.4 in T-transect plot 3) and cover (mean 47% sd 20 in T-transect plot 1, and 48 sd 18 in T-transect plot 3) were similar along the trail edges and the interior plots.

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 were well grouped per trail, while in Aconcagua the three trails were 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).

![Fig. 3](https://example.com/fig3.png)

**Fig. 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 only at a single elevation.

![Fig. 4](https://example.com/fig4.png)

**Fig. 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).
We found that non-native occurrence decreased significantly with increasing distance to the trail edge and distance to the trailhead (Fig. 5a, 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, favored the occurrence, richness and cover of non-natives (Fig. 5c, 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, which increased with increasing NMDS1 axis value. The highest values of the NMDS1 axis correspond to Cordón del Plata, indicating that there were more non-natives in this area than in Aconcagua. The NMDS1 axis had no influence on the cover (Fig. 5f, 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 favored non-native richness but had no significant effect on occurrence and cover (Fig. 5h; Supplementary material, Table S4). Finally, elevation was negatively correlated with richness and cover, but did not influence non-native occurrence (Fig. 5i, 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).

We found that dung density did not vary as a function of distance to the trail edge, nor to the trailhead (Table S6).

**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 flow. The fact that dung density did not vary significantly with distance to the trail suggests that the observed effect of trail distance may be more related to human traffic than to the effect of livestock. 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 could be due competitive release and/or an increased propagule pressure, two factors commonly associated with linear disturbance such as trailsides. However, average native cover and native richness were similar between trail edge plots and interior plots, suggesting that competitive release between native and non-native plants does not explain the distribution of the latter in our study area; instead, propagule pressure resulting from hiker traffic (Pickering and Mount 2010) may be more important.

Although the trails influenced the presence of non-natives, contrary to our expectations, they did not affect non-native richness and cover. This observation suggests that when non-natives are present, they do not exhibit differences in richness and cover at different distances to the trail. This result could be partially explained by the ecosystem characteristics of our study area, including treeless vegetation dominated by low and sparse shrubs, grass and forbs that may not preclude dispersed use by visitors and animals (Leung 2012; Barros and Pickering 2017; Barros et al. 2020). Dispersed use, i.e. trampling in the

| VECTORS      | NMDS1  | NMDS2  | $r^2$ | 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.
area beyond the hardened surface of trails (D’Antonio and Monz 2016), could extend disturbance and seed dispersal beyond the trail boundaries, promoting non-native success beyond trails, which could explain why we did not find significant declines in non-native richness and cover with increasing distance from the trail. This conclusion is supported, in part, by the lack of correlation between distance to the trail and the density of livestock dung, suggesting that livestock is indeed not confined to the trails.

These findings here contrast with those found by Liedtke et al. (2020), who reported both a higher non-native richness and cover close to the trail. These contrasting results could be due to different patterns in recreational use, hiking and livestock grazing in both regions, resulting from a different vegetation cover.

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**Fig. 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 0.95% confidence intervals. Position of points on the y-axis is equal to the partial fit (position on the regression line) plus the corresponding residual.
Indeed, one can expect trail users to remain closer to the trail in forests, as are found in the south-central Andes of Chile studied by Liedtke et al. (2020) than in the short vegetation of the dry high Andean steppe in our study region in Argentina.

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 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 disperse 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.

Non-native success has been reported to vary according to the composition of the native vegetation (e.g. Milbau et al. 2013; Pollnac and Rew 2014; Alexander et al. 2016). Our results indicate that the richness and occurrence of non-natives increased with higher values of NMDS1, which represents changes in native plant composition correlated with precipitation. The first NMDS axis separated the sites in two groups, Cordón del Plata and Aconcagua Park. Plant communities of Cordón del Plata, an area with higher precipitation and native richness (83 native species in Aconcagua vs. 140 in Cordon del Plata Park), had also greater richness of non-native species per plot than those of Aconcagua. A limitation of our study is that we cannot establish a causal mechanistic link of native composition and non-native success given that both native and non-native species may both respond to underlying differences in climatic conditions and or other environmental features between both parks. Further experimental and observational studies along stress gradients in the region would be required to disentangle the potential mechanisms (i.e., allelopathy, facilitation, competition) by which native composition could affect non-native success in these regions.

Nevertheless, our observational data indicate a positive correlation 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 Chilean Andes, as this species provides suitable microhabitats (e.g. smoother temperature 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 has been observed in other regions (Averett et al. 2016; McDougall et al. 2018; Liedtke et al. 2020).

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 (Tromboto 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, 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.

**Conclusions**

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 influence of hikers and non-native herbivores on plant invasions contributes not only to understand 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, management of livestock to limit habitat use and transit to existing trails should be a key strategy, as intensive off-trail trampling and grazing can increase the richness and cover of non-native plants in these environments with high conservation value.

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 (G洛-RIA) to understand the processes governing plant invasions and species distributions at local and global scales.

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**Authors’ contributions** MAA, AAB, DPV, JJL, and VA designed the study; MAA, AAB, and LJB carried out the field work and identified the plant species; REMW obtained the climatic data; MAA, AAB, DPV, and VA analysed the data and wrote the article. All authors contributed to the discussion and critical review of the article.

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**Data availability** The datasets generated during and/or analysed during the current study are available from the corresponding author upon request.

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