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Beyond the Trail—Understanding Non-Native Plant Invasions in Mountain Ecosystems

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ABSTRACT

Aim: We aimed to examine the abiotic, biotic and anthropogenic drivers of non-native plant species distribution along hiking trails in mountainous regions.

Location: Nine mountain regions across six continents, including North America (USA), South America (Argentina and Chile), Europe (Sweden, Norway, Czech Republic), Africa (South Africa), Asia (China) and Oceania (Australia).

Time Period: Data were collected between 2016 to 2022 during the summer season.

Major Taxa Studied: Vascular plants.

Agustina Barros, Eduardo Fuentes Lillo and Jonas J. Lembrechts contributed equally to the manuscript. Agustina Barros and Eduardo Fuentes Lillo should be considered joint first authors.

Methods: We implemented a standardised sampling design (MIREN trail survey) with T-shaped sample sites placed parallel to trails and perpendicular to adjacent vegetation. We examined the main drivers (abiotic, biotic and anthropogenic factors) affecting non-native species' presence, richness and cover.
Results: At the global scale, abiotic (climatic) variables explained most of the variation in non-native species richness. In contrast, biotic factors were the most important for the presence and cover of non-native plants. Anthropogenic factors, including distance to the trail, use intensity and livestock grazing, were also important but to a lesser extent than the main factors. While the total number of non-native species differed across regions, the patterns explaining plant invasions were consistent.
Main Conclusions: Our regional study identified mountain trails that are particularly vulnerable to plant invasions. Our findings suggest that under future scenarios of climate change, increased anthropogenic pressure and heightened livestock activity, the presence of non-native species beyond trail edges may become more frequent. This highlights the need to restrict off-trail activities in areas of high conservation value.

1 | Introduction

Over the past 15 years, there has been increasing attention on the distribution and abundance of non-native plant species in mountain ecosystems (Iseli et al. 2023). Although mountains are still less invaded than lowland regions, a growing body of work has shown that they are not inherently resistant to biological invasions (Alexander et al. 2016; Fuentes-Lillo et al. 2023). Human infrastructure plays a significant role in the upward migration of non-native species into mountains, and there is a mounting body of literature that demonstrates how roads (Seipel et al. 2012; Lembrechts et al. 2017; Haider et al. 2018; Fuentes-Lillo et al. 2023) and railroads (Rashid et al. 2021) may facilitate the encroachment of non-native plants into mountain environments.

The ongoing disturbance caused by the construction and maintenance of human infrastructure reduces native vegetation cover and releases resources, favouring the establishment of non-native plants able to rapidly spread through their often short life cycles and rapid growth (Kalwij et al. 2008; Pickering and Mount 2010; Lembrechts et al. 2017). Traffic along this infrastructure increases the probability of propagule transport as vehicles can disperse non-native seeds from the lowlands (Ansong and Pickering 2013). Due to these major impacts, most global research has focused on how motorised traffic facilitates plant dispersal into mountains, while nonmotorised touristic activities have been relatively neglected, although they have become a critical vector of plant invasions in many mountain regions worldwide (Balmford et al. 2009; Barros et al. 2022).

Recreational hiking trails are a crucial component of the capillary network of touristic movement in mountains, distributing visitors even to the most remote areas (Ballantyne and Pickering 2015) and highest elevations, and are particularly impactful in regions with high volumes of foot traffic. In addition, in many mountains in the world that lack roads or rail infrastructure, foot paths are vital connectors that are used extensively by local communities and for seasonal movements of shepherds and livestock for transhumance pastoralism (Hashmi et al. 2017). Given that these visitors and livestock are known vectors of non-native plant seeds (Pickering and Mount 2010), these trails could play a crucial role in the encroachment of non-native plants into pristine ecosystems. Nevertheless, few studies have tackled this issue and those that have done so have been limited primarily to regional scales (Barros and Pickering 2014; Rowe et al. 2018; Liedtke et al. 2020; Alvarez et al. 2022; Wedegärtner et al. 2022).

According to recent studies (Liedtke et al. 2020; Barros et al. 2022), trailsides exhibit lower numbers of non-native species along the elevational gradient as compared to roadsides, and the effect of disturbance on the vegetation results in less distinctness than on roadsides. The reasons for the lower plant invasion in trails could be related to the lower propagule pressure and disturbance intensity compared to roads (Liedtke et al. 2020; Jolivet et al. 2022). On average, hikers transport fewer seeds than vehicle traffic, and the frequency of trail use is often lower than that of roads (Pickering and Mount 2010; Ansong and Pickering 2013). Additionally, hiking trails create less intensive disturbance across a smaller area than roads, which further reduces the opportunities for trailside invasion (Wolf and Croft 2014; Ballantyne and Pickering 2015; Liedtke et al. 2020). Furthermore, most trails are constructed without the use of imported building material (if constructed at all), which limits the construction disturbances, excludes an invasion pathway from remote sources, and reduces changes in soil, nutrient and water regimes often seen along roads (Newsome et al. 2013).

Although these facts suggest that trails are less susceptible to mountain plant invasions compared to roads, the fact that they provide a linear connection to higher elevations means that they still pose a risk of facilitating plant invasions into alpine habitats. Indeed, recent studies consistently show declines in non-native species richness with distance from the trail head, as a response to harsher climate factors, but also to decreasing propagule pressure (Liedtke et al. 2020; Barros et al. 2022). High-elevation habitats are usually less invaded, especially given that most non-native species are introduced in the lowlands and would need a broad climatic tolerance to succeed across the whole elevation gradient (Alexander et al. 2011, 2016). However, the native vegetation may be more susceptible to invasion due to its slower growth and lower competitive ability in general, making it more likely that non-native species with sufficient climatic resistance could successfully invade from the lowland non-native species pool to the alpine zone (Lembrechts et al. 2014). Additionally, facilitative interactions are more frequent in high-elevation habitats, and there is already evidence of native vegetation facilitating non-native species under harsh climatic conditions (Cavieres et al. 2007; Alvarez et al. 2022).

Another distinctive feature of mountain trails above the treeline or in areas with low stature vegetation is that hikers often wander off trails because of the lack of physical barriers (e.g., areas with high canopy cover) and trails are not often distinguishable, particularly when they are not formally designed (Barros and Pickering 2015). As well, domestic livestock (e.g., horses, cows and sheep) can form parallel informal trails when browsing and grazing in alpine grasslands (Barros and Pickering 2015). This may increase the propagule pressure away from trails by facilitating seed dispersal (e.g., via clothing, fur and faeces) and establishment by disturbing soil and native vegetation (Ansong and Pickering 2013; Liedtke et al. 2020; Alvarez et al. 2022). It can also alter microclimatic conditions including changes in humidity through local soil compaction and less protection against low temperatures through reduced plant cover (Cole 2004).

Given the potential of trails to facilitate plant invasions in less disturbed habitats, there is an urgent need to test how climatic, biotic and anthropogenic factors may impact non-native plant establishment across different mountain regions. The insights gained from global generalities, informed by regional specifics, can be used to adapt trail construction design and management, and decrease the risk non-native plant invasions pose to vulnerable areas often traversed by trails. Here, we conducted the first multi-regional study examining the influence of climatic, biotic and anthropogenic factors on shaping non-native plant species distributions along mountain trails. We used a standardised sampling design (Liedtke et al. 2020) developed by the Mountain Invasion Research Network (MIREN), along 55 trails across nine regions on six continents. Our hypotheses were that non-native species distributions along trails follow similar patterns as those found along roads (e.g., Seipel et al. 2012; Haider et al. 2018), characterised by steep declines in non-native presence, richness and cover with decreasing temperature and distance from the trailhead, as well as reduced presence in adjacent vegetation. In addition, we assumed that biotic factors such as shrub and tree canopy cover, as well as non-native livestock presence, play a distinct role in driving region-specific invasion patterns.

2 | Methods

The MIREN trail survey (Liedtke et al. 2020) is a worldwide vegetation monitoring effort that covers nine mountain regions on six continents, including countries in North America (USA), South America (Argentina and Chile), Europe (Sweden, Norway, Czech Republic), Africa (South Africa), Asia (China) and Oceania (Australia) (Table 1). Within this project, we brought together data from a total of 55 trails. Trails varied in length from 3 to 22 km, with an average of 6.6 ± 1.2 km, and covered an average elevation gradient of 1100 m, ranging from 595 m a.s.l. in China to 1780 m a.s.l. in Chile (Table 1). The survey sites included montane to alpine vegetation, encompassing forests, shrublands, grasslands and tundra vegetation, and covered five of the nine main global biomes.

Sampling was conducted using sample sites set up at regular elevational intervals, starting from the trailhead and ending at the highest point of the trail, with the number of sample sites per trail of at least 10, yet depending on the region (Table 1). Each sample site consisted of three plots with a size of 2 × 10 m forming a T-shape. The first plot was established parallel to the trail

TABLE 1 | Characteristics of the nine mountain regions surveyed in this study, including their location, number of surveyed trails (# surveyed trails) and sample sites, elevational range, trail length, number of all non-native species recorded in the region (# non-native species) and number of occurrences (# occur.).

Region	Coordinates	# surveyed trails	Elevation range (m a.s.l.)	Number of sample sites	Cumulative trail length (km)	# non-native species	# occur.
Argentina (Arid Andes, Mendoza)	−32° S, 69° W	6	2417–3973	122	45	30	752
Australia (Mt. Wellington, Tasmania)	−42° S, 147° E	3	110–1262	60	14.2	47	148
Chile (South-central Patagonia)	−38° S, 71° W	20	131–1910	202	100	41	765
China (Changbai Mountains)	42° N, 127° E	1	2005–2600	13	4.2	4	14
Czech Republic (Krkonoše)	50° N, 15° E	3	788–1590	40	20	6	11
Norway (Hjerkinn)	62° N, 9° E	8	700–1755	80	19.8	6	31
Sweden (Abisko)	68° N, 18° E	8	424–1491	98	63	5	73
South Africa (Witsieshoek, Maloti-Drakensberg)	−28° S, 28° E	1	2595–3224	10	6.20	4	34
USA (Montana)	45° N, 109° W	5	1905–3139	58	32	14	51

at the start of the first vegetation. The second plot was set up perpendicular to the trail, beginning in the middle of the edge of the first plot, and thus reaching from 2 to 12 m away from the trail. The third plot spanned 12–22 m from the trail (Figure 1c). Across our 9 regions and 55 trails, we monitored 680 sample sites and more than 2000 plots.

In each plot, all vascular plants, both native and non-native species, were identified and their ground cover visually estimated on a scale from 0 to 8 (0 = 0%, 1 = 0%–1%, 2 = 2%–5%, 3 = 6%–25%, 4 = 26%–50%, 5 = 51%–75%, 6 = 76%–95%, 7 = 96%–99%, 8 = 99%–100%). We also visually estimated the percentage cover of tree, shrub, herb layer, native species, non-native species and overall vegetation using the same scale. The scale followed the original MIREN survey protocol for roads (Haider et al. 2022) and accounts for the fact that observers tend to visually estimate extreme cover values more accurately than intermediate ones. For all percentage cover data, we transformed the rank cover values sampled to the median percent values in each rank. Note that with this approach we prioritise efficiency over accuracy to allow application in more regions; we thus warn the reader to interpret cover percentages as a rough estimate only.

The sampling was done in each region at the peak of the growing season. The classification according to species origin (native or non-native) for each region was determined using local literature, checklists and contributors' expertise. We also checked the status of the species using the GLONAF database (Global

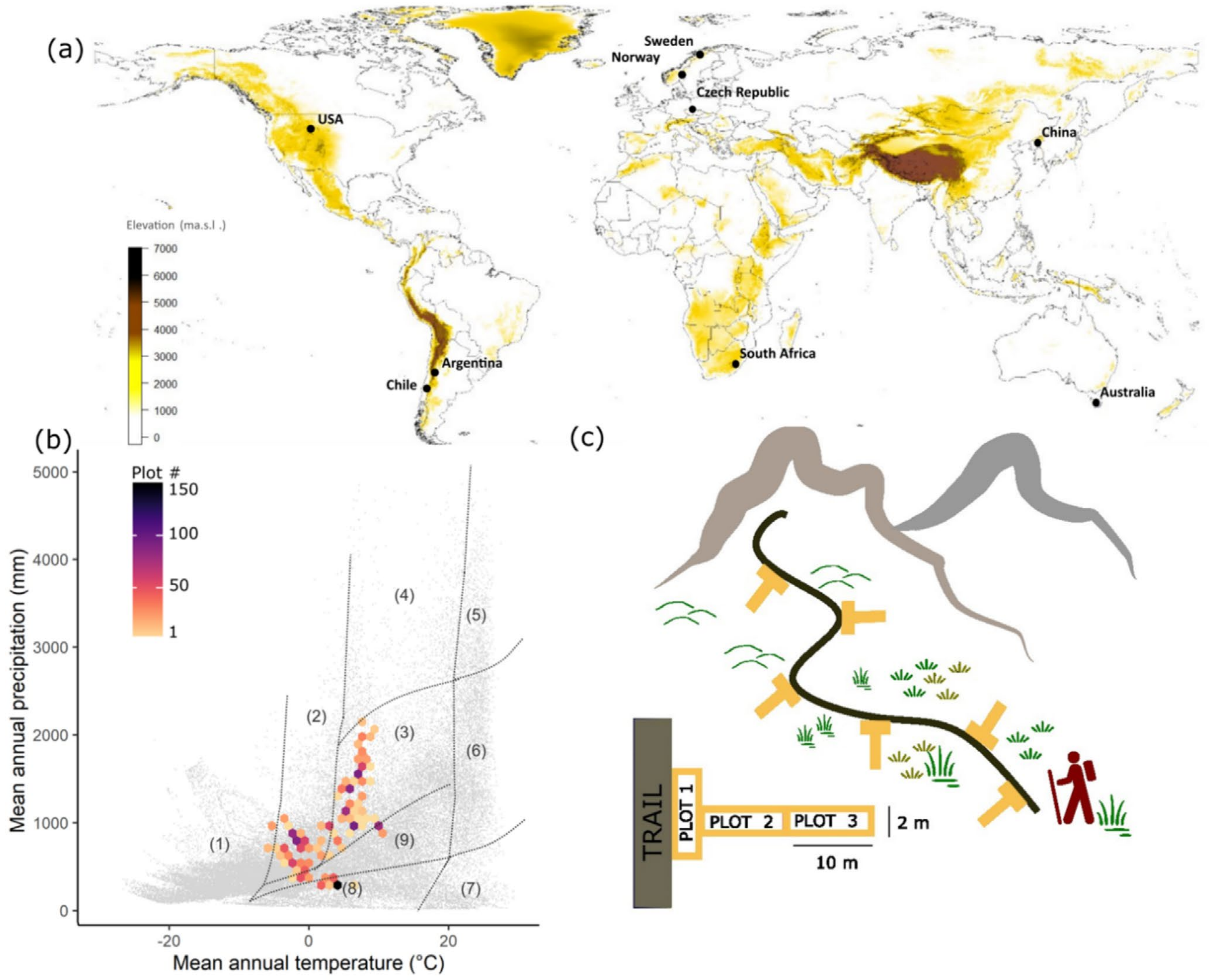

FIGURE 1 | (a) Map of surveyed trail locations on a global map of elevation (in m a.s.l.), (b) distribution of surveyed sample sites in climatic space and within the 9 Whittaker biomes. Colours of hexagons indicate the number of plots at each climatic location, and the environmental space is divided into 40 × 40 bins. Small grey dots in the background represent the global variation in climatic space (obtained by sampling 1,000,000 random locations from the CHELSA world maps at a spatial resolution of 2.5 arc minutes). Overlay with dotted lines and numbers (from 1 to 9) depict a delineation of Whittaker biomes (adapted from Whittaker 1975): (1) tundra and ice, (2) boreal forest, (3) temperate seasonal forest, (4) temperate rainforest, (5) tropical rainforest, (6) tropical seasonal forest/savanna, (7) subtropical desert, (8) temperate grassland/desert, (9) woodland/shrubland. (c) Layout of the MIREN survey design for trails. Sample sites are located at equal elevation intervals, with at least 10 sample sites along each trail. Each sample site consists of three plots, the first one (plot 1) runs parallel to the trailside, and the second and third plots are perpendicular to the first and lead into the adjacent vegetation. Only a few sample sites are shown in the figure for clarity.

Naturalised Alien Flora; glonaf.org), but we decided to use the regional checklists as the data in GLONAF for some of our surveyed regions (e.g., South America) was incomplete (van Kleunen et al. 2019). We also recorded the location, elevation and distance to the trailhead using a handheld GPS. For a full version of the protocol, see Liedtke et al. (2020).

2.1 | Response and Explanatory Variables

We used three metrics as response variables: plot-level presence of non-native species, non-native species richness and non-native species cover. As explanatory variables, we considered a set of abiotic, biotic and anthropogenic variables which are described below.

2.1.1 | Abiotic Variables

Wherever possible, we used downscaled bioclimatic variables from CHELSA (Karger et al. 2017) as available internally from within the MIREN network. These bioclimatic variables were downscaled from a 30-arcsecond (~1 km) to a 1.2-arcsecond (~30 m) resolution using high-resolution topographic layers. We used four bioclimatic layers including mean annual temperature (Bio1), maximum temperature of the warmest month (Bio5), minimum temperature of the coldest month (Bio6) and annual precipitation (Bio12) (Karger et al. 2017). These bioclimatic variables were chosen on the basis that they are known to be good predictors of the distribution of non-native plants in mountain ecosystems and do not exhibit multicollinearity (Lembrechts et al. 2019). Downscaling was done using a geographically weighted regression (GWR) approach (Lu et al. 2017) as described by Lenoir et al. (2017) and Lembrechts et al. (2017), based on elevation, slope, aspect (separately as northness and eastness), distance from the ocean and potential solar radiation to downscale the macroclimatic layers. These variables have shown good results for interpolating climate in previous studies (Buytaert et al. 2006; Ashcroft et al. 2012; Lenoir et al. 2017). For more details on the downscaling approach, see Wedegärtner et al. (2022). For South Africa and Tasmania, the original CHELSA data at a 30-arc sec resolution was used, as for these regions the downscaled versions were not available. To examine the influence of climatic variables across different spatial scales, abiotic variables were divided into two components: a regional mean and a local deviation. The regional mean was calculated as the average of each climatic variable within each region, providing a constant value representing regional conditions (for comparisons across regions). The local deviation was then derived as the difference between each site's value and this regional mean, representing local-scale variation (for comparisons within regions).

2.1.2 | Biotic and Anthropogenic Variables

We selected the following vegetation parameters as explanatory factors: native species richness and the cover of native species, shrubs and trees for each plot. For anthropogenic variables, we used a set of proxies related to human disturbance, including (i) the distance to the trailhead (i.e., the vertical distance of each sample site to the start of a trail), (ii) distance to the trail edge (ordinal scale ranked as plot 1—trail, 2—intermediate and 3—far), (iii) evidence of non-native livestock and other non-native mammals estimated from dung presence (including cows, horses, sheeps and hares for the regions where they are non-native), (iv) trail-use intensity (low, medium and high), and (v) geographic distance to the nearest potential introduction point of non-native species, such as huts, ski resorts and parking sites. Trail-use intensity was defined by the local researchers of each region and validated through park visitor count data and, as such, was as much as possible standardised between regions. To calculate the distance to introduction points, we georeferenced all infrastructure sites that fell within a distance of 500 m from the trail and then used the nearest distance tool in QGIS (QGIS Development Team 2023) to estimate the distance of each plot to the closest introduction point.

2.2 | Analyses

All analyses were conducted in R 4.2.3 (R Core Team 2023).

To determine the main drivers contributing to the presence, richness and cover of non-native plant species along the surveyed mountain trails, we used a generalised linear mixed model (GLMM), using the *glmmTMB* package (Brooks et al. 2017) for each of the response variables as a function of the abiotic (Bio1, 5, 6, 12 [both across and within]), biotic (native species richness, native species cover, tree canopy cover, shrub cover) and anthropogenic predictor variables (distance to trailhead, distance to trail, trail-use intensity, distance to introduction point and non-native herbivory) described above. All metric predictor variables were scaled with a mean of zero and a standard deviation of one to make regression coefficients directly comparable. The unit of analysis was the individual plot within a sample site. Due to the large number of predictors, no interactions were tested.

To account for the hierarchical nature of our data, and since we were initially interested in assessing the global pattern, we used the sample site (transect identity) nested within trail identity nested in the region as the random factor in the models. To assess whether the relative importance of the effects of the different variables varies in each region, we also ran regional models, considering the sample site nested within the trail as random effects. Data limitations prevented us from including the same hierarchical set-up as random slopes into these regional models.

The presence/absence of any non-native plant species in a plot was modelled with a binomial distribution with a logit link function. Non-native plant species richness was modelled with a Poisson distribution with a log link function, and non-native plant cover with a beta distribution with a logit link function. For each model, zero inflation and overdispersion were analysed using the *DHARMa* package (Hartig and Hartig 2017), and the magnitude of multicollinearity of predictors was checked by calculating variance inflation factors (VIF) using the *Performance* package (Lüdecke et al. 2021). If the VIF of any predictor exceeded the value of 5, that predictor was removed from the model. Subsequently, to identify the optimal model for each response variable, we applied a model selection approach based on the Akaike information criterion (AIC). To achieve this, we used the *dredge* function from the MuMIn package (Barton 2016), which generates a set of models with all possible combinations of predictors and calculates the AIC for each. The model with the lowest AIC was selected as the best model. The predictions of the models were extracted based on the final models using the *ggeffect* package (Lüdecke et al. 2021).

For each of our three response variables, we determined the proportion of variance explained by each set of predictor variables (e.g., abiotic conditions, including BIO1, 5, 6 and 12) using a variance partitioning approach (Legendre 2012). Marginal R^2 values of fixed factors (predictors) and conditional R^2 values of the complete models were calculated using the *R.squared.GLMM* function of the *MuMIn* package (Barton 2016). The variance explained by a set of predictor variables was calculated as the difference between the variance explained by the full model (including abiotic, biotic and anthropogenic variables) and the variance explained by a model without the given set of abiotic variables, using the marginal R^2.

3 | Results

A total of 683 sites (2112 plots) were surveyed across 55 trails in nine mountain regions, with a greater number of sampled sites in the Southern Hemisphere (58%) compared with the Northern Hemisphere (42%, Table 1). Across all surveyed sites, a total of 118 non-native species were recorded (Table S1). Overall, mountains in the Southern Hemisphere had a higher number of non-native species (e.g., Australia 47, Chile 41, Argentina 30) present compared with Northern Hemisphere mountains (e.g., USA 14, Norway and Czech Republic 6, Table 1). The most common non-native species were forbs and grasses, with some species occurring in over half of the regions including *Taraxacum officinale* agg., *Trifolium repens* and *Poa pratensis* (Table S1). Non-native herbivores were recorded at 24% (488) of the surveyed sites across three regions, including Argentina, Chile and Norway. The majority (71%) were domestic livestock (cattle, horses, mules and sheep), followed by the European hare (*Lepus europaeus*, 29%). Where present, it was recorded across the three plots (trail edge to interior plot).

The richness of non-native plants was mainly explained by abiotic variables, which accounted for 44% of the variation (Table 2). Non-native richness increased significantly with the regional maximum temperature of the warmest month (Bio 5 across), and with decreased regional and local minimum temperatures (Bio6 across, within; Figure 2a,b). The presence of non-native species and non-native plant cover had a lower correlation with abiotic variables (25.7% and 13%, respectively), but there were some significant effects (Tables 3 and 4). The presence of non-native species increased with increasing regional mean annual temperatures (Bio1 across) and regional maximum temperatures of the warmest month (Bio5 across; Figure 3a,b) while non-native cover increased with local mean temperature (Bio1 within) and local maximum temperatures of the warmest month (Bio5 within; Figure 4a,b).

TABLE 2 | Model parameters of the best GLMM for non-native species richness per plot along hiking trails, based on 1653 sample sites, and with region nested in trail nested in sample site as a random term (Region: Trail: Sample site, 653; Trail: Sample site, 52; Region, 9). Bio1 = annual mean temperature, Bio5 = maximum temperature of the warmest month, Bio6 = minimum temperature of the coldest month. Non-native herb. Yes: Non-native herbivores are present in the region. The bioclimatic variables included two components: A regional mean (Bio across), calculated as the average of the climatic variable within each region, and the local deviation (Bio within) derived as the difference between each site's value and the regional mean.

	Estimated	Std. Error	z value	Pr(>|z|)	Explained variance
Intercept	−0.968	0.292	−3.310	**< 0.001**	
Native richness	0.156	0.016	9.612	**< 0.001**	25.7% Biotic
Native cover	0.003	0.002	1.716	**0.021**	
Shrub cover	−0.002	0.003	−0.546	0.584	
Distance to trail head	−0.236	0.601	−0.393	0.694	20.4% Anthropogenic
Trail intensity low	−0.230	0.252	−0.913	0.361	
Trail intensity medium	0.159	0.215	0.744	0.456	
Plot 2	−0.187	0.087	2.145	**0.031**	
Plot 3	−0.123	0.092	1.337	**0.018**	
Non-native Herb. Yes	−0.001	0.346	−0.003	0.997	
Bio 1 (within)	−0.001	0.060	−0.002	0.998	**44% Abiotic**
Bio 5 (across)	0.446	0.200	2.222	**0.026**	
Bio 6 (across)	0.458	0.188	2.434	**0.014**	
Bio 6 (within)	0.032	0.069	0.466	**0.048**	

Note: Significant values ($p < 0.05$) are indicated in bold.

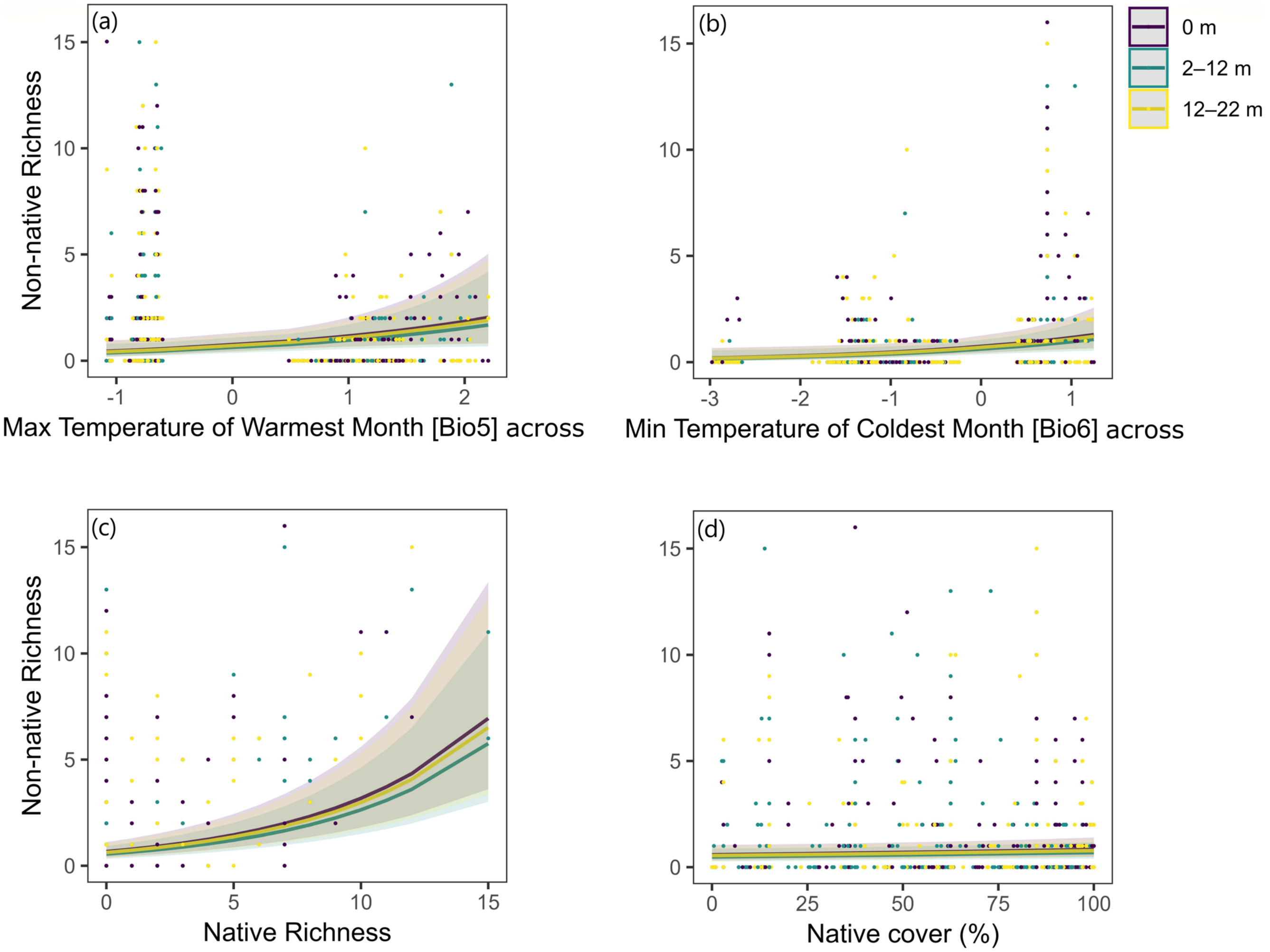

FIGURE 2 | Non-native plant species richness as a function of (a) regional maximum temperature of warmest month; (b) regional min temperature of coldest month; (c) native plant richness; (d) native cover; and distance to the trail edge (indicated by coloured lines). Purple corresponds to the plot parallel to the trail (0 m), green to the intermediate plot (2–12 m), and yellow to the far plot (12–22 m). Dots represent plot-level observations; lines represent model predictions with their confidence intervals.

Additionally, we found that the presence of non-native herbivores (mainly composed of domestic livestock) had a positive effect on the presence of non-native species (Figure S1), but with the regional results only significant for the Chilean Andes (Table S2). Anthropogenic components ranked second in explaining the variance of non-native species presence and cover (28% and 19.2%, respectively) and they were third in explaining differences in non-native richness (20.4%; Tables 2–4). We observed a significant pattern with distance from the trail edge, where all the analysed response variables decreased as we moved away from the trail (Tables 2–4). Trail use intensity was also positively related to non-native cover, but distance to the trailhead was not significant for any of the response variables (Tables 2–4).

Finally, biotic parameters showed a high impact on the presence and plant cover of non-native plants, accounting for 46.4% and 38.7% of the variance, respectively (Tables 3 and 4). Native species richness emerged as the most important biotic factor explaining non-native species distributions, showing a strong positive association with non-native richness, presence and cover (Tables 2–4, Figures 2c–4c). Total native plant cover, shrub cover, and canopy cover generally showed positive associations with non-native plants (Figures 2d and 3d). An exception was shrub cover, which was negatively associated with non-native plant cover (Figure 4d). In all cases, however, the strength of these relationships was weak (Tables 2–4).

The results of the regional models largely confirmed our findings from the global models (Tables S2–S7, Figure S2). For example, the richness of non-native plants decreased with distance from the trail edge in all regions except for South Africa (Table S3). The presence of non-native species increased with native plant richness in all regions except for the Czech Republic and Norway (Table S2). Similarly, non-native plant cover decreased with shrub cover in Argentina, China and South Africa (Table S4).

4 | Discussion

Non-native plant invasions along mountain trails worldwide exhibited notable consistencies with those observed in earlier studies along mountain roads (e.g., Seipel et al. 2012; McDougall et al. 2018). In particular, we observed a consistent and significant decrease in the presence of non-native species and

TABLE 3 | Model parameters of the best GLMM for presence/absence of non-natives along hiking trails, based on 1653 sample sites, and with region nested in trail nested in sample site as random term (Region: Trail: Sample site, 653; Trail: Sample site, 52; Region, 9). Bio1 = Mean annual temperature, Bio5 = Maximum temperature of the warmest month, Bio6 = Minimum temperature of the coldest month. Non-native herb. Yes: Non-native herbivores are present in the region. The bioclimatic variables included two components: A regional mean (Bio across), calculated as the average of the climatic variable within each region, and the local deviation (Bio within) derived as the difference between each site's value and the regional mean.

	Estimate	Std. Error	*z* value	Pr(>|*z*|)	Explained variance
Intercept	−2.300	0.269	−8.561	**< 0.001**	
Native richness	0.027	0.031	0.861	**0.029**	**46.4% Biotic**
Shrub cover	0.003	0.003	0.925	**0.035**	
Canopy	0.009	0.002	3.583	**< 0.001**	
Distance to trail head	0.040	0.058	0.695	0.487	28% Anthropogenic
Trail-use intensity low	−0.274	0.268	−1.021	0.307	
Trail-use intensity medium	0.022	0.228	0.100	0.920	
Plot 2	−0.409	0.124	−3.279	**0.001**	
Plot 3	−0.585	0.132	−4.415	**< 0.001**	
Non-native Herb. Yes	0.715	0.308	2.316	**0.020**	
Bio 1_(across)	0.257	0.124	2.065	**0.038**	25.7% Abiotic
Bio 1 (within)	0.116	0.100	1.158	0.246	
Bio 5 (across)	0.823	0.215	3.822	**0.001**	
Bio 5 (within)	−0.126	0.107	−1.181	0.237	
Bio 6 (within)	0.024	0.081	0.234	0.422	

Note: Significant values ($p < 0.05$) are indicated in bold.

TABLE 4 | Model parameters of the best GLMM for non-native cover along hiking trails, based on 1653 observations, and with region nested in trail and transect as random term (Region: Transect: Trail, 653; Transect: Trail, 52; Region, 9). Bio1 = Mean annual temperature, Bio5 = Maximum temperature of the warmest month, Bio6 = Minimum temperature of the coldest month, Bio12 = Annual precipitation. The bioclimatic variables included two components: A regional mean (Bio across), calculated as the average of the climatic variable within each region, and the local deviation (Bio within) derived as the difference between each site's value and the regional mean.

	Estimated	Std. Error	*z* value	Pr(>|*z*|)	Explained variance
Intercept	1.500	0.295	5.083	**< 0.001**	
Native richness	0.055	0.006	9.204	**< 0.001**	**38.7% Biotic**
Shrub cover	−0.009	0.001	−5.892	**< 0.001**	
Canopy cover	0.001	0.001	2.156	**0.031**	
Distance to trail head	−0.164	0.248	−0.65	0.515	19.2% Anthropogenic
Trail intensity low	−0.561	0.065	−8.624	**< 0.001**	
Trail intensity medium	0.408	0.042	9.539	**< 0.001**	
Plot 2	−0.179	0.038	4.657	**< 0.001**	
Plot 3	−0.075	0.040	1.871	**0.042**	
Bio 1 (within)	−0.063	0.017	−3.58	**< 0.001**	13% Abiotic
Bio 5 (within)	0.076	0.036	2.092	**0.036**	
Bio 5 (across)	0.195	0.226	0.863	0.388	
Bio 6 (across)	0.106	0.138	0.773	0.439	
Bio 12 (across)	−0.010	0.038	−0.274	0.783	

Note: Significant values ($p < 0.05$) are indicated in bold.

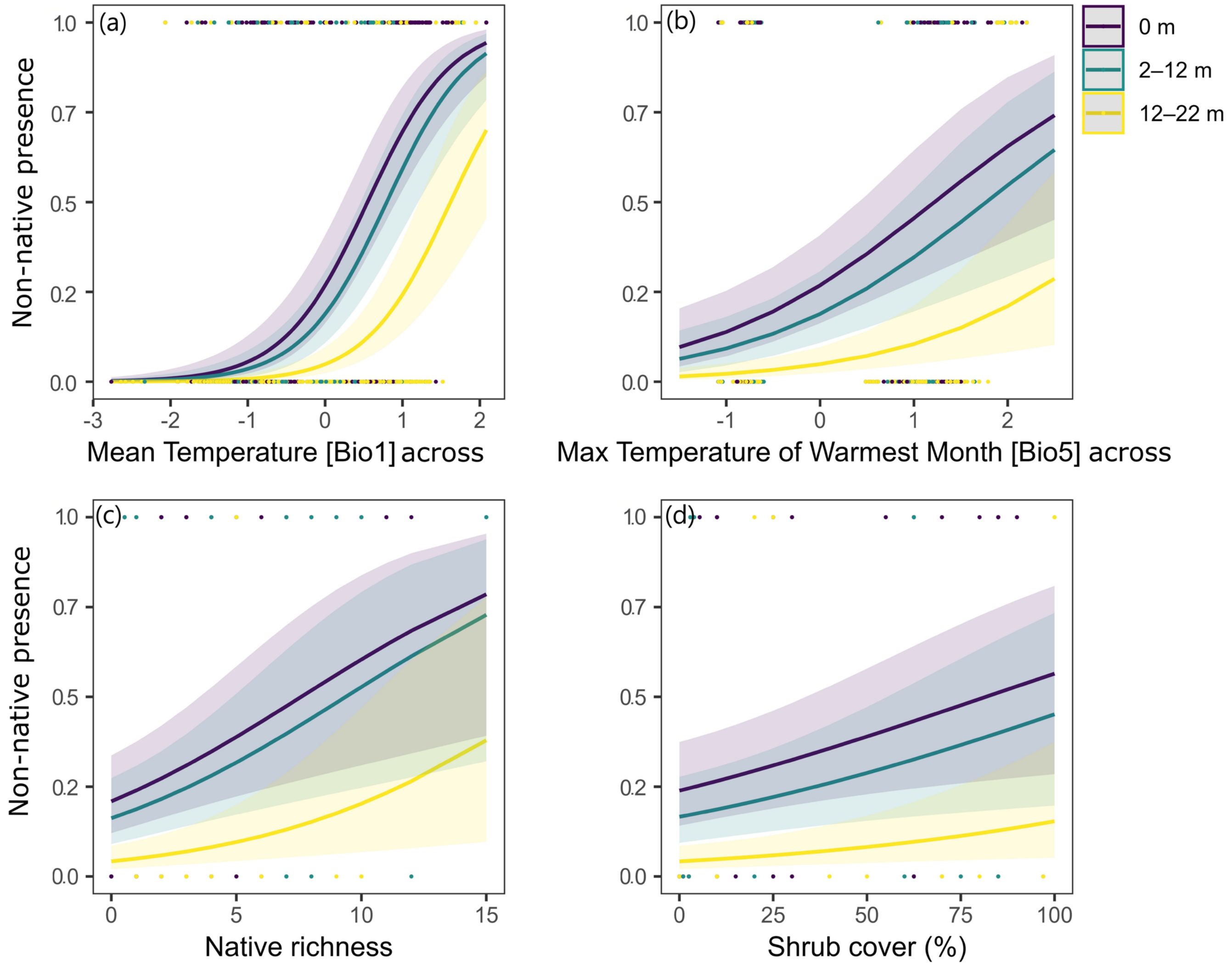

FIGURE 3 | Predicted global non-native presence as a function of (a) regional mean annual temperature; (b) regional maximum temperature of the warmest month; (c) native plant richness; (d) shrub cover; and distance to the trail. Purple corresponds to the plot parallel to the trail (0 m), green to the intermediate plot (2–12 m), and yellow to the far plot (12–22 m). Dots represent plot-level observations, lines represent model predictions with their confidence intervals.

non-native richness with lower maximum temperatures (i.e., at higher elevations and latitudes) and a consistent decline with increasing distance from the trail edge (see Figure S1). These findings support the concept of a 'double filter' imposed by disturbance and climate factors related to elevation, as described for mountain roads by McDougall et al. (2018). This means that non-native species from the lowland species pool can use structures like trails as dispersal corridors into relatively pristine mountain ecosystems. Yet, they are gradually filtered out with increasing harsher climatic conditions including lower temperatures, when moving away from the trail head (Alexander et al. 2011). A second filter is set by the distance to the road or trail edge that is associated with reduced disturbance levels and increased biotic resistance from the native species (Wells et al. 2012; McDougall et al. 2018).

4.1 | The Influence of Native Vegetation

Our study found that native species richness had a strong impact on the distribution of non-native species along the trails with a positive association for all non-native response variables assessed. Additionally, at the global scale, our results showed a weak positive relationship between native cover variables (total, shrubs and canopy) and non-native presence and richness. The counterintuitive relationship found between non-native species richness and both native species richness and total native cover is likely driven by the underlying variation in local environmental heterogeneity. Plots with greater heterogeneity, resulting from factors such as microtopography and disturbance or woody vegetation acting as ecosystem engineers, may create a broader range of microhabitats, increasing the availability of niche space for both native and non-native species (Souza et al. 2011; Kleinhesselink et al. 2014; Cavieres 2021). Additionally, in stressful environments, native species can ameliorate conditions, thereby facilitating the establishment and spread of non-native species. This facilitation can lead to positive associations between native biodiversity and invasion success (Cavieres 2021). At the same time, the widely accepted notion that higher native diversity acts as a barrier to species invasions (e.g., Tilman 1997) may not apply in mountain environments, where most species

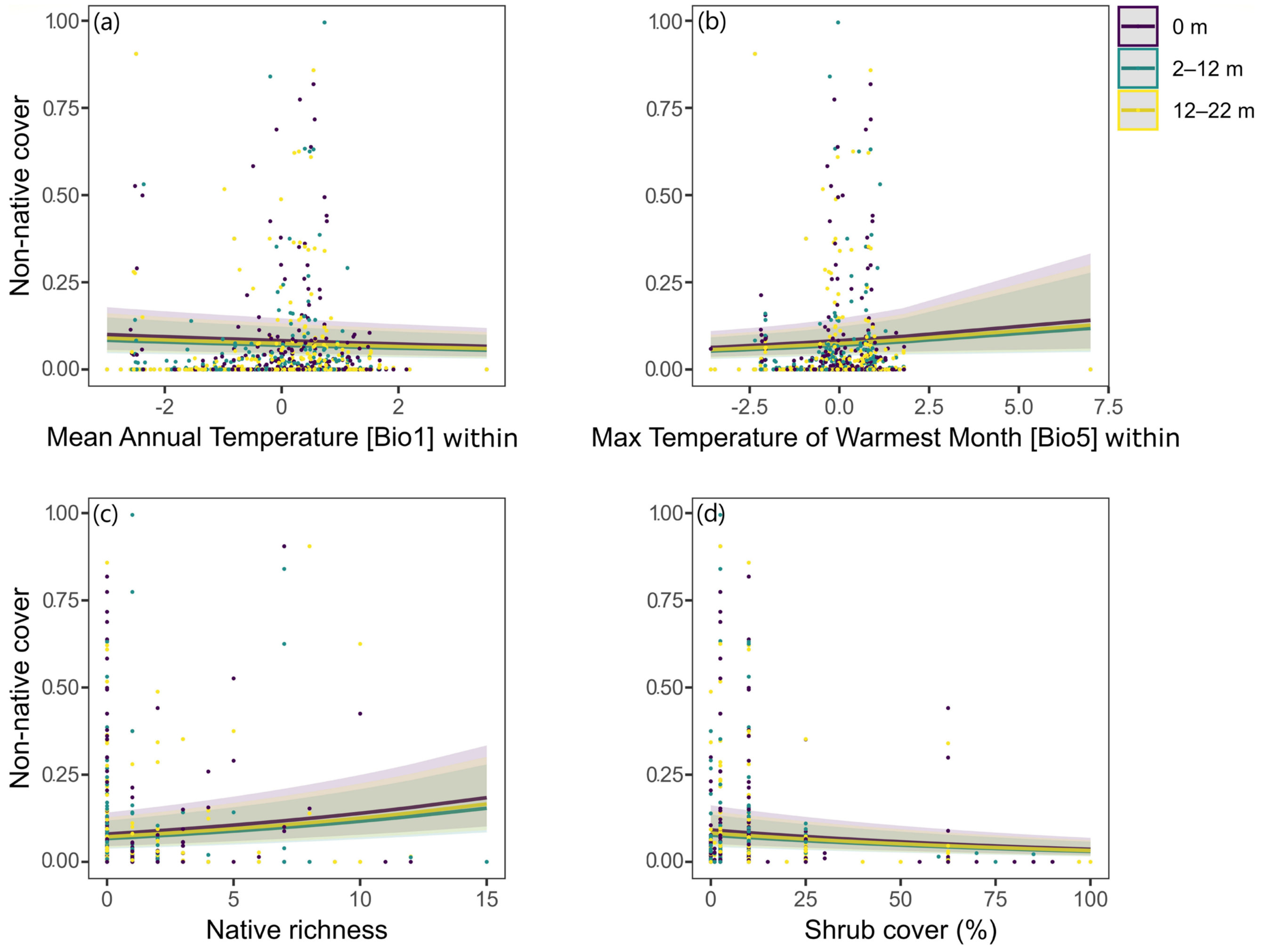

FIGURE 4 | Predicted global non-native plant cover as a function of (a) local mean annual temperature; (b) local maximum temperature of the warmest month; (c) native richness; shrub cover (d); and distance to the trail. Purple corresponds to the plot parallel to the trail (0 m), green to the intermediate plot (2–12 m), and yellow to the far plot (12–22 m). Dots represent plot-level observations, lines represent model predictions with their confidence intervals.

are small and may lack the competitive ability to exclude new arrivals.

In relation to canopy cover, an alternative explanation of the positive association with non-natives can be the underlying correlation between canopy cover and elevation, with lower elevation sites, which are likely more invaded, also tending to support greater tree cover (Pauchard and Alaback 2004; Fuentes-Lillo et al. 2021). The positive biotic interactions were not observed for all variables in our study, with native shrub cover negatively related to non-native cover, supporting previous studies conducted in mountain regions (e.g., Pollnac and Rew 2014; Averett et al. 2016; Kirkpatrick et al. 2024). This negative relationship can be partly attributed to local competitive interactions such as shading that may reduce light availability for the increase in cover or abundance of non-native plants (Averett et al. 2016; McDougall et al. 2018; Fuentes-Lillo et al. 2021). There are exceptions to this pattern, like in the high arid Andes where low-stature cushion shrubs may facilitate both the establishment and success of non-native herbs under harsh conditions (Cavieres et al. 2005).

4.2 | The Role of Trails and Domestic Livestock

Our study found overall similarities to studies on mountain roads in relation to anthropogenic disturbance: at increasing distances from trail edges, the presence, cover and richness of non-native species are reduced. Despite these similarities, we did find some discrepancies in the relative importance of anthropogenic factors (Barros et al. 2022). While global and regional analyses on mountain roads have shown that anthropogenic disturbance and elevation are the main factors shaping plant invasions, our data from mountain trails showed that the relative importance of anthropogenic variables, such as distance from the trail edge and trail use intensity, were lower compared to either biotic or abiotic parameters. The lower effects of trailside compared to roadside disturbance could be linked to the distinct nature of trails.

Trails typically cause less disturbance and less alteration to the adjacent vegetation compared to roads (Müllerová et al. 2011). Additionally, many mountain trails are predominantly formed by trampling or simple vegetation removal and often do not involve the addition of foreign materials like gravel, asphalt or deicing salt, which are commonly seen along roads, resulting in a smaller impact on trailside soil chemistry and disturbances related to the construction work (Müllerová et al. 2011). Moreover, mountain trails may have a smaller effect on microclimatic conditions than mountain roads due to their narrower width, smaller change in albedo, lesser soil compaction and water runoff, and lesser impact on snow cover compared to roads, as demonstrated in a study in the northern Scandes mountains (Lembrechts et al. unpublished).

Although the lesser impacts, distance to trail edge showed a consistent pattern with non-native species. In addition, trail use intensity favoured non-native cover, possibly related to a higher propagule pressure exerted by hikers through the unintentional dispersal of non-native seeds on their equipment (Pickering and Mount 2010) and greater trampling disturbance (Barros and Pickering 2014), both factors known to facilitate the success of non-native plants (Fuentes-Lillo et al. 2021). Adding to trail disturbances, domestic livestock was important in explaining the presence of non-native plants, supporting previous regional studies along mountain trails (Liedtke et al. 2020; Alvarez et al. 2022). It is well known that livestock can act as a vector for the dispersal of non-native propagules along trails, including towards higher elevations (Ansong and Pickering 2013). Also, grazing can significantly alter plant and soil structure, nutrient availability (including inputs through manure), and reduce competition by creating disturbed habitats with bare-soil microsites (Pickering et al. 2010). The high importance of livestock grazing has been demonstrated in a meta-analysis that found this as one of the principal factors explaining the increase in non-natives over disturbances such as anthropogenic fires and soil impacts (Jauni et al. 2015). Because disturbance from domestic livestock can often extend beyond trail edges, as evidenced by previous studies (Barros and Pickering 2015), and what was observed in our study for the three regions where domestic livestock was documented, it is important to consider this factor when managing plant invasions.

At the regional scale, the positive association between domestic livestock and non-natives was only significant for the Chilean Andes site, highlighting the importance of considering ecological context and grazing history (Marchetto et al. 2021) when assessing its influence on plant invasion. In the Andes, domestic livestock is known to play an important role in the dispersal and establishment of non-native plants at higher elevations, as many local communities currently use these areas to graze their cattle during the summer months (Duchicela et al. 2024). This transhumance activity is called 'veranada' and is an important part of the culture of Andean communities, but contributes to the presence of these non-native plants in the region (Pauchard and Alaback 2004; Barros and Pickering 2014). In the European Alps, although livestock activities have become less frequent, they remain widespread in some areas. There is also a significant legacy of these activities, such as abandoned farms, which serve as propagule sources at higher elevations (Dullinger et al. 2003; Mascetti et al. 2023). By contrast, in the Maloti-Drakensberg in South Africa, where extensive communal rangeland transhumance occurs between lower elevation (*c.* 1500 m a.s.l) and higher elevation areas (> 2800 m a.s.l) seasonally, there is no evidence at this point of livestock being vectors of non-native species, possibly due to the competitive resilience of the high elevation tussock alpine grasslands–shrublands against invasion (Turner et al. 2021).

4.3 | Regional Consistency and Management Implications

Finally, our findings demonstrated relative consistency across regions. While the total number of non-native species differed significantly, with notably lower levels in Eurasia where many global mountain invaders originate (and thus are classified as native species; Alexander et al. 2016), the relationships with abiotic, anthropogenic and biotic factors remained remarkably consistent. Such intercontinental consistency has been observed along mountain roads as well (Seipel et al. 2012; Barros et al. 2022), suggesting that patterns of non-native species invasion into mountain areas largely adhere to the same rules globally. Additionally, not only did the relationships remain remarkably constant, but the identity of non-native species across the regions was relatively comparable as well (Barros et al. 2022). Indeed, ruderal and competitive forb species of European origin (e.g., *Cerastium arvense*, *Hypochaeris radicata*, *Rumex acetosella*, *Taraxacum officinale* agg. and *Trifolium repens*) were often among the most dominant non-native species in multiple regions, in line with patterns in alpine areas worldwide (Alexander et al. 2016).

With the increasing pressures imposed by human activities (mainly tourism and recreation) in mountainous regions, it is expected that hiking trails will further contribute to the spread of non-native species, especially considering the likely rise in the number of mountaineers, hikers and trail runners both within and outside protected areas. Our findings do indicate that the design and utilisation of mountain trails can mitigate their role as pathways for non-native species. Specifically, the construction of trails can take advantage of the native shrub cover potential to act as barriers against the spread of non-native plants (Liedtke et al. 2020). Additionally, preventing the presence of domestic animals, whether as livestock or as means of transportation, can decrease both the introduction of propagules and the likelihood of disturbance-related establishment (Alvarez et al. 2022). If the latter cannot be avoided, taking additional precautions such as the use of weed-free hay for livestock could still result in important reductions in the impact of trail use by livestock (Rew and Larson 2022).

While we emphasise that most of the observed non-natives are not (yet) invasive in these mountain ecosystems, and hiking trails have important benefits for humans as well as under some conditions for native plant species (Wedegärtner et al. 2022), it is as always beneficial to educate trail users about their roles in shaping those ecosystems. Additionally, maintaining and marking trails to encourage hikers to adhere to established paths whenever possible can limit trail networks to specific sections of protected areas and hence prevent pathways for non-native plant establishment (Rew and Larson 2022). Finally, the strong negative relationship of non-native diversity with climate again suggests that up till now, cold-climate high elevation areas still remain relatively free of non-natives. This creates opportunities for relatively low-cost prevention rather than eradication of non-natives in those areas, although it should be noted that the nature of trails as dispersal corridors makes such a task difficult to achieve as long as the lowland non-native species pool is not controlled.

5 | Conclusions

While we found that anthropogenic variables had a lesser impact on non-native plant species distribution, richness and cover along mountain trails compared to previously described trends on mountain roads, our findings do call for caution for mountain ecosystem conservation and tourism management. Our assessment is the first to show that mountain trails are acting as conduits for non-native plants into mountain areas worldwide. Given the fact that mountain trails are often much more widespread in mountains than roads, and also expand into more vulnerable and protected areas, these trails bring substantial risks for plant invasions into relatively pristine mountain ecosystems. Moreover, our findings showed that non-native species are surprisingly weakly constrained to trailsides, potentially due to the fact that trail users (human or animal) go off trail more often than most road traffic (Barros and Pickering 2014). Biotic factors play a crucial role in explaining the presence and cover of non-native plants. In some cases, a positive relationship between native plant diversity and non-native plant occurrence has been observed, suggesting that facilitative interactions may modulate the distribution of non-native plants in mountain ecosystems. We thus end with the recommendations to restrict the expansion of trail networks, educate hikers to remain on trails, and otherwise continue monitoring, especially in vulnerable areas of high biodiversity and human activity.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The scripts and Excel file used to generate the analyses for this paper are accessible through the Dryad repository: https://doi.org/10.5061/dryad.2rbnzs807.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.