



Hiking trails shift plant species' realized climatic niches and locally increase species richness

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Abstract

Aim: The presence and use of trails may change plant species' realized climatic niches via modified abiotic and biotic conditions including propagule transport, allowing competition-pressed alpine species to expand their rear edges towards warmer locations and lowland species to extend their leading edges towards cooler locations. We investigated whether mountain trails indeed act as corridors for colonization and shift species' realized climatic niches, resulting in higher species richness in trailsides.

Location: Dovrefjell and Abisko area in the Scandes mountains of Norway and Sweden.

Methods: We surveyed plant community composition and disturbances along 16 hiking trails in summer 2018 (Dovrefjell) and 2019 (Abisko). We linked changes in species' realized climatic niches to their climatic optimum and variation in species richness to climate, trail effects and resident plant community characteristics.

Results: Plant species richness was on average 24% greater in trailside than in interior vegetation plots. Proximity to trails accounted for 9% and climatic harshness for 55% of variation in species richness explained in our model. Trailsides increased in richness, especially in relatively species-poor sites and close to introduction points (each accounting for 24% of variation in our model of species gains). Shifts in rear edges and optima of realized climatic niches along trails related to species' undisturbed climatic optimum, with alpine species being more likely to move into warmer locations. While some disturbance-associated species shifted their leading edges towards colder locations, contrary to expectations this was not the case for lowland species. Overall, shifts in climatic niches resulted in more species' niches overlapping in trailsides than in the interior vegetation.

Main conclusion: Trails can locally increase species richness by creating opportunities for colonizing species and weaker competitors. Because of prevailing disturbance, they may even provide opportunities for persistence and downward expansion of alpine species, aiding conservation efforts.

KEYWORDS

alpine plants, biotic interactions, climate gradient, disturbance, mountain trails, realized niche, species range shifts

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1 | INTRODUCTION

Understanding how climate and anthropogenic disturbance influence plant communities in mountains is necessary to protect these ecosystems (IPBES, 2019). While mountain ranges are hotspots of biodiversity and endemism (Steinbauer et al., 2016), they experience rapid warming, especially around the annual 0°C isotherm (Pepin & Lundquist, 2008). Additionally, mountains undergo shifts in land use (Körner et al., 2006) and experience increasing pressure through recreational activities and associated infrastructure such as hiking trails (Debarbieux et al., 2014).

Species range shifts into previously unsuitable higher elevation habitats are expected with climate warming under the assumption of niche-conservatism (Pearman et al., 2008). As strong competitors move their leading range edge into new locations, alpine plant species might lose ground due to increased competition at their rear range edge (Gottfried et al., 2012; Grabherr et al., 1994). However, a plant species' realized climatic niche, and thus spatial distribution in an area, is determined by a much wider set of ecological processes, including dispersal rate (Engler et al., 2009), habitat modification and resulting changes in biotic and abiotic interactions (Lenoir et al., 2010). As hiking trails may facilitate propagule transport (Mount & Pickering, 2009) and influence competitive and facilitative relationships between species through increased disturbance (Bates, 1935), a better understanding of trail effects on species' realized climatic niches and resulting changes in species distribution and richness is called for.

For plants colonizing new locations in high-latitude mountain systems, competition is considered especially important at lower elevations with milder climate, while at higher elevations facilitation of the colonizer by the extant vegetation is thought to be dominating (Bertness & Callaway, 1994; Choler et al., 2001; Paquette & Hargreaves, 2021). Disturbance can disrupt competition and facilitation through removal of plant biomass and creation of gaps in the vegetation (Lembrechts, Pauchard et al., 2016; Nystuen et al., 2014). Where competition is most important, disturbance may lead to competitive release, with gaps in the vegetation promoting establishment by newcomers. In harsher environments, gap formation is expected to reduce facilitation by lessening environmental amelioration by neighbouring plants (Bertness & Callaway, 1994; Lembrechts et al., 2015). Reduced competition in milder locations could result in downward shifts in rear edges of (competitively excluded) alpine species (Chardon et al., 2019; Lenoir et al., 2010; Normand et al., 2009) and thus changes in plant species' realized climatic niche and spatial distribution. Competitive release may not only be limited to the mild end of the climate gradient, though, as there is evidence for a continued importance of competition in alpine plant communities, with gaps increasing colonization even under harsh climatic conditions (Graae et al., 2011; Lembrechts, Pauchard et al., 2016).

Competition and resistance to colonization are influenced by characteristics of resident plant communities (Auffret et al., 2010; Graae et al., 2011; Pollnac & Rew, 2014). Differences may stem

from the vegetation structure of a site (Giorgis et al., 2016), the vegetation's susceptibility to disturbance (Graae et al., 2011; Milbau et al., 2013), resource availability (Davis et al., 2000), direct biotic interactions (Cavieres et al., 2008) and species richness as an expression of environmental factors, microheterogeneity and biotic interactions (Elton, 1958; Levine & D'Antonio, 1999; Peng et al., 2019). Herb-dominated and willow shrub-dominated communities are most hospitable for colonization in high-latitude mountain ecosystems (Graae et al., 2011), while dwarf shrub- and lichen-dominated ones, such as *Empetrum nigrum* communities, are more resistant due to their dense growth (Pellissier et al., 2010) and allelopathic properties (Nilsson, 1994).

In the European Alps, lowland species exhibited larger upwards shifts of range edges and a greater increase in abundance than alpine species (Rumpf et al., 2018). Lowland species were also more likely to show establishment lags (Rumpf et al., 2019). As anthropogenic disturbances appear to favour successful colonization by lowland species (Lembrechts, Alexander et al., 2016; Lembrechts, Pauchard et al., 2016), Alexander et al. (2018) hypothesize that such disturbances might decrease establishment lags. Where disturbance facilitates the expansion of species' realized climatic niches, this should lead to a greater number of species' climatic niches overlapping and, therefore, a locally increased species richness.

Mountain trails can be described as features of linear disturbance (Suárez-Esteban et al., 2016) that cut through mountain ecosystems and may influence species' realized niches through disruption of competition and facilitation, and by promoting the transport of diaspores. The construction and use of hiking trails disturbs vegetation mechanically, often resulting in bare soil patches and modified soil conditions (Bates, 1935; Gellatly et al., 1986; Marina et al., 2010), and opening up sites for colonization (Monz, 2002). Both hikers and animals using trails can act as vectors of dispersal by transporting diaspores clinging to footwear, clothes and equipment of people (Huiskes et al., 2014; Mount & Pickering, 2009; Ware et al., 2012) and feet and fur of animals or embedded into their faeces (Bråthen et al., 2016; Fischer et al., 1996). Tourism infrastructure such as cabins, trailheads and ski lifts may act as sources from which propagules of lowland or non-native species spread into mountain areas (Pickering et al., 2007).

Higher plant species richness in trailsides compared with the surrounding vegetation could result from change in realized climatic niches and high diaspore input. This has been observed in different ecosystems (Benninger-Truax et al., 1992; Suárez-Esteban et al., 2016, and references therein), and trails have been shown to promote the spread of non-native species in mountain areas (Anderson et al., 2015; Liedtke et al., 2020). In Arctic, Antarctic and alpine systems, however, findings are contradictory, with decreases in vascular plant species richness along trails in some cases (Crisfield et al., 2012), and in other cases either no clear effect (Jägerbrand & Alatalo, 2015; Monz, 2002) or effects depending on community type, soil moisture (Gremmen et al., 2003), trail type (Hill & Pickering, 2006; Nepal & Way, 2007) and use intensity

(Benninger-Truax et al., 1992). We therefore, need a better understanding of when and to what extent trails affect the colonization of lowland and alpine species into new areas in alpine ecosystems.

In this paper, we examine the effects of hiking trails on species richness, species' realized climatic niches and colonization in an alpine ecosystem. We surveyed the presence and cover of all vascular plants, as well as trail effects along 16 trails spanning steep climatic gradients in two mountain areas. We used this data to model regional species richness, determine the extent to which trails modulate species richness patterns and compare species' realized climatic niche in trailsides and the interior vegetation—undisturbed vegetation away from trails. We hypothesized that: (a) trails act as corridors of colonization for species in mountain ranges, resulting in larger species richness at trailsides; (b) how species colonize new areas along trails is affected by their climatic niche, with lowland plants expanding towards colder locations and alpine plants shifting to warmer locations as competition decreases through disturbance; and (c) in addition to regional drivers of biodiversity, site characteristics such as the recipient community, disturbance and dispersal influence local colonization along trails.

2 | METHODS

2.1 | Study regions

We conducted vegetation surveys along mountain trails in two popular hiking areas in Scandinavia. The Abisko area is situated in Northern Sweden (68.3°N; 18.8°E) and Dovrefjell approximately 700 km south in Southern Norway at 62.2°N; 9.5°E (Figure 1a–d). Both areas are accessible by road and train and are popular tourist destinations with many visitors exploring on foot, mostly following trails (Gundersen et al., 2019; Karlsson, 2016).

At Fokstugu weather station in Dovrefjell (62.11°N, 9.29°E, 979 m.a.s.l.), the mean annual temperature was 1.0°C and mean annual precipitation 445 mm (2002–2019). In Abisko (68.36°N, 18.82°E, 388 m.a.s.l.), the corresponding values were 0.5°C and 340 mm (Norsk Klimaservicesenter, 2020; SMHI, 2020). Both areas are located on the lee-side of mountain ranges, with landscapes shaped by the Weichselian glaciation events (Holdar, 1959; Paus et al., 2011). The bedrock in Abisko area is mostly metamorphic with some acidic and ultrabasic intrusions; in Dovrefjell, it is composed of calcium-rich phyllites. Soils are predominantly thin podzols developed on deposits of glacial till (SGUs Kartvisare, n.d.; Sjögersten et al., 2003), allowing for a rich flora, especially in calcium-rich locations (Gjærevoll, 1979; Koltzenburg & Schipperges, 2014).

The tree line and forest below largely consist of mountain birch (*Betula pubescens*). Low-alpine plateaus host dwarf shrub communities and lichen heaths dominated by *Empetrum nigrum*, *Vaccinium uliginosum*, *V. vitis-idea*, *B. nana* (and *Arctostaphylos uva-ursi* at Dovrefjell), lichens and bryophytes, with considerably denser and more widespread lichen heath in Dovrefjell than in Abisko. The

vegetation at higher elevation is a mosaic of dry heath, meadow vegetation, snow beds and sparsely vegetated boulder and scree fields (De Wit et al., 2014; Sjögersten et al., 2003). Vascular plant cover was above 75% in most plots; vascular species richness was highly variable (ranging from 2 to 56 and 1 to 58 species in Dovrefjell and Abisko, respectively). The elevation gradient in the Abisko area spans from 341 m.a.s.l. (Lake Torneträsk) to 2096 m.a.s.l., the top of Sweden's highest mountain (Kebnekaise); at Dovrefjell it spans from 659 m.a.s.l. (Dombås) to 2286 m.a.s.l. (Snøhetta mountain).

Sami people traditionally used both areas for reindeer herding (Bergstøl & Reitan, 2008; Emanuelsson, 1987). Today, such practices only take place in the Abisko area (Gabna - Sametinget, 2021). Sheep are grazing in Dovrefjell in summer (kilden.nibio.no, 2021), and a small population of muskoxen is present west of the E6 highway. Trails are used for hiking, and to a lesser extent for biking; in Dovrefjell, some trails are also used for horse riding. The average width of the examined trails was 2.5 m, and the trail surface was mostly bare soil interspersed with remaining vegetation.

2.2 | Data collection

2.2.1 | Field surveys

We surveyed a total of 16 trails, eight in each region, following the trail survey protocol from the Mountain Invasion Research Network (MIREN) as outlined in Liedtke et al. (2020). Trails were surveyed early July to early September, in 2018 for Abisko and 2019 for Dovrefjell. Along each trail, we placed 10 T-shaped transects at intervals of equal elevation from the trailhead to the highest occurrence of vascular plant species along the trail, or the highest point of the trail feasible if this occurred below the limit of vascular vegetation (Figure 1e). Each so-called T-transect consisted of three 2 m × 10 m plots, with the trailside (T) plot directly adjacent to the trail and parallel to its edge forming the short side of the T. Perpendicular to this, the mid-plot (M) and farthest away the interior vegetation plot (F) form the long side of the T (see Figure 1e–f). We are, therefore, capturing a gradient from strongly trail-influenced vegetation (T) to interior vegetation that was not visibly influenced by the trail (F). For each plot, we determined the presence of vascular plant species and estimated their cover (see Appendix S1) alongside that of total vascular vegetation, herbs and forbs, shrubs, dwarf shrubs, bryophytes, rocks and bare soil. We measured the visible extent of mechanical disturbance from trampling exceeding the trail edges and surveyed the number of gaps in the vegetation with exposed soil encountered along a line transect crossing the middle of the plot (see Appendix S1: Figure S1.1). The number of gaps and their representative size were subsequently used to calculate an index of the area covered by gaps (see protocol in Appendix S1). Information about the conservation status of plant species was added to determine whether any threatened species were especially affected by trails (Norwegian Red List, 2015; Swedish Red List 2020, 2020). In each area, three species were listed as near threatened.

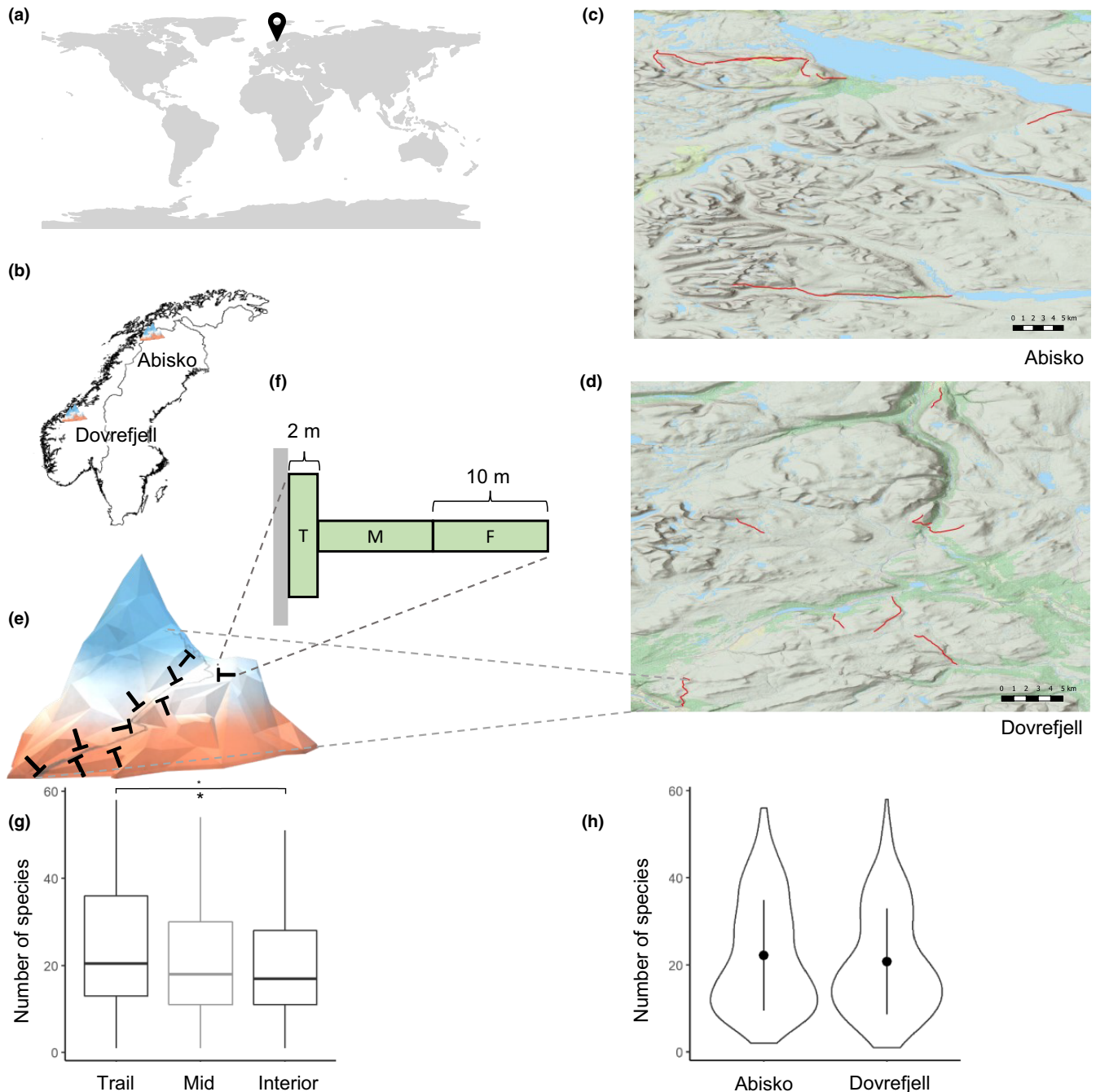


FIGURE 1 Schematic map of (a) the location of the study areas in northern Europe and (b) within the context of Scandinavia, with more detailed maps of surveyed hiking trails in (c) Abisko and (d) Dovrefjell. (e) Shows the study design of 10 T-transects at regular elevation intervals along a trail and (f) the trailside (T), mid- (M) and interior vegetation (F) 2×10 m plots that constitute each T-transect. Panel (g) shows the median number and interquartile ranges of species per plot type (with the asterisk denoting a significant difference at the $p < .05$ level between T and F plots, and M plot in grey, as it was not included into the comparison, and (h) depicts the number of species per 20m^2 plot in the two research areas, with mean (circle), standard error (line) and density function (area). Note for (e) and (f): Trails and T-transect plots are not to scale

2.2.2 | Climate and GIS data

To obtain functionally relevant bioclimatic predictor variables for our models (Elith & Leathwick, 2009), we used high-resolution topographic layers to downscale CHELSA bioclimatic layers (Karger et al., 2017; Karger et al., 2018) with a 30-arcsecond (~ 1 km) resolution and produce temperature at 1.2-arcsecond ($\sim 30\text{m}$) resolution.

Downscaling followed a geographically weighted regression (GWR) approach (Lu et al., 2011) as described by Lenoir et al. (2017) and was based on elevation, slope, northness, eastness, distance from the ocean and potential solar radiation. These predictor variables have shown good results for predicting temperature in previous studies (Ashcroft & Gollan, 2012; Buytaert et al., 2006; Fridley, 2009; Lenoir et al., 2017). The downscaling process is described in Appendix S1.

To obtain plot-based estimates of climatic harshness, we applied a principal component analysis to high-resolution annual mean temperature, maximum temperature of the warmest month and minimum temperature of the coldest month, as these were highly correlated (see [Appendix S2](#): Table S2.1). The first principal component captured 87% of the variation in climate data and was strongly and negatively correlated with mean annual temperature ($r = -0.97$, $p < .001$) and minimum temperature ($r = -0.98$, $p < .001$), but less so with maximum temperature ($r = -0.53$, $p < .001$). Using this principal component, a climatic harshness value was assigned to each plot.

To determine the distance to the nearest potential propagule introduction source for each plot, we downloaded all roads, railways and buildings for a bounding box surrounding our trails from Open Street Map using the 'osmdata' package (Padgam et al., 2017) and calculated the Euclidian distance. If no such anthropogenic features were present along a trail, additional propagule introduction by humans was considered most likely at the trailhead and, therefore, the distance from there to each plot, along a hiking trail, was taken as distance to the nearest potential introduction source.

2.3 | Analyses

2.3.1 | Trails as corridors of colonization in mountain ranges

We compared median species richness in trailside, intermediate and interior vegetation plots with a Friedman test and paired Wilcoxon signed-rank tests with a Bonferroni correction (Hollander & Wolfe, 1973). For each transect, we compared the presence of species in trailside and mid-distance plots with those found in the associated interior vegetation plot to quantify the number of species lost and gained. We tested for differences in median number of species lost and gained and between trailside and mid-distance plots again using paired Wilcoxon signed-rank tests.

Next, relationships between plot-level species richness and distance to trail, regional drivers of species richness such as microclimate, distance to potential introduction sites and the research area were analysed with generalized linear mixed-effect models (GLMMs, with a Poisson error distribution) using the 'glmmTMB' package (Brooks et al., 2017). Transect nested within trail was chosen as based on a selection of the random effects model with lowest Akaike Information Criterion (AIC, Akaike, 1974) starting with the most complex possible random effects structure as described in Zuur et al. (2009). We modelled species richness as a function of climatic harshness, distance from trail edge, distance to nearest introduction point, research area (Abisko vs. Dovrefjell) and the interactions of distance from the trail, climatic harshness and distance to introduction point. Then, we employed backward model selection based on AIC to find the optimal model for species richness using the 'MASS' package (Venables & Ripley, 2002). To determine how much of the variation in richness each of the predictor variables explained, we constructed nested partial models and used a variance partitioning approach (Legendre & Legendre, 2012).

2.3.2 | Range shifts along trails

For all species with more than 6 occurrences in each plot type (i.e. trail, mid, interior) in both research areas, we calculated the rear edge (warmest occurrence), leading edge (coldest occurrence), climatic range and optimum position (mean occurrence along the gradient weighted by species cover, as outlined in Lembrechts, Alexander et al., 2016) along the gradient of climatic harshness. To evaluate how proximity to a trail can influence realized climatic niche, we determined species-specific shifts in rear edge, leading edge, optimum and climatic range between trailside and interior vegetation plots. The influence of a species' realized niche on range shifts was tested through linear regression analysis, modelling changes in rear edge, leading edge, climatic range and optimum as a function of a species' climatic optimum in the interior vegetation.

2.3.3 | Site-level drivers of colonization

To examine how the interplay between regional drivers of richness and site-level properties influences colonization along trails, we calculated the difference in species richness between each pair of interior vegetation and trailside plots and modelled this change in richness using a linear mixed-effect model with a Gaussian error distribution (Bates et al., 2015). We included regional drivers of

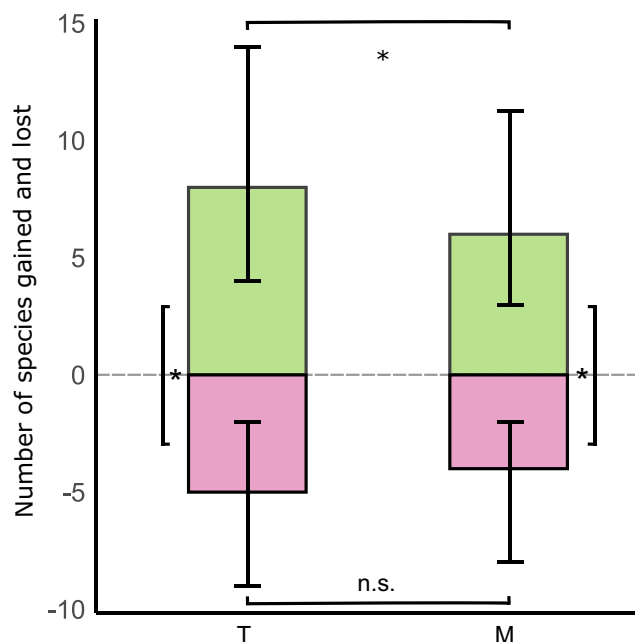


FIGURE 2 Bar plots of median and interquartile ranges of number of species gained (green, positive values) and lost (pink negative values) for trailside (T) and mid-distance (M) vegetation relative to the number of species present in interior vegetation. We compared lost with gained, within T and M, respectively, and differences in lost and gained between T and M. Significance of each pairwise Wilcoxon comparison with Bonferroni correction at the $p < .05$ level is denoted by an asterisk (full summary table [Appendix S2](#): Table S2.5)

colonization (distance to introduction source, interaction between climatic harshness and research area), site-level properties related to disturbance by trails (disturbance extent into the vegetation, gap index and total vegetation cover), properties of the recipient plant community (species richness of the interior vegetation, herb cover and dwarf shrub cover of the colonized plot) into our beyond optimal model. To find the best model, we again used AIC-based backward model selection. Trail identity was included as a random effect after determining the optimal random effects structure using AIC. Contributions of the different variables were analysed using variance partitioning.

3 | RESULTS

3.1 | Trails as corridors for colonization

We found a total of 325 species of vascular plants, of which 296 could be identified to species level (Appendix S2: Tables S2.2 and S2.3). The number of species per plot varied considerably within both regions, but their means were rather similar (Figure 1h; Abisko, 24.0 ± 13.5 [SD]; Dovrefjell, 23.4 ± 13.9). Plots next to trails had on average 24% more species than plots in the interior vegetation (Figure 1g; median 4 [95% CI: 1–6] species more; Appendix S2: Table S2.4). Trailside and mid-distance plots gained more species than they lost (Figure 2; trailside: median 3 [95% CI: 2–4] mid-distance: median 2 [95% CI, 1–3] more species gained than lost; Appendix S2: Table S2.5), and trailside plots gained on

average two more species than the mid-distance plot (Figure 2; Appendix S2: Table S2.5).

Species that were frequently gained in trailside plots included grasses such as *Poa annua*, *Phleum alpinum* and *P. alpina*, low-stature forbs such as *Sibbaldia procumbens* and *Euphrasia frigida*, and some species associated with agriculture such as the forbs *Trifolium repens* and *T. pratense*, but also occasional occurrences of red-listed species that were not found in the interior plots, such as *Draba lactea* and the orchid *Platanthera obtusata* (see Appendix S2: Tables S2.2 and S2.3).

Variation in species richness may stem from a multitude of interacting drivers. Our best GLMM captured 17% of the variation observed (marginal R^2). Of this explained variance, climatic harshness was the main determinant of plot-based species richness (Figure 3; 55%, with greatest richness at lowest climatic harshness; see Appendix S2: Tables S2.6 and S2.7 for model parameters and variance partitioning), followed by study area (10%, with greater richness in Dovrefjell than in Abisko) and distance from trail (9%, with higher richness at trailsides). Distance to introduction source only explained 1% of the variance in our model of plot-based richness.

3.2 | Trail influence on occupied climatic niches

Shifts in realized climatic niche when growing close to trails could be examined for 73 species from Abisko and 54 from Dovrefjell; this included 37 species sufficiently present in both study areas (Figure 4; see Appendix S2: Tables S2.8–S2.11, Figures S2.2–S2.7). Shifts were species- and area-specific. While shifts in optimum were small for some species, over half of them shifted their optimum towards warmer locations (Dovrefjell 59%, Abisko 53%) close to trails. The rest of the species shifted their optimum towards colder locations. In Dovrefjell, the shares of species that expanded their rear edges towards warmer (28%) or retracted towards colder (26%) locations were similar, and the proportion of stable rear edges was high (47%), whereas in Abisko more species lost ground at their rear edges (57%) and the proportion of stable rear edges was lower (23%). More species expanded their leading edges towards colder locations (Dovrefjell 30%, Abisko 38%) rather than losing ground (Dovrefjell 22%, Abisko 28%) but a relatively high proportion of species had leading edges that remained stable (49% and 33%). Considering the 37 species shared between areas, 35% of species consistently shifted their optimum towards warmer locations and 21% shifted towards colder locations in both areas. The remaining species (44%) responded inconsistently between areas (see Figure 4a,b).

Linking direction and magnitude of shift to information about species climatic preferences, we found that climatic optimum in the interior vegetation predicted changes in species' realized climatic niche in trailsides. In trailsides, alpine species were more likely to shift their rear edges and optima towards warmer locations and lowland species towards colder locations (Figure 5; Table 1; see Appendix S2: Table S2.12). For example, alpine species such as *Luzula multiflora* and *Silene acaulis* shifted their optima towards warmer locations,

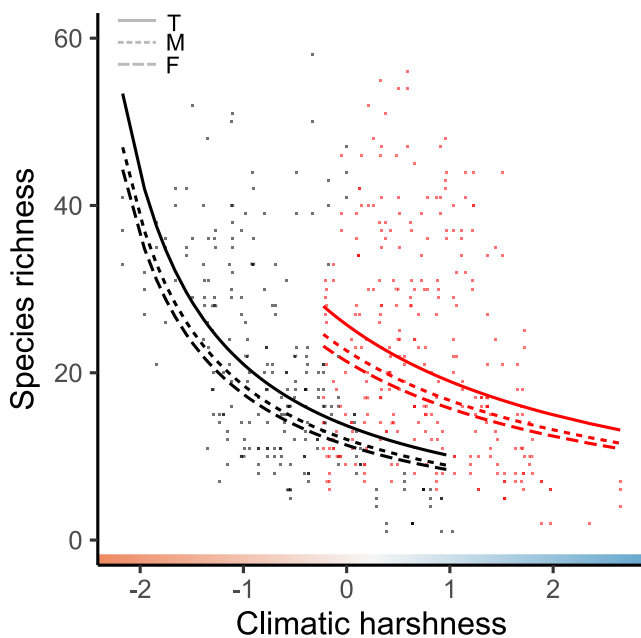


FIGURE 3 Predicted species richness as function of climatic harshness and distance from the trail for Dovrefjell (black line) and Abisko (red line). Raw data from Dovrefjell (black dots) and Abisko (red dots) are plotted as is, to show variability among recorded plots. The coloured bar at the bottom illustrates the climatic harshness gradient from warmer (red) to colder (blue)

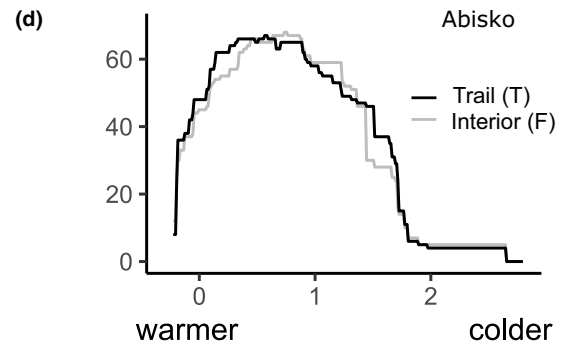
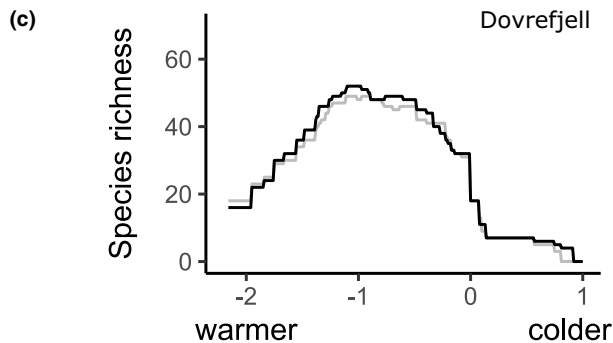
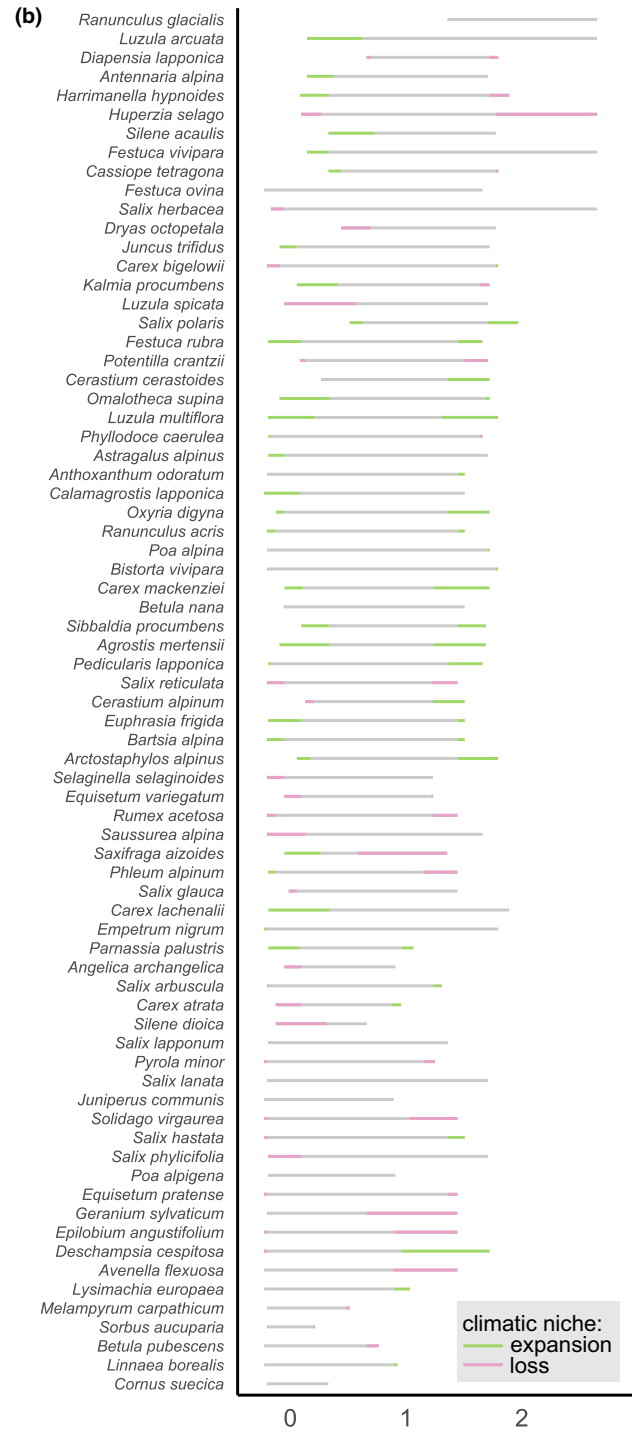
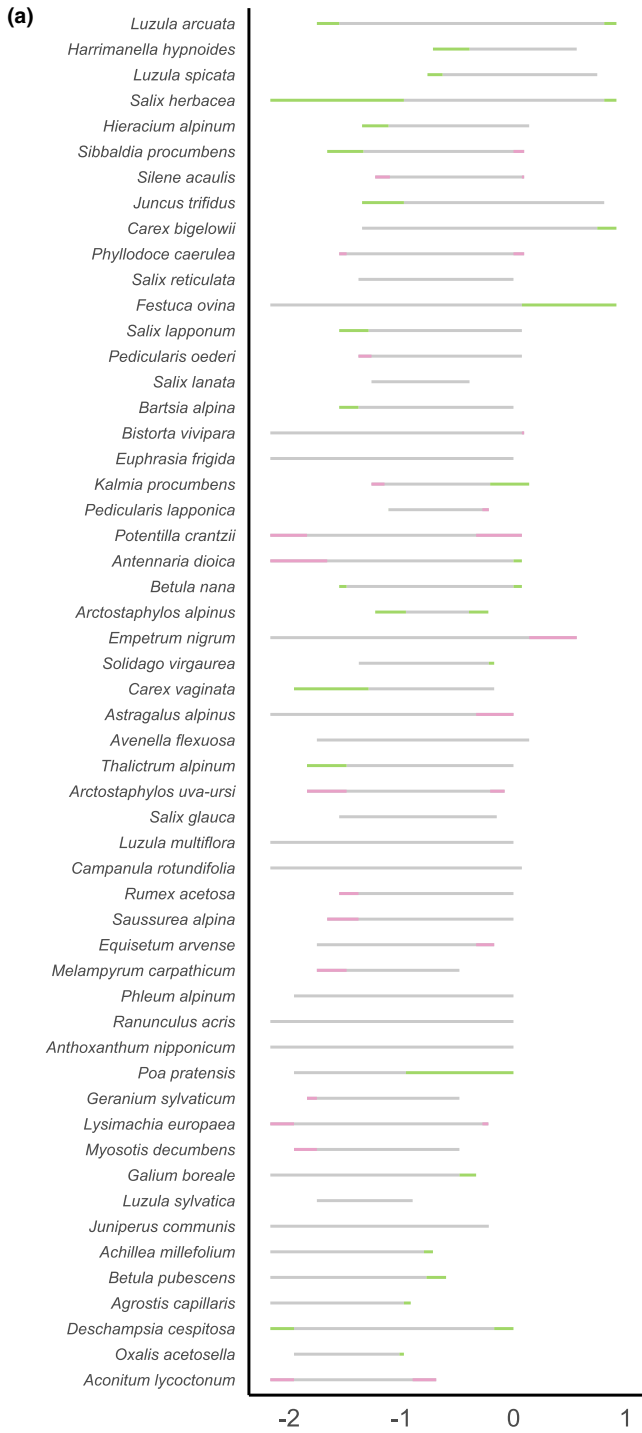


FIGURE 4 Species range changes along trails in comparison with the interior vegetation, with pink parts of the bar denoting a loss of range along trails, green range expansion along trails, and grey ranges occupied both along the trails and in the interior vegetation in (a) Dovrefjell and (b) Abisko area. Species are ordered according to their optimum in the interior vegetation, with those found at the coldest locations on the top. Cumulative number of species ranges overlapping at any given point (i.e., species richness) along the climatic gradient in the interior vegetation (grey) and in trailsides (black) are shown in (c) Dovrefjell and (d) Abisko

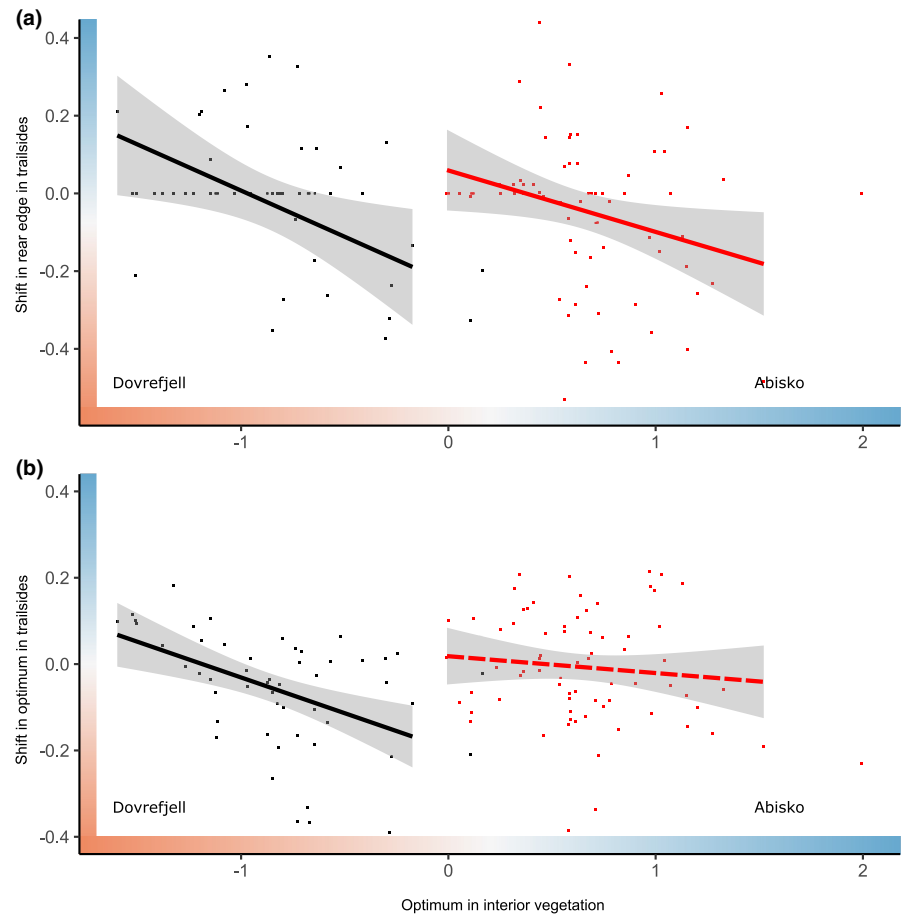


FIGURE 5 Predicted shifts between interior vegetation and trailsides (with 95% confidence intervals) in (a) rear edges and (b) optimum of species plotted against each species' optimum in the interior vegetation along the climatic gradient studied in the Dovrefjell ($n = 52$, black) and Abisko ($n = 72$, red) areas. Solid lines denote significance at $p < .05$. The colour gradient on the axes illustrates the climatic gradient from warmer (red) to colder (blue). Positive values on the x-axis correspond to harsher climate. Positive values on the y-axis represent shifts towards colder locations in trailsides

and lowland species such as *Geranium sylvaticum* and *Juniperus communis* towards colder locations along trails. The general pattern was consistent across the two areas, but with stronger support from Dovrefjell; for Abisko only the rear-edge shifts were statistically significant. No general pattern for leading edge shifts could be found, but in the Abisko area many species with their optimum in the sub-alpine range (e.g. *Bartsia alpina*, *Omalotheca supina* and *Sibbaldia procumbens*) showed an expansion of their leading edge towards colder locations along trails (Figure 4a,b). Plotting species ranges in the interior vegetation and along trails (Figure 4c,d) illustrates how the cumulative change in ranges can lead to an increase in richness by allowing more overlapping species ranges at a given climatic locality.

3.3 | What drives differences in richness between interior and trailside plots?

The best LMM of the difference in species number between interior and trailside plots accounted for 25% of variation (see Appendix S2: Tables S.2.13 and S.2.14). Increases in species richness next to

trails were greater when closer to introduction points such as trail-heads (variances explained by all factors are summarized in Table 2). Distance to the nearest introduction point accounted for 24% of the variation explained by the model. Interior vegetation species richness explained 24% of variation in differences between trailside and interior vegetation with largest gains in less rich communities. When keeping all other factors constant, the gain in trailside species richness increased with increasing herbaceous cover, while more dwarf shrubs close to trails led to smaller gains or in extreme cases even to a loss of species. Gap area was negatively related to gain in richness at trailsides, while trailsides were more likely to increase in richness in sites with a higher total vegetation cover or with a larger disturbance extent. Factors associated with disturbance through trails added up to explaining 21% of the variance in the model.

4 | DISCUSSION

Contrary to previous observations in cold ecosystems (Crisfield et al., 2012; Gremmen et al., 2003; Jägerbrand & Alatalo, 2015;

TABLE 1 Model parameters from linear models of shifts in climatic optimum, rear edge, leading edge, climatic range of vascular plant species in the trailside compared with the interior vegetation after removal of outliers in Dovrefjell ($n = 52$) and Abisko ($n = 72$), as a function of species' climatic optimum in the interior vegetation

	Dovrefjell				Abisko			
	Optimum	Rear edge	Leading edge	Amplitude	Optimum	Rear edge	Leading edge	Amplitude
Intercept	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	-0.00 (0.00)
Optimum interior vegetation	-0.17 (0.05)	-0.24 (0.09)	-0.02 (0.09)	0.21 (0.14)	-0.04 (0.04)	-0.16 (0.07)	0.04 (0.10)	0.20 (0.13)
n	52	52	52	52	72	72	72	72
Adj. R^2	0.19	0.09	-0.02	0.03	-0.00	0.05	0.00	0.02

Note: The standard error of coefficients is given in parentheses. Significance at the $p < .05$ level is denoted by bold lettering.

Monz, 2002), trailsides in the Scandes mountains had higher species richness than the surrounding vegetation. Trail effects appeared to have resulted in increased overlap in species' ranges due to transport to new locations and competitive release. Many alpine species shifted their rear edges and climatic optima towards warmer locations in trailsides. For lowland species' leading edges, no general shift was detected. Trailside plots close to introduction points and with fewer species in the interior vegetation had a larger increase in species number, and species gain was higher when the interior plot was dominated by herbaceous and lower in dwarf shrub-dominated vegetation. Altogether, this highlights that trails in the Scandes mountains provide plants with opportunities to shift realized niches, resulting in greater local plant species richness.

4.1 | Trails increase species richness

We observed a higher species richness in trailside plots than in the interior vegetation. An increased overlap in species' realized climatic niches along the climatic gradient contributed to this increase in species richness, with trails acting as conduits for seed transport and providing seedling establishment opportunities. Higher richness and expansion of alpine species' ranges towards lower elevation were also found along mountain roads in Scandinavia. There, roads led to a lower cover of *E. nigrum* and moss, which otherwise may inhibit germination and establishment (Lembrechts et al., 2014). Higher species richness along trails contrasts with other studies from cold ecosystems, all finding no or negative effects (Crisfield et al., 2012; Gremmen et al., 2003; Jägerbrand & Alatalo, 2015; Monz, 2002). However, we surveyed 16 trails extending more than 100km and cutting through a variety of alpine communities, capturing the effects of trails on species richness across a larger spatial scale than previous studies. Our study emphasizes that the impact of trails on species richness should not be underestimated, especially when taking into consideration that trails often reach more remote and climatically extreme locations (Liedtke et al., 2020). While research has mostly focussed on the role of trails as corridors for the invasion of non-native species into mountain areas (e.g. Liedtke et al., 2020), we suggest that they also allow alpine species to colonize new locations.

4.2 | Climatic niche shifts along trails

Trails influenced the realized climatic niche of species. For alpine species, the expansion of their rear edge towards warmer locations is a sign of competitive release caused by disturbance (Chardon et al., 2019; Herrmann et al., 2021). Trailsides may thus potentially help preserve populations even under the condition of lowland plants moving into alpine habitats (Chardon et al., 2019). Corridors along trails could, therefore, act as temporary escape routes for alpine species such as *Harrimanella hypnoides*

TABLE 2 Direction of effect of factors retained in the best linear mixed model on change in species number between interior vegetation and trailside plots, and percentage of variance explained

Driver	Species gains ↑ or losses ↓ at trails relative to interior vegetation	Variance explained [%]
Distance to introduction point	↓	24.0
Interior vegetation species richness	↓	23.9
Vegetation cover	↑	9.5
Dwarf shrub cover	↓	9.4
Herb cover	↑	7.0
Gap index	↓	7.0
Disturbance extent	↑	4.9

Note: R^2 values on which the calculated variances are based and additional information regarding coefficients and shared variances can be found in [Appendix S2: Tables S2.13 and S2.14](#).

and *Sibbaldia procumbens*, which prefer low-stature neighbours (Coker, 1966). However, as trailsides only comprise a small fraction of the total mountain area, it remains unclear how stable the observed changes in realized niche are over time, as they might be the result of source-sink dynamics (Lembrechts, Alexander et al., 2016). Overall, our observations of downward shifts of alpine plants with disturbance corroborate patterns found along trails in the Rocky mountains (Chardon et al., 2019), but expand those by relating rear-edge shifts of the whole community to their optimum along the climatic harshness gradient. Contrary to our expectations, lowland species' leading edges did not generally shift towards colder locations in trailsides. However, trails allowed lowland species to increase in abundance particularly in colder parts of their niche, which resulted in a shift of climatic optima towards colder locations. In contrast to our findings, mountain roads allowed native lowland species to expand their leading edges towards higher elevations in the same ecosystem (Lembrechts, Alexander et al., 2016). Our results suggest that many lowland species might (a) benefit less from disturbances by trails than alpine species (Le Roux et al., 2013), (b) have their leading edge detected at their true temperature limit as trails reached higher elevations than roads which might provide truncated climatic gradients, (c) might be insufficiently equipped to deal with additional stresses in the alpine zone such as drought and wind exposition or (d) that the disturbance intensity of trails in our research area was too weak to break down limiting biotic resistance at the upper range edge of lowland species (Graae et al., 2011; Lembrechts, Pauchard et al., 2016; Milbau et al., 2013).

We did, however, find that some species expanded their leading edges towards colder locations along trails. This included the trampling-resistant grass *Deschampsia cespitosa*. In Abisko we saw that, for example, the forbs *Cerastium cerastoides*, *Omalotheca supina*, *Oxyria digyna*, *Sibbaldia procumbens*, *Euphrasia frigida* and *Bartsia alpina* expanded from the sub-alpine belt towards the alpine zone. Many of these species are associated with snowbeds (Coker, 1966; Taylor & Rumsey, 2003; Totland & Schulte-Herbrüggen, 2003; Väre et al., 1997), which are moist environments; they may, therefore, be favoured by increases in moisture along trails resulting from

soil compaction and funnelling of precipitation (Kuss, 1986; Tuomi et al., 2020), while, for example, *Cerastium cerastoides* and *Euphrasia frigida* are known to explicitly benefit from disturbances (Nylén & Totland, 1999; Totland & Schulte-Herbrüggen, 2003). This underlines that trails can allow disturbance-adapted species to move into colder locations.

4.3 | Where do trailsides gain species?

Characteristics of the recipient plant community influenced the gain of species in the trailside compared with the interior vegetation. In sites with species-poor interior vegetation, which in our study was dominated by graminoids like *Luzula arcuata*, *Carex bigelowii* and *Juncus trifidus*, the prostrate dwarf shrub *Salix herbacea*, the herb *Ranunculus glacialis* or by dwarf shrubs, trailsides gained more species, while in more species-rich sites frequently associated with meadows and willow shrub communities, trailsides gained fewer species. Decreasing establishment with higher diversity was also found by Olsen & Klanderud, 2014. Richer communities may already accommodate a broader range of niches than poorer ones due to higher in-site environmental variability, and thus the net effect of disturbance on niche availability might be weaker or even negative (Hofer et al., 2008; Palmer & Dixon, 1990). At similar levels of richness, a larger cover of herbaceous vegetation was associated with larger and more dwarf shrubs with smaller increases of species richness in trailsides. This corroborates experimental studies of establishment in different vegetation types after disturbance finding higher resistance of dwarf shrub heaths to colonization but greater invasibility of meadows dominated by herbaceous vegetation (Graae et al., 2011; Milbau et al., 2013; Opedal et al., 2021). Distance to the closest potential point of propagule introduction, such as ski lifts or trailheads, also had a strong effect, with a greater gain of species in trailsides close to introduction points concurring with findings of Pickering et al., 2007. The fact that t function as corridors for colonization in alpine ecosystems aligns with their role played in other ecosystems such as coniferous mountain forests in North America (Benninger-Truax et al., 1992).

Disturbance is known to create microsites for germinations and subsequent establishment also in alpine systems (e.g. Lembrechts, Pauchard, et al., 2016). However, under harsh climatic conditions the establishment in large gaps could be too difficult for successful establishment, as theoretically predicted by Lembrechts et al. (2015). Our findings lend careful support to this prediction, as richness in trailsides increased less in plots with larger gaps yet was positively associated with a larger area over which disturbance was spread.

5 | CONCLUSION

While disturbance and trampling on paths evidently suppress plants, our findings demonstrate that trailsides may also offer opportunities for alpine species, weaker competitors and disturbance-associated species, through competitive release and propagule transport. Changes in species ranges along trails increased plant diversity in trailsides in our study, which underscores their importance as corridors of colonization for notably weaker competitors and alpine species. As communities showed differential reactions to disturbances along trails, a further integration of such field findings into management is called for in the planning of trails. However, the species richness enhancing effects of trails should be considered in a broader perspective, as disturbances may also destroy rare communities or rare and trampling-sensitive species. In this context, species- and region-specific understanding of trail effects is required.

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CONFLICT OF INTEREST

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at <http://doi.org/10.6084/m9.figshare.17040770>.

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BIOSKETCH

The research team is part of the Mountain Invasions Research Network (MIREN), which aims to understand the effects of global change drivers such as climate and land-use change on species' distributions and biodiversity in mountainous areas. We perform observational and experimental studies along elevation gradients to evaluate and quantify the processes and mechanisms that shape mountain plant communities at regional to global scales. One part of our focus is evaluating the effects of trails on plant communities in mountains around the globe. More information about our work in Scandinavia can be found on the [MIREN trails Scandinavia webpage](#).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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