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RESEARCH ARTICLE

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Anthropogenic disturbance modifies long-term changes of boreal mountain vegetation under contemporary climate warming

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Abstract

Aims: Accelerating high-latitude climate warming drives shrub expansion in open landscapes and alters species distributions and compositions of plant communities. Simultaneously, various land use practices cause disturbance to the vegetation. However, not much documentation exists on how long-term intensive land use disturbance modifies high-latitude vegetation under climate warming. Here, we study how the composition of boreal mountain plant communities has changed during three decades in response to heavy land use disturbance, related to ski resort construction and management, and how these changes compare to those observed in adjacent less disturbed communities.

Location: Iso-Syöte, Finland.

Methods: We resurveyed vegetation along four elevational gradients (240–426 m a.s.l.) on a boreal mountain in 2013–14. After the original study in 1980, half of the gradients were subjected to continuous heavy land use disturbance, while the other half remained only slightly disturbed. All the gradients experienced a similar amount of macroclimatic warming over time. We analysed temporal changes in plant group covers, species richness and species' elevational range means in relation to disturbance levels and elevation.

Results: Under slight disturbance, the cover of shrubs increased on the originally open upper slopes and elevational range means of several species shifted upward. In contrast, heavy disturbance resulted in a uniform, yet modest, shrub cover increase along the whole elevational gradient and promoted both up- and downward shifts of species. Bryophyte cover decreased considerably over time, regardless of the disturbance level. Species richness increased throughout, yet more under heavy disturbance.

Conclusions: Long-term changes in boreal mountain vegetation are substantially influenced by heavy land use disturbance compared to less disturbed sites where the vegetation changes are more comparable to those expected under a warmer climate.

Therefore, along with the climatic effects, land use effects on vegetation are important to consider in management actions and in projections of future vegetation.

KEYWORDS
anthropogenic disturbance, boreal mountain, boreal treeline ecotone, land use disturbance, long-term vegetation changes, plant community, shrub expansion, ski resort, vegetation resurvey

1 | INTRODUCTION

The vegetation of high-latitude and mountain environments is changing as a response to a warmer climate. Most conspicuous vegetation changes include shrub expansion (Elmendorf et al., 2012; Myers-Smith & Hik, 2018), as well as advancement of treelines (Holtmeier & Broll, 2005; Harsch et al., 2009) and species ranges towards the north and higher elevations (Lenoir et al., ccc; Parolo & Rossi, 2008; Myers-Smith & Hik, 2018; Rumpf et al., 2018; Steinbauer et al., 2018). At the same time, various land use practices modify vegetation in these environments (Vittoz et al., 2009; Providoli & Kuhn, 2012), often in concert with climate change (Lenoir et al., 2010; Dainese et al., 2017; Guo et al., 2018; Maliniemi et al., 2018; Hedwall et al., 2019). However, plant community responses to long-term land use disturbances during the recent climate change are little documented or understood (but see Brice et al., 2019; Danneyrolles et al., 2019) even though this is essential under rapidly changing environmental conditions. Particularly rare are the studies that consider both the entire community composition (canopy, shrub, field and ground layers) and cover over a sufficiently long time period (decades). These aspects are of high importance in order to better understand the often slow temporal dynamics of high-latitude plant communities with a generally high share of ground-layer species (Callaghan et al., 2004; Maliniemi et al., 2018, 2019).

One widely distributed form of local land use that often causes severe disturbance in the vegetation, is the construction and management of tourist attractions, such as ski resorts (Roux-Fouillet et al., 2011; Holtmeier & Broll, 2018; Bacchiocchi et al., 2019). In forested areas, this typically means a reduced or completely removed tree layer while the understorey vegetation is retained to varying degrees. The clearing of the tree layer strongly alters the microclimate (De Frenne et al., 2019), allowing solar radiation and wind flow near the soil surface (Holtmeier & Broll, 2005). Ski piste management and the use of artificial snow may affect snow cover duration, chemical properties of the soil, freezing conditions during the cold season and thermal conditions throughout the year (Rixen et al., 2004; Roux-Fouillet et al., 2011; Bacchiocchi et al., 2019). The managed snow cover and mechanical damage, e.g., due to grooming, has also been shown to cause dieback of dwarf shrubs (Stoeckli & Rixen, 2000). Given the relatively slow process rates and long recovery time of high-latitude vegetation, these kinds of disturbances with relatively short intervals and large areal extent can destabilise the system and shift the compositional trajectories of vegetation (Turner et al., 1993). Therefore, by strongly altering site conditions, disturbances due to ski resort infrastructure may also be expected to considerably influence climate-driven vegetation changes, such as shrubification.

Shrub expansion is one of the most evident responses to climate warming in open high-latitude landscapes (Myers-Smith et al., 2011; Scharnagl et al., 2019). However, improved light conditions and enhanced wind dispersal of seeds due to tree clearance, longer-lasting burial under snow, or certain levels of soil disturbance may alone facilitate the establishment of good competitors, such as taller shrubs (Myers-Smith et al., 2011; Tilman, 1988). Importantly, warmer conditions can further accelerate the growth response of shrubs to the increased light (De Frenne et al., 2015). Thus, the combined effects of warming and certain levels of disturbance can be expected to enhance shrub abundance, unless the disturbance is too severe and begins to limit shrub growth (Verma et al., 2020). Increasing shrub cover is further associated with changes in local abiotic conditions (e.g., hydrology and nutrient cycling) but also to changes in understorey species composition, e.g., reduced cover of small species and species richness by plant–plant interactions (Pajunen, Oksanen & Virtanen, 2011; Wallace & Baltzer, 2020).

Late-successional forest communities in European boreal mountains are often relatively species-poor and dominated by Norway spruce (*Picea abies*), dwarf shrubs (*Vaccinium* spp.) and a moss layer with a few dominant species (*Hylocomium splendens*, *Pleurozium schreberi*). However, it is well known that natural or anthropogenic disturbances (e.g., fire or various silvicultural practices) can, at least temporarily, increase local species richness in boreal forests (Peltzer et al., 2000; Kumar et al., 2018). In arctic-alpine landscapes, in turn, disturbances due to ski resort management have been shown to have no or negative effects on species richness (Bacchiocci et al., 2019).

In undisturbed boreal mountain landscapes, tree and shrub cover thins out towards higher elevations giving way to open slopes and mountain tops that can maintain a tundra-like vegetation. Although it can be generally expected that species shift towards higher elevations in response to a warmer climate (Lenoir et al., 2008; Steinbauer et al., 2018) and that the shift is stronger the lower species were situated historically (Rumpf et al., 2018), it has been found possible that disturbances modify these range shifts. According to Lenoir et al. (2010), disturbance due to habitat modification and the consequent release in competition could also cause a downward shift of species that are filling only part of their potential distributional range along the elevational gradient. Agreeing with this, Guo et al. (2018) found that loss of forest cover caused downward shifts in species' elevational distributions suggesting that land use disturbances may complicate recognition and interpretation of climate-driven vegetation changes.

Here, we study how heavy land use disturbance, due to the construction and management of a ski resort, influences long-term vegetation changes along elevational gradients and compare the observed changes to those occurring along only slightly disturbed gradients. In 2013–14, we resurveyed plant communities along four elevational gradients on a boreal mountain in northern Finland that were originally surveyed in 1980–81. Each gradient started from a closed forest, changed gradually into more open slopes, and reached the nearly treeless top. Right after the original survey, half of the slopes and the whole top were partly cleared of trees to accommodate ski resort infrastructure and were thus subjected to a relatively heavy disturbance that continued until the resurvey. In contrast, the other half of the slopes was located outside the resort and was only slightly disturbed. This unique setting allowed us to analyse long-term impacts of different disturbance levels on the boreal mountain plant communities within a similar environmental context and under a similar impact of macroclimatic warming. More specifically, we analysed temporal changes in the cover of different plant groups, species richness and species' elevational range means in relation to heavy vs slight disturbance and elevation.

We hypothesised that heavy disturbance has a strong influence on the long-term vegetation changes that are expected under a warmer climate. Under slight disturbance, we predicted to observe changes that are frequently reported as a response to warmer conditions, such as advancement of taller shrubs on the originally open upper slopes and upward movement of low-elevational species. In contrast, we predicted that heavy disturbance and the tree cover removal result in an increase of taller shrubs along the whole elevational gradient and cause both upward and downward movements of species in the long term. We further predicted that heavy disturbance reduces the cover of dwarf shrubs and ground layer species (bryophytes and lichens) but enhances species richness due to species introductions.

2 | METHODS

2.1 | Study area and vegetation resurvey

The study area, Iso-Syöte (65,62°N, 27,60°E), is situated in the northern boreal zone in Finland and covers approximately 4 km^2 (Figure 1a). Reaching 432 m a.s.l., the top of Iso-Syöte rises among the highest mountain tops in the upland region of Northern Ostrobothnia and has one of the southernmost elevational treelines in Finland. The vegetation of Iso-Syöte represents typical boreal forest vegetation with coniferous forests, dwarf shrubs and forest mosses. In 1980–81, the vegetation of Iso-Syöte was surveyed along four elevational gradients, each from a different compass point (Mikkonen-Keränen, 1982; Figure 1b). Gradients started from the late-successional forests at the foot of the slope, mainly of *Hylocomium–Vaccinium myrtillus*-type, and changed gradually into more open *Calluna–Empetrum–Vaccinium*-type towards the upper slopes. Certain species typical for treeless tundra, such as *Arctous alpina*, were found at the small-extent top.

Right after the original vegetation survey, a ski resort was built on the NE and SE slopes and on the top of Iso-Syöte (Figure 1c,d). The NE vegetation gradient was situated in the immediate vicinity of the ski routes and lifts, while the SE gradient was situated next to paved roads, numerous cabins and a hotel. Although the specific disturbance types are partially different between these gradients, they generally represent heavy mechanical and physical land use disturbance. For most parts of the gradients, trees were cut or thinned out and forest understorey vegetation was typically disturbed by infrastructure maintenance or building yet was not completely removed (Appendix S1). No artificial revegetation or seeding was done during the study period. Based on the field observations, no prominent or directional variation in disturbance intensity was observed along the slopes. The maintenance and extensions of the ski resort infrastructure continued until the vegetation resurvey in 2013–14. Thus, the vegetation on NE and SE slopes (240–395 m a.s.l.) and on the top (405–426 m a.s.l.) were influenced by relatively heavy mechanical disturbance for over three decades. Consequently, the SE and NE slopes are regarded as "heavily disturbed" gradients. In an apparent contrast, the SW and NW slopes (250–395 m a.s.l.) remained nearly unbuilt over time (Figure 1c, d, Appendix S1). Only a few hiking trails crossing parts of the slopes were established during the study period. The vegetation on these slopes was protected from any kind of management since 1910 and for the most part also prior to this (Metsähallitus, 2004). A visual inspection on site during the resurvey confirmed the absence of land use disturbance. Thus, these gradients are regarded as "slightly disturbed." Sample plots at the heavily disturbed top are treated separately in the analyses. Thus, the heavily and slightly disturbed slopes have comparable elevational range.

For the resurvey in 2013–14, elevational gradients were relocated to the same position as indicated by the original map (Figure 1b). The original survey plots situated along the gradients were not permanently marked in the field, but plot coordinates were obtained from digital maps using the plot-wise information on elevation, slope and aspect in the original publication (Mikkonen-Keränen, 1982). In the vegetation resurvey, we used the same methods as in the original survey to estimate the species composition. Vascular plants, bryophytes and lichens (Appendix S2) were estimated for the 1 m × 1 m vegetation plots using a percentage cover scale. Species not found on the plot but present within a radius of 5 m from the plot centre were recorded and given the minimum cover value (0.25%). Soil pH was additionally measured in the resurvey of the 1 m × 1 m plots. Of the in total 54 1 m × 1 m vegetation plots, 22 were located on slightly disturbed slopes, 22 on heavily disturbed slopes and 10 on the top. Most often two vegetation plots were placed every 5–15 vertical metres along each slope and more frequently on the top. The cover of shrub layer species and tree canopy were recorded from 30 m × 30 m plots surrounding 43 1 m × 1 m plots. Of the larger plots, 16 were located on the heavily disturbed slopes, 17 on the slightly disturbed slopes and 10 on the top.

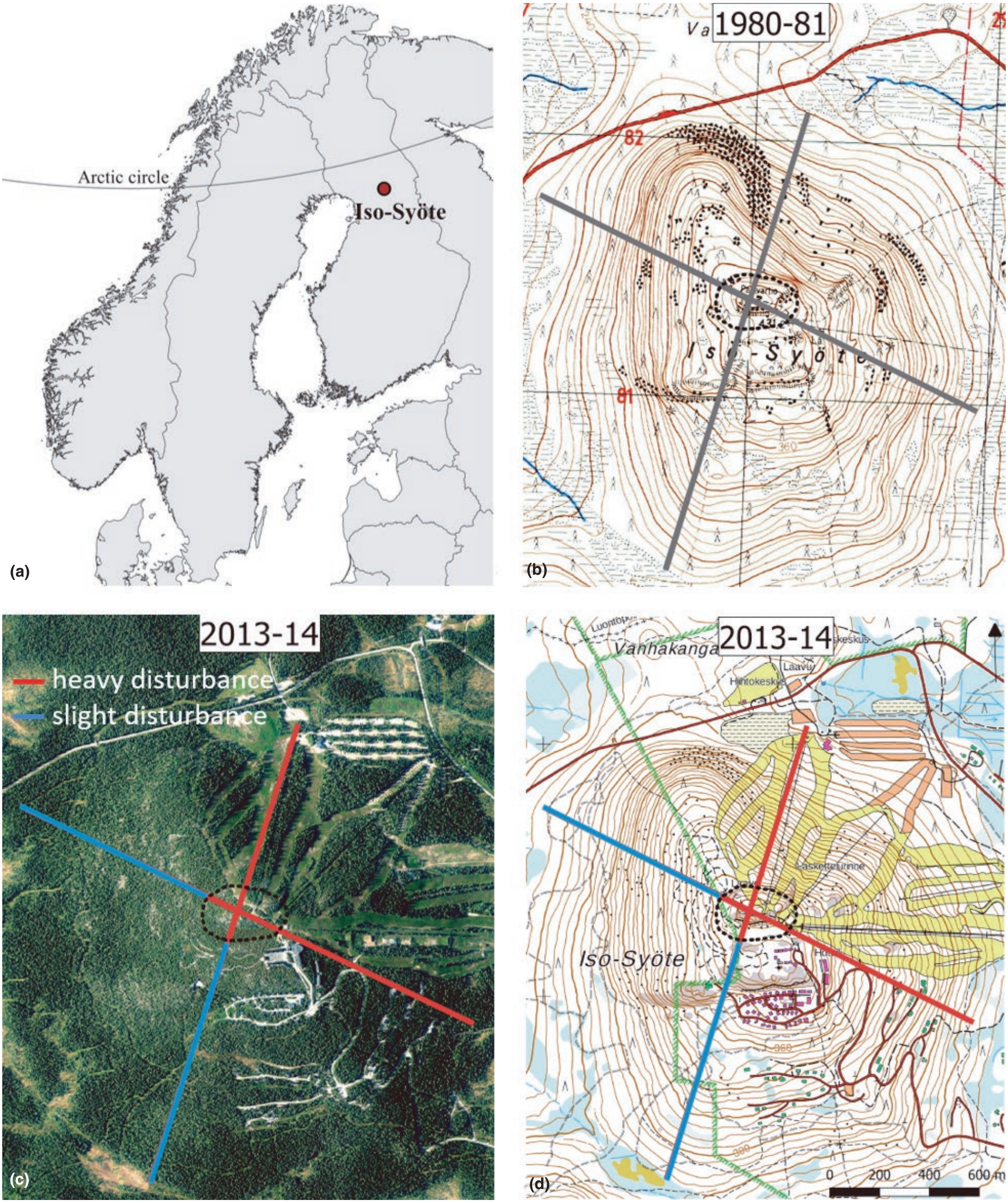

FIGURE 1 Maps of the study area. (a) Location of Iso-Syöte in Finland. (b) Iso-Syöte during the original survey in 1980–81. Vegetation was sampled along four elevational gradients, indicated by the grey lines. Black dashed line marks the extent of the originally more open top. (c, d) Iso-Syöte during the resurvey in 2013–14. Right after the original survey, vegetation on NE and SE slopes and on the small-extent top was subjected to heavy disturbance (red lines), due to the construction and maintenance of a ski resort, that continued until the resurvey. Vegetation on SW and NW slopes (blue lines) remained less disturbed and devoid of any kind of management since 1910. Here, hiking trails can be regarded as a source of slight disturbance. Green dashed line in (d) indicates the border of a national hiking area founded in 2000

The vegetation plots in this study can be regarded as quasi-permanent (Kapfer et al., 2017) and thus, the comparisons of vegetation between the surveys are affected by a relocation error. This may cause pseudo-turnover in species composition, which adds random error to the observations of temporal change in vegetation. The presence of random error may increase the risk of not detecting real temporal changes yet is unlikely a source of a systematic error (Kopecký & Macek, 2015; Kapfer et al., 2017). In our case, considering the relatively detailed information on gradient and plot locations, we estimated that the relocation error for the 1 m × 1 m plots is generally <20 m. Due to the larger plot size, the estimates of shrub and canopy layers and of species richness are less affected by the relocation error.

Original and resurveyed species data were taxonomically harmonised before the analyses, i.e. synonyms were identified, and certain bryophyte and lichen species were treated collectively (Appendix S2). Because the studied vegetation is composed of relatively few species, most of which are common and identifiable in the field, we find it unlikely that the observed vegetation changes would reflect systematic error between the observers. To analyse temporal changes, species were grouped into the following morphological groups: shrubs (including both tall and low-growing shrubs), dwarf shrubs, graminoids, herbs, bryophytes, and lichens. Absolute cover values (%) were calculated for each group by summing the cover values of species in the group. In order to detect elevational shifts of biogeographical species groups, vascular plants were classified into four different general biogeographic categories: temperate–boreal, boreal, boreal–hemiarctic or hemiarctic after Engelskjøn, Skifte and Benum (1995). A class could be assigned for 93% (67 out of 72 species) of the vascular plant species (Appendix S2).

2.2 | Environmental data

E-OBS raster data (10 km × 10 km; Cornes et al., 2018) were used to calculate temporal changes in mean annual temperatures, annual precipitation and annual thermal sums (summed from daily temperatures exceeding the +5°C threshold during the growing season) in the Iso-Syöte area. Data on annual reindeer numbers in the herding district containing Iso-Syöte were obtained from the Natural Resources Institute Finland and converted into grazing pressure (reindeer/km^2). Temporal differences in climate and grazing pressure variables were calculated using 15-year averages prior to each survey.

2.3 | Statistical analyses

To have an overall view on the long-term compositional changes in communities under slight and heavy disturbance, we used non-metric multidimensional scaling (NMDS) ordination, based on Bray–Curtis distances and plot-level data ($n = 43$) on species' covers, from the R package *vegan* (Oksanen et al., 2019). Stable and adequate stress solution (stress > 0.2) was reached using three dimensions ($k = 3$). Correlation vectors of elevation and shrub cover were fitted to the ordination to find out if compositional changes correlate with elevation or the expected increase of shrubs. The goodness-of-fit of the fitted vectors was estimated using 999 permutations. Due to repeated sampling, permutations were not allowed within paired plots.

We used generalised linear mixed-effects models (GLMM) to analyse the effects of time, disturbance level and elevation on vegetation changes. The first set of models was built for the slope data that are comparable in elevational gradients between different disturbance levels (240–395 m a.s.l.). We built separate models for seven cover (%) variables (trees, shrubs, dwarf shrubs, graminoids, herbs, bryophytes and lichens) and four species richness variables (total, vascular plant, bryophyte and lichen richness). Time (original survey vs resurvey), disturbance level (slight vs heavy), elevation (m a.s.l.) and their interactions were added as fixed factors in the models. We were particularly interested in whether the response variables had changed over time (T) and whether these changes were dependent either on the disturbance level ($T \times D$) or elevation ($T \times E$) or on both the disturbance level and elevation ($T \times D \times E$). Plot identity was added as a random factor to control for the repeated sampling. Aspect could not be used as a random factor because half of the potential combinations were lacking (i.e. neither level of disturbance was found in all aspects). However, none of the disturbance levels were entirely directed to either north or south. This reduces the possible influence of the aspect together with the long summer days and low sun angles, which have been shown to even out differences between the aspects to some extent in the study area (Winkler et al., 2016). Model fits and normality of residuals were examined using diagnostic plots. There was no substantial spatial autocorrelation in the residuals of any model (Appendix S3). All cover variables were modelled with a Gaussian distribution. Four variables (shrub, graminoid, herb and lichen cover) were $\log(x + 1)$-transformed to improve the model fit and the predictions of these models were back-transformed to the original response scale. Total species richness and lichen richness were modelled with a Poisson distribution while vascular plant and bryophyte richness fitted better with a Gaussian distribution that can be applied for counts when models are complex and when linear model assumptions can be fulfilled (Warton et al., 2016) The effect of predictor terms on response variables was assessed based on p-values (<0.05). Model fits were visualised with confidence intervals based on the standard errors. The possibility of non-linear responses along the elevational gradient was considered in preliminary examinations, which revealed no considerable non-linear patterns for any of the studied response variables. The second set of models was built for the same response variables (excluding graminoids and herbs, abundances of which were very low) at the heavily disturbed top (405–426 m a.s.l.). For these models, time (original survey vs resurvey) was added as a fixed factor. Plot identity was added as a random factor to account for repeated samplings. All the models were run using the R package *glmmTMB* (Magnusson et al., 2020).

We used the slope data to test whether temporal shifts in species' elevational range means were influenced by the level of disturbance and species' mean elevational position during the original survey (e.g., whether low-elevational forest species shifted their range means more than species with originally higher elevational position). We first calculated weighted elevational range mean for each species (including vascular plants, bryophytes and lichens), on both slightly and heavily disturbed slopes during both surveys. Species' abundances (percent cover) were used as weights. We then built a generalised linear mixed-effects model to explain species' elevational means during the resurvey by their elevational means during the original survey, disturbance (slight vs heavy) and their interaction. Species identity was added as a structural term in the random-effects part of the model. Only species that were present at least three times during both surveys were included in this analysis. Model fit and normality of residuals were examined using diagnostic plots. Additionally, we estimated temporal shifts in the weighted mean elevations of biogeographic plant groups under both disturbance levels using *t* tests for weighted means from the R package *weights* (Pasek, 2018). All statistical analyses were performed using the R software (R Core Team, 2019).

3 | RESULTS

Mean annual temperature, as a 15-year average prior to each survey, rose by 1.5°C during the study period (from 0.08 to 1.61°C), while annual precipitation increased only marginally (c. 610–658 mm, Appendix S4a, b). Annual thermal sums increased 16% between the surveys (from 878 to 1,044°Cd, Appendix S4c). Grazing pressure remained relatively low and constant (c. 1.5 reindeer/km^2, Appendix S4d). The mean ± *SE* soil pH in the resurvey was 3.67 ± 0.04 on slightly and 4.24 ± 0.11 on heavily disturbed gradient.

The NMDS ordination suggested that the original slope communities (which were later subjected to different disturbance levels) had relatively similar composition, while the original composition of top communities differed from that of slope communities (Figure 2). However, under long-term exposure to different disturbance levels, the composition of slope communities became dissimilar in relation to their original compositions. Expectedly, the NMDS suggested that the shift was stronger under heavy disturbance. Moreover, the composition of top communities became more similar to the composition of slope communities.

Generalised linear mixed-effects model fits indicated that the elevational patterns of all the plant group covers were originally rather similar between the slopes that were later subjected to either slight or heavy disturbance (Figure 3). However, these patterns changed prominently during the three decades. The expected decrease in canopy cover over time was prominent under heavy disturbance (Table 1; $T \times D$), being strongest at lower elevations (Figure 3a). Surprisingly, a similar temporal change in the elevational pattern was observed also under slight disturbance (Table 1; $T \times E$, Figure 3a). The cover of shrubs clearly increased over time, but this response was affected by both the disturbance level and elevation: shrubs increased towards the top under slight disturbance, whereas the increase was more uniform along the heavily disturbed slopes (Table 1; $T \times D \times E$, Figure 3b). The covers of dwarf shrubs, graminoids and herbs changed over time in terms of their elevational distribution (Figure 3c–e, Table 1; $T \times E$).

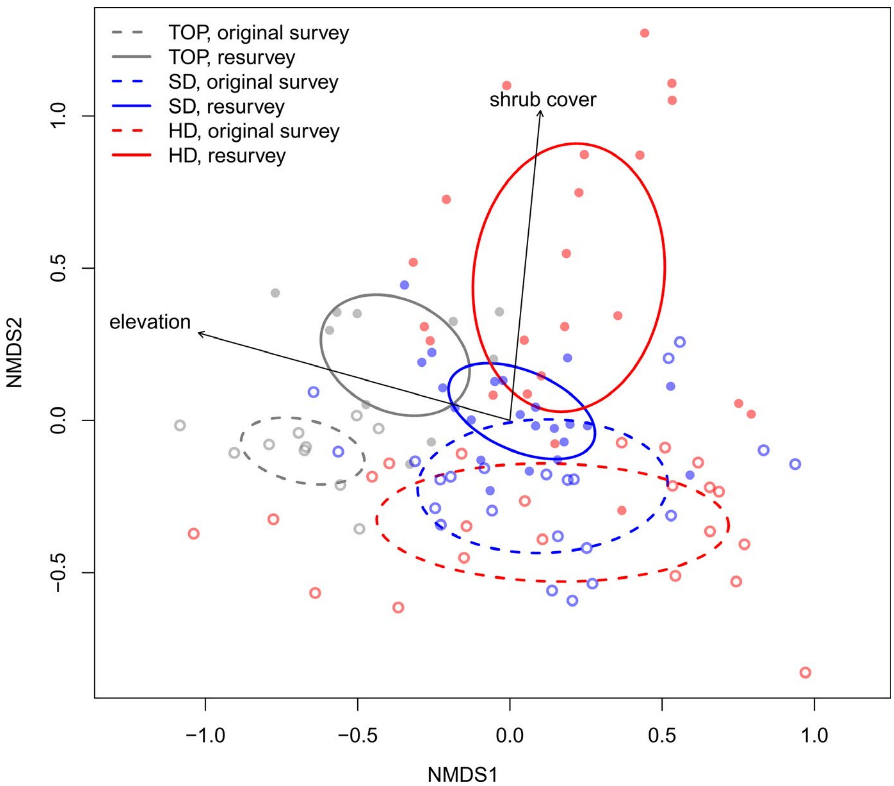

FIGURE 2 Compositional changes over time. The non-metric multidimensional scaling (NMDS) ordination shows the composition of communities subjected to slight (SD) and heavy disturbance (HD) and the corresponding original communities. Ellipses are 1 standard deviation for group centroids. Temporal shifts in the community composition seem most pronounced under heavily disturbed slopes and at the top. The composition of top communities has shifted towards the composition of more forested slope communities over time. Temporal shifts in community compositions correlate with increased shrub coverage ($r^2 = 0.28$, $p = 0.001$) and elevation ($r^2 = 0.44$, $p = 0.001$; ordination plots with the third axis in Appendix S5). Stress = 0.15

Non-overlapping confidence bands indicate that dwarf shrubs also gained ground at lower slopes under slight disturbance (Figure 3c), whereas graminoid increase was strongest at the upper slopes under heavy disturbance (Figure 3d). Bryophyte cover decreased strongly at lower slopes, regardless of the disturbance level, leading to temporal changes in their elevational distribution (Table 1: *T* × *E*, Figure 3f). Lichen cover tended to decrease only slightly on the heavily disturbed upper slopes (Figure 3g), yet this change was not significant. Total species richness increased prominently under both disturbance levels over time but even more so under heavy disturbance (Table 1; *T* × *D*, Figure 4a). Here, the increase of total species richness was primarily due to the increased number of vascular plants (Table 1; *T* × *D*, Figure 4b). Bryophyte richness increased under both disturbance levels (Table 1: T, Figure 4c) and lichen richness only little on the slightly disturbed upper slopes (Table 1; *T* × *D*, Figure 4d). At the heavily disturbed top, canopy cover decreased over time, while shrub cover, total species richness, vascular plant richness and bryophyte richness increased (Table 2).

Species' elevational position during the original survey and the level of disturbance had significant effects on species' weighted mean elevation during the resurvey ($X^2 = 19.8$, $p < 0.001$ and $X^2 = 9.5$, $p = 0.002$, respectively; Figure 5). However, the magnitude of change in mean elevation was different between the disturbance levels (original mean elevation × disturbance level: $X^2 = 5.5$, $p = 0.019$). Species with an originally lower mean elevation shifted upwards over time regardless of the level of disturbance (confidence bands diverge from the 1:1 line that represents no temporal change in mean elevation in Figure 5). Many species with originally higher mean elevation shifted downwards under heavy disturbance, whereas such a trend was not detected on slightly disturbed slopes. Additional analyses for biogeographical groups showed that the weighted mean elevation of temperate–boreal, hemiarctic–boreal and hemiarctic vascular plant groups shifted upwards under slight disturbance, whereas under heavy disturbance, the mean elevation of the hemiarctic group shifted downwards (Appendix S7).

4 | DISCUSSION

We resurveyed the vegetation of a boreal mountain along four elevational gradients that had been originally surveyed before the construction of ski resort facilities in the 1980s. Between the surveys, climate warmed in the study area for over two decades, which was expected to affect the vegetation. Half of the gradients were taken for ski resort facilities, while the other half remained relatively

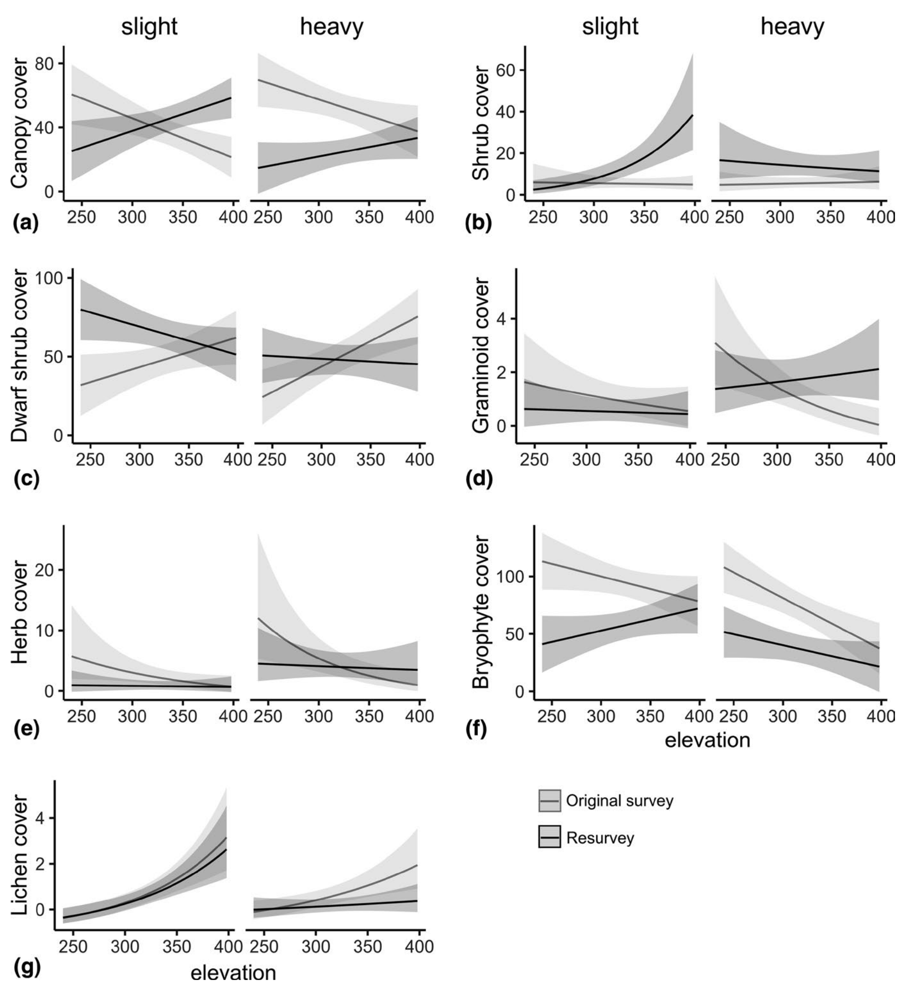

FIGURE 3 Fits of generalized linear mixed-effects models with 95% confidence bands for the cover (%) of (a) canopy, (b) shrubs, (c) dwarf shrubs, (d) graminoids, (e) herbs, (f) bryophytes and (g) lichens along the elevational gradient on slightly and heavily disturbed slopes during the original survey and the resurvey. Model summaries (including estimates, standard deviations and pseudo-R^2 values) are in Appendix S6

TABLE 1 Results from generalized linear mixed models testing the effects of time (original survey vs resurvey), disturbance (heavy vs slight), elevation (m a.s.l.) and their interactions on different plant group covers (%) and species richness. *df* = 1

	Time (*T*)		Disturbance (*D*)		Elevation (*E*)		*T* × *D*		*T* × *E*		*D* × *E*		*T* × *D* × *E*	
	X^2	*p*	X^2	*p*	X^2	*p*	X^2	*p*	X^2	*p*	X^2	*p*	X^2	*p*
Canopy cover	3.8	0.051	0.9	0.348	0.2	0.645	15.4	<0.001	20.2	<0.001	0.1	0.745	0.6	0.431
Shrub cover	25.2	<0.001	0.0	0.945	2.6	0.108	0.0	0.907	2.8	0.094	4.4	0.036	7.3	0.007
Dwarf shrub cover	2.1	0.152	2.0	0.163	2.6	0.104	4.4	0.038	14.1	<0.001	2.1	0.152	0.0	0.951
Graminoid cover	0.0	0.919	4.4	0.036	4.2	0.040	5.4	0.020	7.2	0.007	0.3	0.600	2.4	0.119
Herb cover	2.2	0.137	11.7	0.001	8.1	0.004	2.4	0.124	5.2	0.023	0.2	0.652	0.1	0.716
Bryophyte cover	34.4	<0.001	13.5	<0.001	8.0	0.004	0.1	0.834	7.1	0.007	6.2	0.013	0.4	0.523
Lichen cover	3.3	0.069	1.5	0.215	35.5	<0.001	1.8	0.178	2.4	0.119	6.2	0.013	1.1	0.304
Total richness	168.0	<0.001	0.1	0.746	5.5	0.024	11.3	0.002	0.1	0.771	8.1	0.007	0.6	0.433
Vascular richness	85.4	<0.001	7.1	0.007	0.0	0.894	19.1	<0.001	0.4	0.538	6.2	0.013	0.1	0.831
Bryophyte richness	57.1	<0.001	16.2	<0.001	6.5	0.011	0.2	0.662	0.1	0.708	0.0	0.951	0.1	0.850
Lichen richness	3.8	0.052	2.1	0.149	30.9	<0.001	4.4	0.036	0.0	0.967	1.3	0.259	0.1	0.718

*Shrubs include both low-growing and tall shrubs.

intact, allowing comparison of the effects of heavy and slight land use disturbance on vegetation changes that had taken place during 34 years. We observed differences in shrub encroachment, species richness and species' elevational shifts between slightly and heavily disturbed gradients. These findings therefore generally support our hypothesis that the level of land use disturbance considerably influences the long-term vegetation changes in a boreal landscape. In the following, we discuss the main findings to establish the role of anthropogenic disturbance as one of the primary drivers modifying boreal plant communities under climate warming and consider implications for management.

Expectedly, shrubs and tree canopy cover increased on the originally open upper slopes under slight disturbance. We interpret these trends to result from the recent climate warming favouring woody plant growth on formerly open habitats (Myers-Smith & Hik, 2018), and the upward shift of treeline ecotones (Harsch et al., 2009). Even though we cannot completely rule out other drivers that may have had effect on these observed changes (e.g., natural succession), the encroachment of trees and shrubs seem to rapidly transform formerly semi-open or open boreal heaths towards more closed forest stands. In contrast, tree cover clearance and continued heavy disturbance tended to limit shrub expansion on the upper slopes and to promote a uniform, yet modest, increase along the elevational gradient. Thus, our results indicate that heavy land use disturbance may limit major expansion of shrubs on formerly open habitats to some degree but can allow their presence at low to moderate abundances under cleared or thinned tree canopies. Taken together, these findings strongly suggest that increases in tree canopies and shrub abundance could be more common in the boreal mountain uplands if there were no constraints due to disturbances.

Contrary to our expectation, the overall cover of dwarf shrubs, mainly composed of ericoids (*Vaccinium* spp.), was not notably affected by the disturbance level and thus, seemed to resist relatively heavy disturbance. Like taller shrubs, dwarf shrubs also may benefit from lighter and warmer conditions (Myers-Smith et al., 2011). Thus, under reduced canopy shade due to heavy disturbance, they could retain at least part of their abundance. According to Zeidler et al. (2016), dwarf shrubs can also benefit from managed snow cover and perform well on ski slopes, which may partly explain the observed results. The increase of dwarf shrubs on slightly disturbed lower slopes coincides with the reduced tree cover. The latter is likely due to a natural dieback of old-growth trees and canopy damage due to pronounced crown snow-loads typical for the study area (Gregow et al., 2008).

There was a notable overall decrease in bryophyte cover between the surveys that depended on elevation. Most pronounced decreases took place on the lower slopes under slight disturbance, coinciding with the increased dwarf shrub cover on slightly disturbed slopes and with increased shrub cover on heavily disturbed slopes. Decreased bryophyte cover may also be a general response to a warmer microclimate, solar radiation damage and evaporation stress due to decreased canopy cover (Busby et al., 1978). The

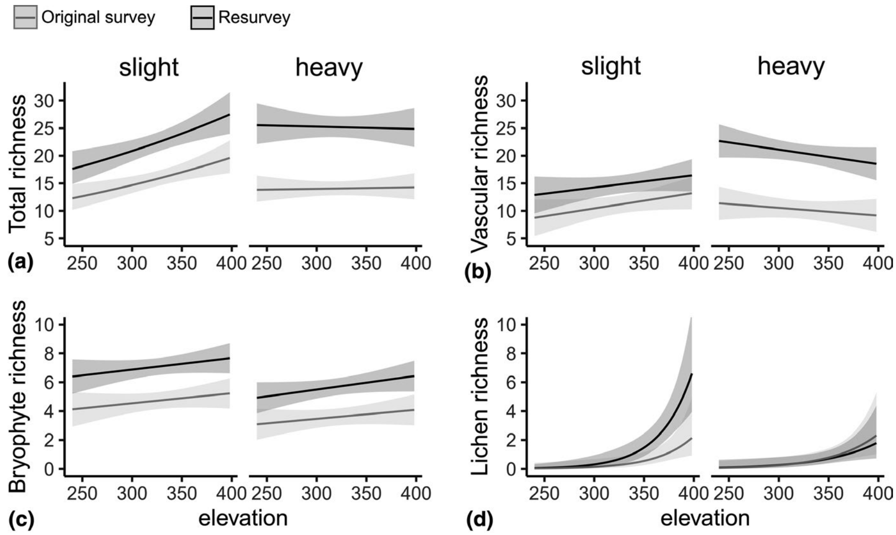

FIGURE 4 Fits of generalized linear mixed-effects models with 95% confidence bands for (a) total species richness, (b) vascular plant richness, (c) bryophyte richness and (d) lichen richness along the elevational gradient on slightly and heavily disturbed slopes during the original survey and the resurvey. Model summaries (including estimates, standard deviations and pseudo-R^2 values) are in Appendix S6

TABLE 2 Mean ± *SD* of plant group covers (%) and species richness at the heavily disturbed top during the original survey and the resurvey, and the temporal change (Δ)

	Original survey	Resurvey	Δ	X^2	*p*
Canopy cover	19.0 ± 9.7	10.3 ± 5.3	−8.7	8.5	0.004
Shrubs[a]	3.0 ± 1.0	11.3 ± 9.1	+8.3	11.6	0.001
Dwarfs shrubs	71.4 ± 19.8	66.3 ± 21.3	−5.1	0.5	0.501
Bryophytes	25.8 ± 27.3	18.5 ± 12.2	−7.3	0.4	0.550
Lichens	6.7 ± 10.3	3.4 ± 4.2	−3.3	0.4	0.539
Total richness	13.7 ± 2.2	19.1 ± 3.3	+5.4	32.3	<0.001
Vascular richness	9.2 ± 1.0	13.6 ± 2.1	+4.4	63.7	<0.001
Bryophyte richness	2.5 ± 1.1	3.9 ± 1.6	+1.4	6.4	0.011
Lichen richness	2.0 ± 1.7	2.7 ± 2.7	+0.7	0.7	0.419

X^2- and *p*-values are derived from generalized linear mixed models that were used to test the effect of time on plant group covers and species richness. $df = 1$.

[a]Shrubs include both low-growing and tall shrubs.

other main ground layer element, lichen cover, tended to decrease towards the top under heavy disturbance, which can be expected because fruticose lichens, especially in dry conditions, are sensitive to disturbances and recover slowly (Klein & Schulski, 2009; Heggenes et al., 2017).

Species' elevational shifts, in terms of their elevational range means, were directed primarily upwards under slight disturbance, which was expected given the warmer conditions (Lenoir et al., 2008; Parolo & Rossi, 2008). Species-specific shifts were stronger in those species that had originally lower elevational position, as also shown by Rumpf et al. (2018). Such clear upward shifts of species and also certain biogeographical groups (Appendix S7) may be highlighted in boreal landscapes where low-lying and short elevational gradients along with the proximity to closed forests may allow relatively rapid movement of species compared to, for instance, alpine environments. However, as anticipated based on Lenoir et al. (2010), our results showed that heavy disturbance promoted several species to expand their elevational range means also downwards. This likely reflects an increased immigration of local species following more open and partially disturbed forest floor vegetation and may also explain the absence of upward shifts in biogeographical group means under heavy disturbance (Appendix S7). Taken together, these patterns strongly suggest that disturbance opens new space for species immigration and thus, contributes to more pronounced elevational shifts of individual species in boreal landscapes.

As expected, the ski resort as a heavy disturbance agent enhanced plant richness in the boreal mountain environment, promoting richness particularly at the lower slopes compared to slight disturbance. It is possible that downward shifts in species' elevational means on heavily disturbed slopes explain species richness increases on lower slopes, in addition to gains of species that benefit from disturbances (e.g., fireweed *Chamaenerion angustifolium* and tree saplings *Populus tremula*, *Salix* spp., and *Sorbus aucuparia*, see Appendix S8e). Even though our results provide robust evidence that disturbed conditions can substantially promote local richness under contemporary climate warming, as suggested also by Harrison (2020), we highlight that enhanced species richness may not necessarily improve other facets of plant biodiversity as locally rich vegetation can become compositionally homogeneous in the longer term (Savage & Vellend, 2015).

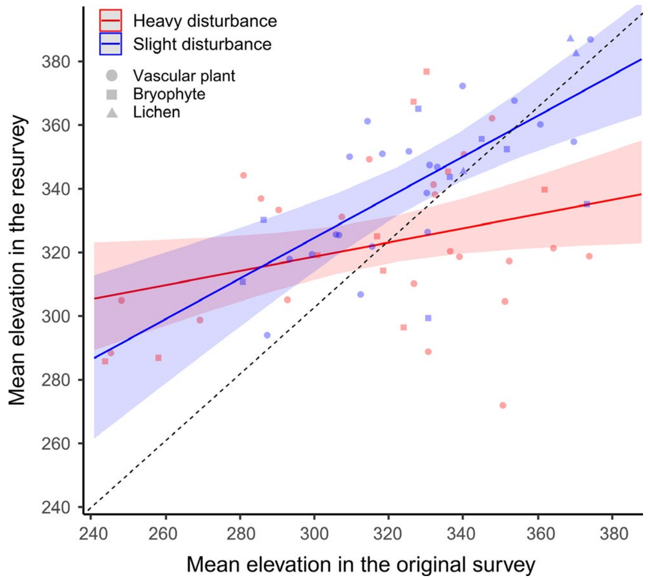

FIGURE 5 Generalized linear mixed-effects model fit with 95% confidence bands for species' weighted mean elevation in the resurvey in relation to their original weighted mean elevation and the disturbance level (SD = slightly disturbed slopes, HD = heavily disturbed slopes). The diagonal dashed line indicates a condition where species' mean elevation is the same for the original survey and the resurvey. Only species that occurred at least three times in both surveys were included in the model (all species-specific shifts in Appendix S8)

Our results indicate that heavy land use disturbances can modify shrub expansion patterns across elevational gradient, shuffle species' elevational distributions and enhance species richness in boreal environments. We therefore suggest that the effects of climate and land use on vegetation should not be assessed separately as this may lead to inappropriate management actions or inaccurate projections on future vegetation (see also Danneyrolles et al., 2019). As disturbance effects may alter the climate–distribution relations, attempts to predict climate change effects on vegetation may be complicated if disturbances are not considered. This may also partly explain inconsistencies in the observed climate-driven vegetation changes across high latitudes (Myers-Smith et al., 2020). The recognition of human disturbance as an important driver behind local scale vegetation dynamics is crucial, since year-round recreational activities will likely increase due to growing tourism (Saarinen, 2007).

The negative effects of ski resorts on mountain environments are relatively well known, being strongest under soil-grading and revegetation by invasive species (Tsuyuzaki, 1994B; urt & Rice, 2009; Roux-Fouillet et al., 2011). Thus, the realisation of a potentially positive effect is an intriguing idea. We find it possible that disturbances owing to mainly tree clearance, but preserving soils and field layer vegetation to some extent, may contribute, at least temporarily, to preservation of species requiring open habitats (see also Steinbauer et al., 2018; Chardon et al., 2019) by limiting shrub and canopy cover development into closed stands. However, even though the previously tundra-like top had remained relatively open due to heavy disturbance, compositional features related to tundra-like communities had declined (i.e. top communities had become more similar to slope communities and certain species typical for treeless habitats shifted towards the mountain top, Appendix S8c). Given that there is evidence for the climate change-induced disappearance of species and communities of formerly open tundra-like habitats on relatively undisturbed boreal mountains (Maliniemi et al., 2018), further research on anthropogenic disturbance mitigating climate change effects in these habitats is timely.

Our results provide new insight into the nature conservation problematics of boreal mountains and have certain management implications. First, our results provide support for the recent expert assessments (Pääkkö et al., 2019) that undisturbed boreal mountain tops are threatened by current climate warming promoting shrub and tree expansion. Second, disturbances due to ski resort maintenance in boreal mountains may limit climate-driven shrub encroachment and even preserve or create habitats for some species that might decrease under warming climate, yet more research is required on this matter. There is still limited consensus or knowledge about the multiple roles of anthropogenic disturbances in the management of boreal mountain environments, and whether they might constitute an ecologically, societally and culturally acceptable climate change mitigation strategy. However, analogous to discussions on the role of grazing as a means of slowing down tundra shrubification (Verma et al., 2020), we find it beneficial and timely to consider if the already ongoing human disturbances could contribute to the preservation of open boreal mountain habitats and recommend that experts developing management plans would pay greater attention to this. Third, we emphasise that the disturbance effects depend on the context (e.g., elevational position) and intensity, and these factors, along with the multiple negative effects that human land use disturbance imposes on the environment must always be considered when developing conservation and management plans.

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AUTHOR CONTRIBUTIONS

TM and RV conceived the ideas and designed methodology; TM collected and analysed the data and led the writing of the manuscript. Both authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data used in this study will be deposited in EVA (European Vegetation Archive).

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SUPPORTING INFORMATION

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

Appendix S1. Photographs of heavily and slightly disturbed sites

Appendix S2. List of all species recorded during the surveys

Appendix S3. Spatial autocorrelation of generalised linear mixed-effects model (GLMM) residuals

Appendix S4. Long-term climate and grazing pressure records

Appendix S5. Non-metric multidimensional scaling (NMDS) plots of the 1st vs 3rd axis and of 2nd vs 3rd axis

Appendix S6. Model summaries (estimates, standard deviations and pseudo-R^2 values) for Figures 3 and 4

Appendix S7. Temporal changes in the weighted mean elevation of biogeographical plant groups

Appendix S8. Species-specific elevational shifts under different disturbance levels

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