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Lost at high latitudes: Arctic and endemic plants under threat as climate warms

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Abstract

Aim: Species' biogeographical patterns are already being altered by climate change. Here, we provide predictions of the impacts of a changing climate on species' geographical ranges within high-latitude mountain flora on a sub-continental scale. We then examined the forecasted changes in relation to species' biogeographic histories.

Location: Fennoscandia, Northern Europe (55–72°N).

Methods: We examined the sensitivity of 164 high-latitude mountain species to changing climate by modelling their distributions in regard to climate, local topography and geology at a 1 km^2 resolution. Using an ensemble of six statistical modelling techniques and data on current (1981–2010) and future (2070–2099) climate based on three Representative Concentration Pathways (RCPs 2.6, 4.5, 8.5), we developed projections of current and future ranges.

Results: The average species richness of the mountain flora is predicted to decrease by 15%–47% per 1 km^2 cell, depending on the climate scenario considered. Arctic flora is projected to undergo severe range loss along with non-poleward range contractions, while alpine flora is forecasted to find suitable habitat in a warmer North. A substantial majority (71%–92%) of the studied species are projected to lose more than half of their present range by the year 2100. Species predicted to lose all suitable habitat had ranges centred in the northernmost (>68°N) part of continental Europe.

Main conclusions: Climate change is predicted to substantially diminish the extent and richness of Europe's high-latitude mountain flora. Interestingly, species' biogeographic histories affect their vulnerability to climate change. The vulnerability of true Arctic and endemic species marks them as highly important for conservation decisions.

KEYWORDS

Alpine, Arctic, biogeographic history, climate change, range contraction, species distribution models

1 | INTRODUCTION

The flora of the high-latitude mountains of Europe is an interesting mix of species with different biogeographic histories from the true Arctic and mid-latitude mountains. Plants inhabiting high-latitude mountains—some of the most vulnerable areas to global warming (Nogués-Bravo, Araújo, Errea, & Martinez-Rica, 2007; Parmesan & Yohe, 2003; Sala et al., 2000)—experience a shorter growing season than elsewhere on Earth due to low air and soil temperatures (Körner, 2016). Cold-adapted flora (Bliss, 1971) is already in decline and is likely to experience further range losses (Lenoir, Gégout, Marquet, Ruffray, & Brisse, 2008; Thuiller, Lavorel, Araújo, Sykes, & Prentice, 2005) and/or range shifts to track suitable climate (Engler et al., 2011; Thuiller et al., 2005).

Recent reviews highlight the necessity of predicting these range changes under climate change (Bonebrake et al., 2017; Urban, 2015) for use in assessments of extinction risk (Lenoir & Svenning, 2015) or climate change adaptation (Hickler et al., 2012). High-latitude mountains encompass both the latitudinal and elevational range limits for a number of species and are thus suitable for investigating climate change-induced range changes (Menéndez, González-Megías, Jay-Robert, & Marquéz-Ferrando, 2014). Many studies show that species are shifting their ranges poleward (e.g., Parmesan & Yohe, 2003, Hickling, Roy, Hill, Fox, & Thomas, 2006) and to higher elevations (e.g., Lenoir et al., 2008, Chen, Hill, Ohlemüller, Roy, & Thomas, 2011) and additional knowledge is needed to help anticipate future range changes (VanDerWal et al., 2013). Despite the importance of high-latitude mountainous regions for preserving their unique flora, few studies have focused on their climate change sensitivity (see Urban, 2015 for a review).

Species' ranges will need to shift in complex ways to track their thermal niches (Burrows et al., 2014). Complexities and uncertainties are emphasized in regional findings of cold-adapted plant species richness in the Scandes Mountains ranging from increases (Klanderud & Birks, 2003) to losses (Engler et al., 2011; Wilson & Nilsson, 2009) and stability (Vanneste et al., 2017). Increases in species richness on the summits of the Scandes are a likely consequence of the upslope shifts in species' upper range limits (Steinbauer et al., 2018). In the European Alps, the species experiencing reductions in abundance and range size are the cold-adapted species of the highest elevations (Rumpf et al., 2018). Though the Scandes flora is predicted to be less sensitive to climate change than other European florae (Engler et al., 2011), with northern range margins potentially exhibiting strong local adaptation (Vergeer & Kunin, 2012), it is believed that mountainous Fennoscandia will experience species loss (Lenoir et al., 2008; Thuiller et al., 2005). Moreover, previous efforts to model species' climate change vulnerability in Europe have mainly been conducted at coarse spatial resolutions (50–75 km: e.g., Bakkenes, Alkemade, Ihle, Leemans, & Latour, 2002, Pearson & Dawson, 2003, Engler et al., 2011, but see e.g., Randin et al., 2009).

In this paper we seek to (a) predict future range and richness patterns for a set of vascular plants occurring at high latitudes and high altitudes, (b) ascertain how species vulnerability manifests in terms of range size reductions under climate change, and (c) determine whether species biogeographic history has an effect on predicted range changes. Species with different biogeographic histories have overlapping macroclimatic niches but different recolonization histories since the last glacial–interglacial cycle (Wasof et al., 2015) and may thus showcase dissimilar responses to changing climate (Pellissier et al., 2016). We expect differential responses arising between the biogeographic history groups due to dissimilar evolution and migration patterns. For example, more northerly species of Arctic origin may be less adapted to warming climate at their southern range margin than the relatively more southerly alpine species at their northern margin, as alpine species generally have broader climate niches and better adaptive abilities (Wasof et al., 2015). We employ an ecologically relevant array of climatic, topographical and geological predictors across a model ensemble. Climate change sensitivity was assessed by quantifying predicted spatiotemporal changes in currently suitable habitat for the studied species (164 species; 195,203 observations) under three climate change scenarios using data on a fine sub-continental spatial scale (1 km × 1 km grid cell). Predictions of range contractions were used to define the species expected to become threatened by climate change by the end of this century.

2 | METHODS

2.1 | Study area

The study was carried out in Fennoscandia, Northern Europe (55–72°N, 5–32°E; Figure 1). This latitudinal gradient—from the northern limits of the temperate biome to the southern limits of the Arctic biome (Heikkinen, 2005)—encompasses a range of climatic conditions from −9.2°C to 9.3°C in annual mean temperatures (as calculated from the European Climate Assessment and Dataset [ECA&D: Klok & Klein Tank, 2009; see Section 2.3). There is a strong east–west gradient in rainfall due to an orographic effect by the Scandes (see e.g., Tikkanen, 2005) and the mean annual precipitation varies from 366 mm to over 3,000 mm. The region is influenced by the North Atlantic current and westerly winds that transfer heat and moisture. Elevation ranges from sea-level coastlines to the highest peaks of the Scandes (2,469 m a.s.l), a region of rugged terrain intensely shaped by glacial and fluvial processes. The area is host to significant topographic heterogeneity from level to steep terrain (Figure 1) associated with a wide range of microclimatic conditions, and many plant species reach their distributional limits in the regions northern parts (see e.g., Corner, 2005). Due to the mainly continuous ice sheet covering the region during the Last Glacial Maximum (c. 23000–18000 years BP; Svendsen et al., 2004) and the East–West orientation of other European mountain ranges, postglacial recolonization was limited (Wasof et al., 2015). Long-distance

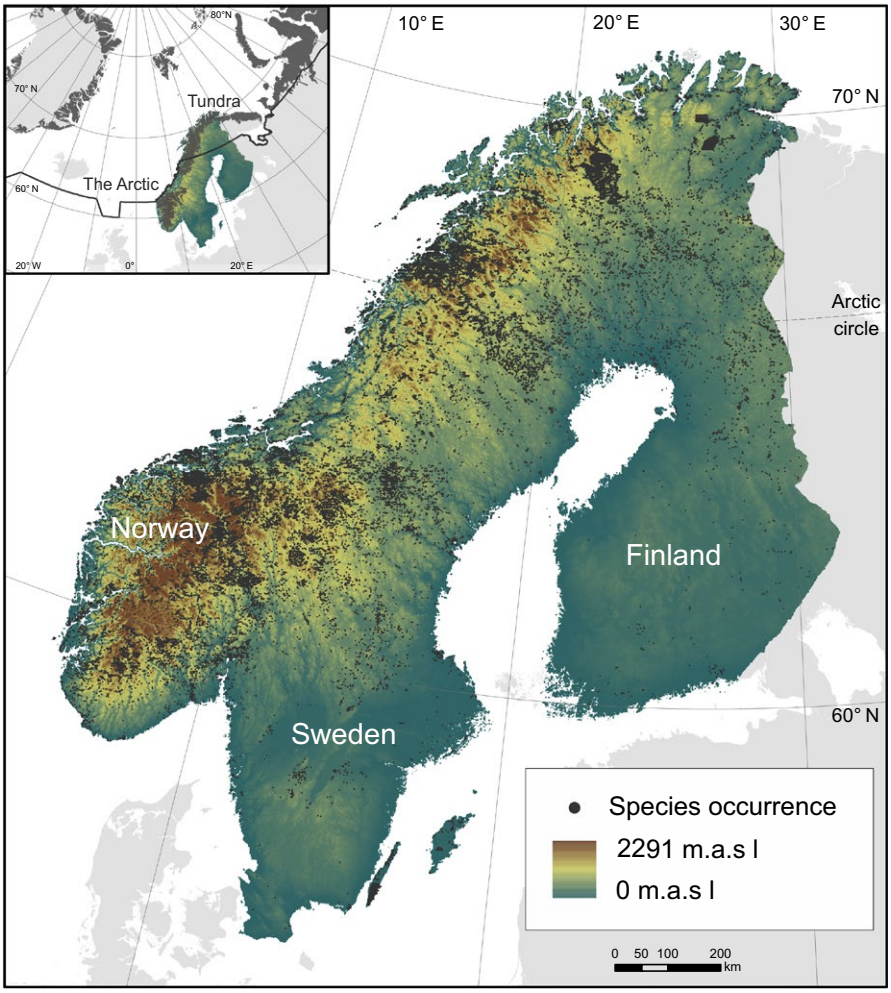

FIGURE 1 The study area relief and location of the vascular plant species occurrence observations (n = 195,211) in Fennoscandia, northernmost Europe. The Scandes can be seen as the "high elevation belt" running along the western side of the peninsula. The inset map shows the study region in relation to the tundra biome (Dinerstein et al., 2017) and the Arctic boundary (Steenhuisen & Wilson, 2013)

recolonization via repeated founder events from southern as well as eastern refugia (Eidesen et al., 2013) may have reduced population adaptability and genetic variation (due to genetic erosion as a consequence of post-glacial recolonization: see Yannic et al., 2014), shrinking the fundamental climatic niche towards colder growing conditions (Giesecke, 2005).

2.2 | Species data

Species occurrence data of high-latitude mountain vascular plant species (defined according to expert opinion and their biogeographic distribution from observation maps) were collected and combined from the national species data banks of Finland, Sweden and Norway (http://www.laji.fi/en/, https://www.artportalen.se/, http://www.artsdatabanken.no/, respectively) and complemented using occurrence data from the Global Biodiversity Information Facility (GBIF; http://www.gbif.org/) and observational data collected in the field by the authors (see Data Accessibility for further information). The online search, undertaken in November-December 2016, was filtered to include only georeferenced occurrences since the year 1990 with a location accuracy of 100 metres. These species occurrences were aggregated to a 1 km × 1 km grid (projection: Transverse Mercator Finland Uniform Coordinate System, epsg: 2,393), creating a dataset of 195,203 occurrences in 31,659 grid cells. Currently, the entire study region has, on average, six species per grid cell (min–max: 0–111). Our analyses were conducted for 164 species with a minimum occurrence of 25 grid cells for which projections could be made (Figure 1; five species were excluded from the analysis; see Supporting Information Appendix S1 for the species list).

2.3 | Environmental predictors

We used a set of predictors describing climate, topography and geology and matching the resolution of the species data to predict their distributions in space and time (1 km × 1 km; see Supporting Information Appendix S2 for further variable descriptions).

We acquired the climatic data for our study region from a high resolution 1 km × 1 km climate data set produced for land surface areas (following Aalto, Riihimäki, Meineri, Hylander, & Luoto, 2017). In brief, monthly average temperatures (1981–2010) were modelled across the study domain based on daily data from 942 meteorological stations (ECA&D: Klok and Klein Tank 2009) and generalized additive modelling (GAM: as implemented in R package *mgcv*; Wood, 2011) utilizing variables of geographical location, topography and water cover. Modelled monthly average air temperature data agreed well with the observations, with root mean squared error

(RMSE) ranging from 0.6 to 1.6°C. To produce gridded monthly precipitation data, a kriging interpolation based on data from 1,076 rain gauges, topography and proximity to the sea was used (R package *gstat*; Pebesma, 2004). A random 10-fold cross-validation conducted over the gauge data indicated reasonable agreement between measured and interpolated precipitation with RMSE ranging from 9.3 to 21.7 mm. Three climatic predictors were derived from the produced monthly datasets and were included in the analyses: growing degree days (GDD5: °C, sum of the monthly mean air temperatures >5°C representing growing season conditions; five degrees was chosen as the appropriate threshold sum for plant growth in this region and for this set of species), temperature of the coldest quarter (TCQ: °C, Dec-Feb representing overwintering conditions), and water balance (WAB: mm, the difference between the annual precipitation sum and potential evaporation representing available moisture; Skov & Svenning, 2004). These climatic predictors were chosen to represent known physiological limits to high-latitude plant distributions including water and energy availability (Körner 2003).

The future climate projections are based on an ensemble mean over 23 global climate models (GCMs) extracted from the Coupled Model Intercomparison Project phase 5 (CMIP5) archive (Taylor, Stouffer, & Meehl, 2012). We explore the implications of three possible future Representative Concentration Pathways (RCPs): 2.6, 4.5 and 8.5 (Van Vuuren et al., 2011). The GCM data represent the predicted average change in mean temperature and precipitation (compared to 1981–2010) over the period of 2070–2099 for each RCP scenario. The GCM data were bilinearly interpolated to the matching resolution of 1 km × 1 km and the predicted change was added to the baseline climate data. The three climate predictors were re-calculated for each RCP scenario (see Supporting Information Appendix S2).

Besides climate, topography and bedrock type exert a strong influence through numerous geomorphological, hydrological and geological processes mediating the growing conditions experienced by plants (Mod, Scherrer, Luoto, & Guisan, 2016; Scherrer & Körner, 2011) and have been shown to improve SDM predictive ability (Austin & Van Niel, 2011). Two topo-edaphic landscape-scale predictors were used. Firstly, the maximum elevational difference within a given 1 km × 1 km grid cell was used to represent topographical heterogeneity, a proxy for microclimatic and habitat variation (hereafter TOPO: Luoto & Heikkinen, 2008). The TOPO predictor was calculated for each cell using ArcGIS software (zonal statistics –function) from a digital elevation model (DEM; combined from national DEMs provided by the land surveys of Finland, Sweden, and Norway) with a resolution of 50 m × 50 m. Secondly, bedrock class was used to represent the calcareousness of geological substrates in a given 1 km × 1 km grid cell (GEO: Dubuis et al., 2013; see Supporting Information Appendix S2). The topo-edaphic data were resampled and reprojected to a matching grid. The GEO predictor was reclassified from a collated 1:1 M geological dataset of the Fennoscandian shield region obtained from the Geological Surveys of Finland, Sweden and Norway.

2.4 | Statistical analyses

Species occurrences were related to the predictor set using six statistical modelling techniques to control for inter-model variability. These included generalized linear modelling (GLM; McCullagh & Nelder, 1989), generalized additive modelling (GAM: Hastie & Tibshirani, 1990), multivariate adaptive regression splines (MARS; Friedman, 1991), boosted regression trees (BRT; Elith, Leathwick, & Hastie, 2008), random forest (RF; Breiman, 2001) and classification tree analysis (CTA; Breiman, Friedman, Olshen, & Stone, 1984). See Supporting Information Appendix S3 for detailed description of models' parameters. We combined presence-only species occurrences with pseudo-absence (PA) data. The ensemble modelling was performed separately for three categories of models depending on optimal amount of PAs. For GAM and GLM, we used 10,000 random PAs (Barbet-Massin, Jiguet, Albert, & Thuiller, 2012). For MARS, we used 1,000 climatically stratified PAs, and for CTA, BRT and RF, we used the same number of climatically stratified PAs as available presences (average, min–max: 1,190, 25–6,274; Barbet-Massin et al., 2012). All models were run under the BIOMOD2 platform (Thuiller, Georges, & Engler, 2013) using R-program (R Development Core Team, 2013) and the chosen set of environmental predictors:

$$\text{Occurrence of species} = \text{GDD5} + \text{TCQ} + \text{WAB} + \text{TOPO} + \text{GEO}. \quad (1)$$

The predictive ability of the models was evaluated using random fourfold cross-validation where, at each run, the models were calibrated with a random subset of 70% of the data and evaluated with the withheld 30%. Occurrences of some alpine species outside the study region, such as in mountainous southern Europe, were excluded from model calibration as dispersal from there to the study region is limited. Using data from Fennoscandia alone are further justifiable by the extensiveness of the study area and the warm range margins it covers. To assess the agreement between observed and predicted occurrences, we used a range of commonly used evaluation metrics: the area under the curve of a receiver operating characteristic (AUC: Fielding & Bell, 1997) and true skill statistics (TSS: Allouche, Tsoar, & Kadmon, 2006).

All data were used for projecting species occurrences over the study domain. Occurrence probabilities were transformed to binary presence/absence predictions using a TSS cut-off maximizing model accuracy defined by Biomod2 (Thuiller et al., 2013). In order to reduce uncertainty related to the choice of modelling technique, we constructed an ensemble of forecasts (Araújo & New, 2007). Here, we chose a majority's vote of a minimum of four out of six modelling techniques to denote a presence value for a given species inside a given 1 km × 1 km grid cell. To find suitable habitats as defined by the set of predictors used, species-specific predictions of presence or absence for each raster cell were then projected into three future climate scenarios. Our predictions assume the optimistic unlimited dispersal scenario which—though not entirely realistic—has been shown to give predictions similar to "optimistic" static models (Dullinger et al., 2012), and provide a good estimate of species

range shifts in Arctic (Alsos et al., 2007) and alpine areas (Engler et al., 2009).

2.5 | Climate change impact measures

To study the effects of climate change on the plant species of the Arctic-alpine realm, we firstly defined the realm as the area of the study region in which grid cells were predicted to be occupied by ten or more high-latitude species in the current time period. The Arctic-alpine realm as defined herein is predicted to experience increases in temperature and rainfall between the years 1981–2010 and 2070–2099, with noticeable differences between the Northern (>65°N) and the Southern (<65°N) Scandes. In RCP 4.5, GDD5 will increase by an average of 111 degree days (°C; 95% interval: 50–177) in the Northern Scandes and by 44 degree days (°C; 95% interval: 3–82) in the Southern Scandes. WAB will increase by an average of 268 mm (95% interval: 194–383) in the North and 294 mm (95% interval: 167–450) in the South. Greater increases in GDD5 in the North can be explained by the fact that the magnitude of climate change is increasing poleward, that is, Arctic amplification (Bekryaev, Polyakov, & Alexeev, 2010). We then proceeded to quantify the effects of these climatic changes on the extent and high-altitude species richness (TSR) of the Arctic-alpine realm. Changes for two other richness thresholds (TSR ≥1 species; TSR ≥100 species) were also explored but are not outlined here (but see Supporting Information Appendix S4).

Here, we refer to the SDM predictions of suitable habitat as predicted species' ranges. Changes in these ranges were estimated separately for all species, but consequently also studied according to species' biogeographic histories. Within the set of high-latitude species, we distinguished four biogeographic history categories: Arctic (number of species in the data = 66); alpine (n = 10); Arctic-alpine (n = 80); and endemic (n = 8), based on current distributions and expert opinion (Anderberg & Anderberg, 2017; Hultén & Fries, 1986). We estimated the mean distance and direction (elevational and latitudinal) of species' range shifts and contractions. We used the weighted centroid of a species' distribution range, calculated as the centre of gravity (COG) of each prediction raster with the R package SDMTools (VanDerWal et al., 2014), to quantify latitudinal change between current and future ranges. The COG of each prediction raster is weighted by area of individual spatial cells, and changes therein can provide great insight into species responses to predicted climate change (VanDerWal et al., 2014). Elevational range change was calculated as the difference in mean elevation between a species' current and future distribution. To decipher whether the biogeographic history of a species has an effect on its future range change, we tested for significant differences in predicted range change across biogeographic groups using nonparametric ANOVA (Kruskal–Wallis test).

We quantified vulnerability as the change in a species' range size (relative change in area of predicted occupancy) between current and future projections (Bakkenes et al., 2002). Range size change was also compared with range overlap between current and future projections to recognize potential for the in situ preservation of species for which range shift would not be required. We utilized a simplistic Red List approach (sensu Thuiller et al., 2005) where regional vulnerability was based on the amount of decline in area of occurrence (number of cells) by 2070–2099 according to the IUCN Red List criterion A3(c) (IUCN Red List Categories, 2001). Though threat status is also driven by other parameters and though our models do not explicitly address the cause of predicted species extinction, this method can provide insights on species' regional vulnerability as any reduction in the range of a species is likely to increase vulnerability (Thomas et al., 2004). Each species was assigned to a regional threat category using the following thresholds: a species is likely to become critically endangered (CR) after a projected range loss of ≥80%, endangered (EN) after a projected range loss of ≥50%, and vulnerable (VU) after a projected range loss of ≥30%. We discuss regional extinction (EX) in terms of habitat loss only (sensu Randin et al., 2009), assigned to species predicted to lose 100% of suitable habitat within the study area.

3 | RESULTS

The models performed well over the four evaluation rounds averaged (standard deviation *SD*) over all (n = 164) species (AUC = 0.93, *SD* = 0.04; TSS = 0.75, *SD* = 0.09). The Arctic-alpine realm is projected to diminish following warming, its extent decreasing 51%–87% by 2100, depending on climate scenario (Figure 2). The currently spatially continuous Arctic-alpine realm (Figure 2a) is projected to contract into two more distinct centres of Arctic-alpine biodiversity following stronger climatic change (Figure 2d). Currently averaging at 58 high-latitude mountain species per grid cell, the mean TSR of the Arctic-alpine realm is predicted to decrease by 15%–47% by 2100 (Figure 2). High TSR regions (≥100 species) are currently found throughout the Scandes but will also shrink, disappearing completely from the Northern Scandes in RCP 8.5 (see Supporting Information Appendix S4).

Current range size is highly variable between species, from 1,235 km^2 to >465,000 km^2 (see Supporting Information Appendix S1). Species vulnerability manifests as predictions of range contraction for over 98% of the species (Figure 3b; see Supporting Information Appendix S5). The mean range contraction averaged across all species ranges from 60% to 92%, depending on climate scenario. We predict that ≥87% of the studied species will be classified as at least VU by the year 2100 (see Supporting Information Appendix S5). Between 20 and 133 species are predicted to be classified as CR (see Supporting Information Appendix S1) and become more restricted to the southern area of the realm via predominantly south-westerly range centre shifts (Figures 3 and 4). Here, 1%–9% of the species are projected to lose all suitable habitat in Fennoscandia by 2100, depending on climate scenario (Figure 3b: see also Supporting Information Appendix S5). No suitable habitat remains in any of the future scenarios for two species: *Antennaria nordhageniana*, endemic to the study region; and *Dryopteris fragrans*,

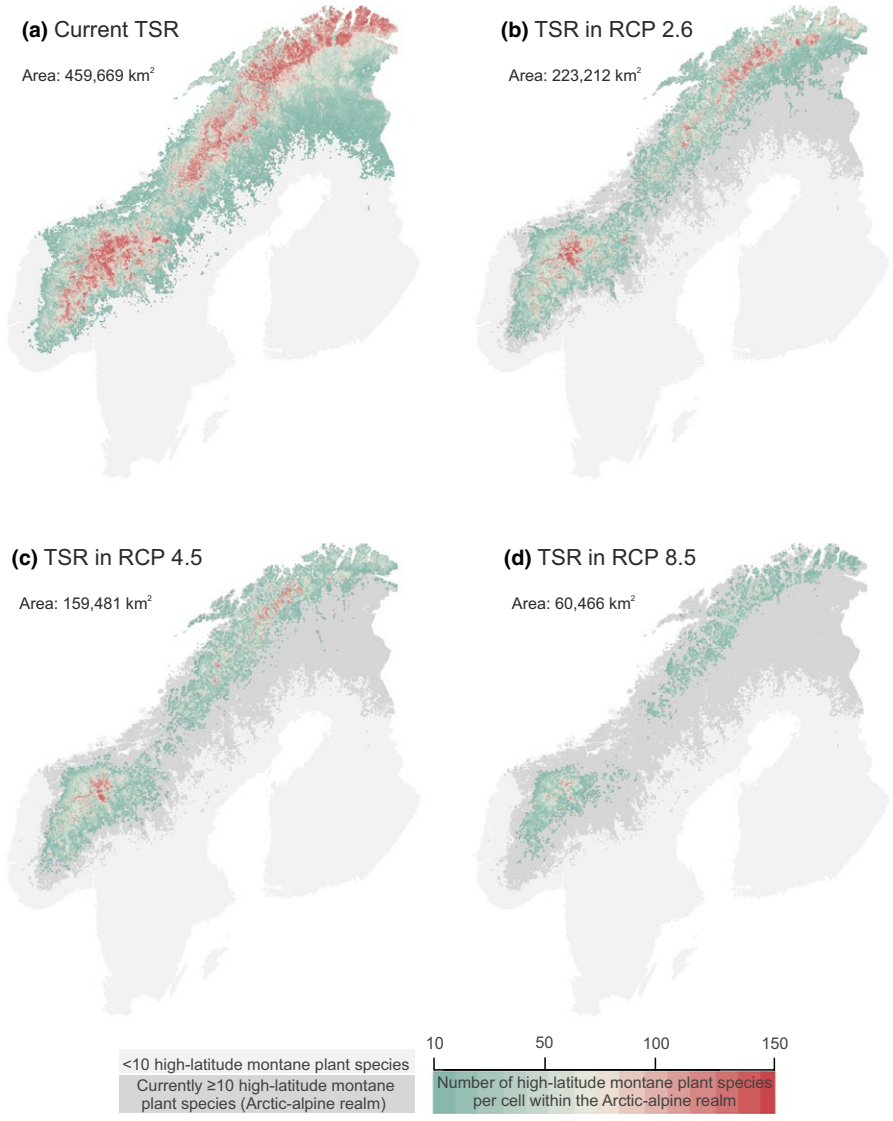

FIGURE 2 Total species richness (TSR) per 1 km × 1 km grid cell within the current Arctic-alpine realm (TSR ≥10 high-latitude and high-altitude vascular plant species) and its area as predicted for the current (1981–2010; a:) and future climate (2070–2099; b: Representative Concentration Pathway (RCP) 2.6; c: RCP 4.5; d: RCP 8.5) in Fennoscandia

rare in Europe (see Supporting Information Appendix S1). Only a few species retain range overlap and gain in all scenarios (Figure 3b).

Non-poleward COG range shifts are projected for 38%–77% of species not predicted to go extinct, increasing with the severity of climate change. The COG range shifts predicted for RCP 4.5 show that the consequences of climate change vary according to biogeographic history (Table 1; See Supporting Information Appendix S6). There were highly significant differences in range loss across the biogeographic history groups (Kruskal–Wallis rank sum test; $p < 0.005$). The average range sizes decrease by 82% for Arctic species compared to a 48% decrease for alpine species (current average range size 142,583 and 156,907 km^2, respectively). The COG range shifts are predominantly southerly for Arctic species but northerly for alpine species (Table 1). A significant difference between the COG shifts of both Arctic and endemic species with alpine species was found in RCP 2.6 (Wilcoxon non-paired rank sum tests; $p < 0.05$). A significant difference between the range change in endemic species and alpine species was also found in RCP 2.6 (Wilcoxon non-paired rank sum test; $p < 0.05$). The species predicted to become EX in RCP 4.5 are Arctic species with a COG in the Northern Scandes (Figure 4; see Supporting Information Appendix S1). The small proportion of the least vulnerable species comprise of Arctic, alpine and Arctic-alpine species with more southerly COGs, shifting in a north-easterly direction (Figure 4). Along with latitudinal shifts, climate change is predicted to cause mainly upslope distribution shifts for ≥98% of species not predicted to disappear, regardless of climate scenario (Table 1). Significant differences in the average elevations across the biogeographic history groups (Kruskal–Wallis rank sum test; $p < 0.05$) became apparent with warming. In particular, there were significant differences between the future average elevations of Arctic species and alpine species (Wilcoxon non-paired rank sum test; $p < 0.05$) as the habitats suitable for Arctic species were found at increasingly higher elevations.

These results are exemplified in the responses of *Ranunculus glacialis* (Glacier buttercup; Arctic-alpine), *Draba nivalis* (Snow whitlowgrass; Arctic), and *Saxifraga adscendens* (Wedge-leaf saxifrage; alpine) to climate change (Figure 5). Range loss is predicted regardless of biogeographic history, but sensitivity appears higher for the

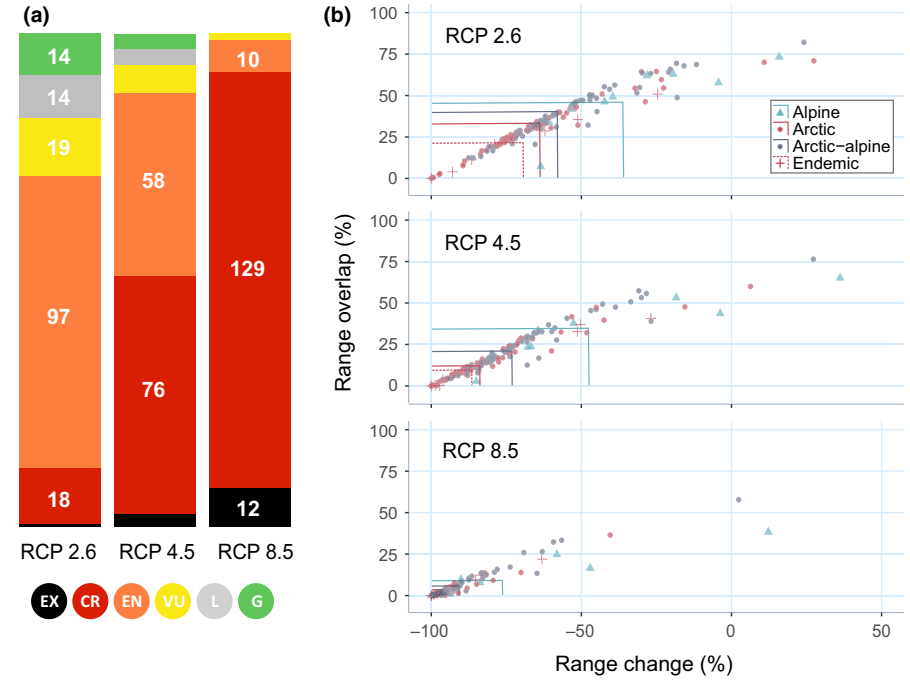

FIGURE 3 (a) Changes in proportions of high-latitude mountainous vascular plant species in each threat category under three climate change scenarios (Representative Concentration Pathway, RCP) between current (1981–2010) and future (2070–2099) conditions. The absolute number of species per threat category is given if that number is >10. Each species is assigned to a threat category according to projected range loss in Fennoscandia: ≥80% = critically endangered (CR); ≥50% = endangered (EN); ≥30% = vulnerable (VU). Species predicted to lose 100% of suitable habitat are likely to become regionally extinct (EX). Species experiencing a range loss <30% are categorized here as L, and species experiencing range gain as G. (b) Range overlap versus relative range size change under three climate change scenarios. The proportion of the current range projected to remain suitable is plotted against the extent of predicted future range expressed as a percentage of current range. Each point represents one of the 164 species modelled. Plot shape distinguishes biogeographical history: alpine, Arctic, Arctic-alpine or endemic. The coloured lines in the plots delineate the averages of range size decline and range overlap per biogeographic history category

Arctic *D. nivalis*. The COGs of their shrinking distributions move south for *D. nivalis* and *R. glacialis*, but for the alpine *S. adscendens* the COG shift is to the north. Mean range elevations move upslope in all scenarios (Figure 5; see Supporting Information Appendix S1).

4 | DISCUSSION

Our results predict substantial reductions in the ranges and richness of mountainous high-latitude flora in Northern Europe. Interestingly, the considerable range changes of individual species appear to be affected by their biogeographic histories. The distributions of these species are projected to shift in unintuitive ways due to differential range contractions (see Loarie et al., 2009; Burrows et al., 2014). Arctic species are forecasted to undergo prominent range loss along with non-poleward range contractions. In contrast, the range centres of alpine species are projected to move poleward. The risk of regional extinction—though moderate and predicted for only one to twelve species depending on climate scenario—was most pronounced for true Arctic and endemic species.

Our findings indicate spatially uneven climate change sensitivity within the Arctic-alpine realm of northernmost Europe (Figure 2). Consequently, the currently continuous Arctic-alpine realm may diverge into two centres of high-latitude mountain flora: one in the Northern Scandes and one in the Southern Scandes. The lower elevations of the central Scandes will become increasingly unsuitable for high-altitude species as the climate warms (Figure 2). Though previous studies suggest high-latitude and high-altitude species to potentially diminish more at southern range margins (e.g., Lesica, McCune, & Ezcurra, 2004) such as around the Southern Scandes, our predictions show a decline especially at northern range margins (see also Gottfried et al., 2012) in the Northern Scandes (Figure 2). Underlying this uneven decline are predictions of warmer growing season conditions especially for the northern extent of the Arctic-alpine realm (>65°N). Our results thus show non-poleward range contractions to be prominent for high-latitude flora (Figure 4). Cooler high elevation regions disrupt the expected poleward movements of species range shifts (Burrows et al., 2014) and consequently draw Arctic species in particular towards the Southern Scandes (see Supporting Information Appendix S6). Though poleward range shifts are still the most frequently reported (see e.g., previous meta-analyses and reviews: Parmesan & Yohe, 2003, Chen et al., 2011; but see also Lenoir & Svenning, 2015), non-poleward shifts have also been detected in Australia (VanDerWal et al., 2013) and in marine environments (Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013).

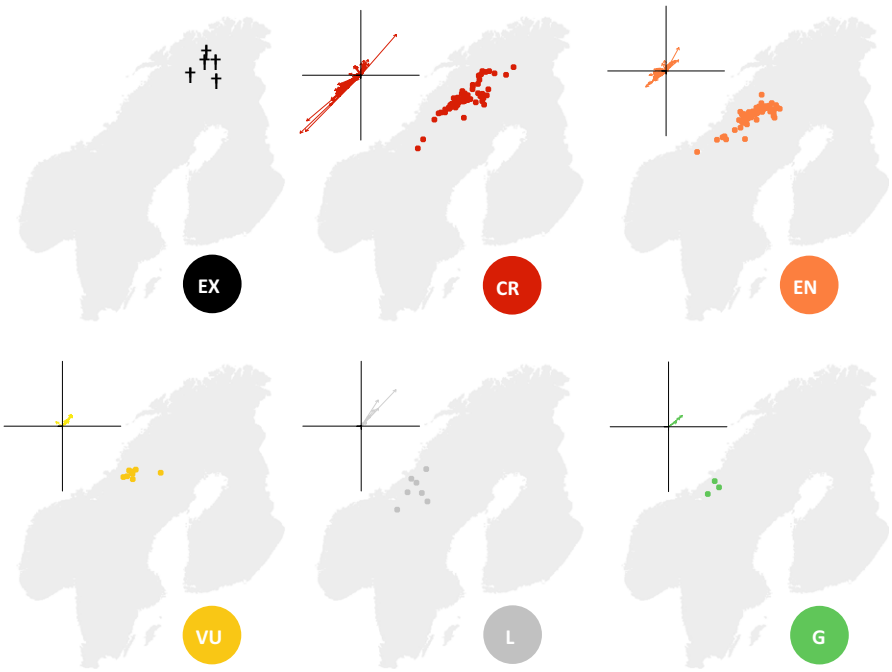

FIGURE 4 Each point represents the current centre of gravity (COG) of a high-latitude and high-altitude vascular plant species grouped according to the IUCN-based categories [proportion of range loss between current (1981–2010) and future (2070–2099) conditions] for Representative Concentration Pathway (RCP) 4.5 (see also Table 1). Each species was assigned to a threat category according to projected range loss in Fennoscandia: ≥80% = critically endangered (CR); ≥50% = endangered (EN); ≥30% = vulnerable (VU). Species predicted to lose 100% of suitable habitat are likely to become regionally extinct (EX). Species experiencing a range loss <30% are categorized here as L, and species experiencing range gain as G. The wind roses summarize the COG shift within each category: the arrows represent the distance and direction of COG change with the axes bars representing a 600 km shift (0, 0–tip)

TABLE 1 The range changes of high-latitude and high-altitude vascular plant species in Fennoscandia between current (1981–2010) and future (2070–2099) conditions for Representative Concentration Pathway (RCP) 4.5

	All modelled species	Arctic	Endemic	Alpine	Arctic-alpine
Number of species	164	66	8	10	80
Range size change (%)	−75 *(−100 to 36)*	−82 *(−100 to 6)*	−76 *(−100 to −27)*	−48 *(−85 to 36)*	−72 *(−100 to 27)*
Range overlap (%)	19 *(0 to 76)*	14 *(0 to 60)*	16 *(0 to 41)*	32 *(3 to 65)*	23 *(0 to 76)*
Euclidean shift (km)	146 *(4 to 822)*	132 *(10 to 822)*	235 *(37 to 697)*	169 *(23 to 526)*	147 *(4 to 425)*
Distance of latitudinal shift (km)	114 *(1 to 624)*	100 *(1 to 624)*	180 *(11 to 555)*	128 *(18 to 366)*	117 *(2 to 321)*
Relative latitudinal shift (km)	−73 *(−624 to 366)*	−78 *(−624 to 90)*	−39 *(−555 to 357)*	54 *(−172 to 366)*	−88 *(−321 to 174)*
Elevational range shift (m)	351 *(−115 to 762)*	382 *(81 to 762)*	320 *(−114 to 617)*	232 *(−34 to 431)*	343 *(103 to 625)*

Note. The average (minimum and maximum are italicized in brackets) range shifts are given for all modelled species and separately for each biogeographic history category; true Arctic; endemic; alpine; or species with both Arctic and alpine biogeographical histories. The changes in range size and overlap (%) refer to the spatial coverage of predictions. The shifts (km) refer to Euclidean shifts between current and future centres of gravity (COG); the distance of absolute latitudinal changes in the COG of a species range; and the relative latitudinal change demonstrates direction with positive values denoting poleward (northerly) COG shifts and negative values denoting non-poleward (southerly) shifts. The elevational range shift (m) describes the change in the average elevation of the species.

FIGURE 5 Contraction of range size and shifts in range centre of gravity (COG; shown as points) of three vascular plant species between current (1981–2010) and future (2070–2099) predictions. *Ranunculus glacialis* (an Arctic-alpine species), *Draba nivalis* (Arctic) and *Saxifraga adscendens* (alpine) to three scenarios of changing climate (Representative Concentration Pathways (RCP) 2.6, 4.5 and 8.5). Species are assigned to a regional Red List threat category according to projected range loss in Fennoscandia: ≥80% = critically endangered (CR); ≥50% = endangered (EN). Range loss <30% is categorized here as L

The current ranges of Arctic species are mainly centred in the Northern Scandes with alpine species relatively more likely to be found in the central or Southern Scandes owing to differences in evolutionary and migration histories (see Supporting Information Appendix S7 for current distributions of species in the four biogeographic history categories; Billings, 1973; Väre, Lampinen, Humphries, & Williams, 2003). Predicted changes for Arctic species contrast with the lesser changes predicted for alpine species that generally have broader climate niches and better adaptive abilities (see Wasof et al., 2015). Similar trends have been observed in the European Alps, where the more thermophilic species benefit from climatic warming whereas cold-adapted species are in decline (Rumpf et al., 2018). The effect of biogeographic history on sensitivity is particularly evident in the optimistic climate scenario (Figure 3b). In the more pessimistic scenarios, stronger climate change impacts may override biogeographic history in affecting species ranges. However, the prominent warming and loss of Arctic-alpine habitat predicted for the northernmost (>68°N) regions of continental Europe is predicted to lead to a disproportionate climate change sensitivity of true Arctic species compared to alpine species (Table 1 and Figure 3b).

A majority of the studied species are predicted to shift their ranges upslope (Table 1; Chen et al., 2011; Klanderud & Birks, 2003; Lenoir et al., 2008; Steinbauer et al., 2018). This could potentially minimize dispersal limitation as the distance between different thermal and vegetation zones are shorter along elevational (than latitudinal) gradients (Körner, 2007). However, the shifting of future suitable habitats to higher elevations is predicted to subsequently also force latitudinal range movements in order to occupy the taller mountains within this landscape. In a warmer future, it is the Arctic species ranges in particular that will need to rise higher—and thus potentially shift further South—to find suitable habitat (Table 1). Underlining the importance of the altitudinal extension and topographic heterogeneity (Elsen & Tingley, 2015; Luoto & Heikkinen, 2008) provided by these upslope shifts to mountainous regions such as the Southern Scandes is that species' dispersal to the North is limited by the Arctic Ocean (Figure 1).

The non-poleward shifts of Arctic species isolate their populations from main distribution areas (see Supporting Information Appendix S6). As this would have potentially significant consequences from genetic and conservation perspectives (Kadmon & Allouche, 2007; Young, Boyle, & Brown, 1996), the northernmost populations of Arctic and endemic species should be highlighted for future conservation decisions. Conservation priorities could focus on assessing the level of local risk or, reversely, locating potential northern refugia for the persistence of the most threatened populations and species as outlined here. As the highest elevations are likely to be increasingly central for biodiversity and provide refugia for species to migrate to as the climate changes (e.g., Randin et al., 2009, Keppel et al., 2012), additional insights into the predicted suitable areas in the Southern Scandes are needed to evaluate how accessible they are for at-risk species and whether other factors such as land use might influence future vulnerability assessments.

Application of the IUCN Red List criteria to our range projections shows that many of the studied species may become severely threatened within this region by the end of this century (Figure 3a). Our predictions of regional extinction are on the more modest side of previous estimates for Fennoscandia predicting more than ten northern or Arctic species to face extinction based only on climatic factors (Sætersdal, Birks, & Peglar, 1998). The risk of local extinction due to range contraction (Thomas et al., 2004) could, however, be further amplified as local stochastic events (such as disturbance, droughts, or disease) can then effect a larger proportion of a species' total population (Thuiller et al., 2005). Furthermore, as species' ranges contract (Figure 5), shifts to newly suitable areas may become more limited and consequently less likely to be realized (Huntley, Collingham, Willis, & Green, 2008).

As modelling and climate scenario uncertainties cannot be fully accounted for (e.g., Elith & Leathwick, 2009; Pereira et al., 2010) our results are not to be taken as precise forecasts. Future range changes are likely to be influenced by other factors than changing climate and topo-geological parameters (e.g., dispersal [Bateman, Murphy, Reside, Mokany, & VanDerWal, 2013]), or biotic interactions (Callaway et al. 2002) not included due to the resolution used [Araújo & Rozenfeld, 2014]). The Red List approach and the 80-year time scale used here may have limitations when evaluating the consequences of slow, persistent threats such as climate change, possibly causing overestimation of species loss (Akçakaya, Butchart, Mace, Stuart, & Hilton-Taylor, 2006; Pacifici et al., 2015; Thuiller et al., 2005). Despite these limitations and possible underestimations of species persistence, the general future patterns predicted across the region may stand.

Our findings demonstrate the significance—and some unexpected effects—of climate change on Arctic-alpine plants and biodiversity. The responses of Arctic-alpine species are reliant not only on the predicted level of warming and regional topography but also biogeographic history. Responses thus deviate from simple poleward-and-upslope contractions which may have significant impacts on the future evolution of these species and efforts to conserve them.

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DATA ACCESSIBILITY

Most of the species occurrence data used here are available from the national species data banks of Finland (http://www.laji.fi/en), Sweden (https://www.artportalen.se/) and Norway (http://www.artsdatabanken.no/), and from the Global Biodiversity Information Facility (GBIF; http://www.gbif.org). Please contact the BioGeoClimate Modelling Lab (see information below) for access to the final projected species distribution surfaces.

The climate observation data is available from the European Climate Assessment & Dataset (Klok & Klein Tank 2009) and the future projections (based on 23 global climate models) from the Coupled Model Intercomparison Project phase 5 (CMIP5) archive (Taylor et al., 2012).

The digital elevation model (DEM) used to make the TOPO variable was combined from national DEMs provided by the land surveys of Finland, Sweden, and Norway. The GEO variable was reclassified from a collated 1:1M geological dataset of the Fennoscandian shield region obtained from the Geological Surveys of Finland, Sweden and Norway.

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BIOSKETCH

The BioGeoClimate Modelling Lab (at the Department of Geosciences and Geography, University of Helsinki) is focused on the spatiotemporal modelling of Earth systems, particularly patterns, processes and interactions concerning biogeography, geomorphology and climatology. Group web page: https://www.helsinki.fi/biogeoclimate.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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