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Hiding from the climate: Characterizing microrefugia for boreal forest understory species

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Abstract

Climate warming is likely to shift the range margins of species poleward, but fine-scale temperature differences near the ground (microclimates) may modify these range shifts. For example, cold-adapted species may survive in microrefugia when the climate gets warmer. However, it is still largely unknown to what extent cold microclimates govern the local persistence of populations at their warm range margin. We located 99 microrefugia, defined as sites with edge populations of 12 widespread boreal forest understory species (vascular plants, mosses, liverworts and lichens) in an area of ca. 24,000 km² along the species' southern range margin in central Sweden. Within each population, a logger measured temperature eight times per day during one full year. Using univariate and multivariate analyses, we examined the differences of the populations' microclimates with the mean and range of microclimates in the landscape, and identified the typical climate, vegetation and topographic features of these habitats. Comparison sites were drawn from another logger data set ($n = 110$), and from high-resolution microclimate maps. The microrefugia were mainly places characterized by lower summer and autumn maximum temperatures, late snow melt dates and high climate stability. Microrefugia also had higher forest basal area and lower solar radiation in spring and autumn than the landscape average. Although there were common trends across northern species in how microrefugia differed from the landscape average, there were also interspecific differences and some species contributed more than others to the overall results. Our findings provide biologically meaningful criteria to locate and spatially predict potential climate microrefugia in the boreal forest. This opens up the opportunity to protect valuable sites, and adapt forest management, for example, by keeping old-growth forests at topographically shaded sites. These measures may help to mitigate the loss of genetic and species diversity caused by rear-edge contractions in a warmer climate.

KEYWORDS

cold-adapted species, marginal populations, microclimate, range contraction, range edge, range shift, rear edge, thermal niche

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1 | INTRODUCTION

Climate warming is shifting species' range margins across the globe resulting in considerable impacts on ecosystems and human well-being (Pecl et al., 2017). However, fine-scale temperature differences near the ground (microclimates) may modify these range shifts (Geiger, Aron, & Todhunter, 2012; Lenoir, Hattab, & Pierre, 2017; Suggitt et al., 2018). For example, it has been proposed that retracting cold-adapted northern species may survive in microrefugia when the climate gets warmer (Hylander, Ehrlén, Luoto, & Meineri, 2015; Rull, 2009). Microrefugia are small areas in the landscape with favourable microclimate condition that allow the local persistence of species at their retracting range margin (Ashcroft, 2010; Keppel et al., 2012; 2015). In the context of current global warming, these are typically sheltered microsites (*sensu* Delcourt & Delcourt, 1988) with a particular climate, for example, topographic depressions, river gorges, wind- or sun-sheltered slopes, denser forest stands or higher elevations (Ashcroft, Gollan, Warton, & Ramp, 2012; Dobrowski, 2011; Lenoir et al., 2017). Hylander et al. (2015) suggest that the existence of climate microrefugia depends on species being limited by one or several climate variables and on these climate variables differing between local and regional scales.

Rear-edge populations inhabiting microrefugia do not only add to the regional species richness but can also host unique genetic diversity within species (Nicastro et al., 2013; Provan & Maggs, 2011; Rebelo et al., 2013). They are therefore disproportionately important for a species' capacity to evolve and cope with environmental change (Abeli, Vamosi, & Orsinego, 2018; Hampe & Petit, 2005). Yet, many rear-edge (low-latitude, low-altitude) populations of cold-adapted species are threatened by global warming (Thuiller, Lavorel, Araújo, Sykes, & Prentice, 2005), and the challenge is to locate, manage and protect microrefugia where rear-edge populations can persist. Thus, identifying climate microrefugia has important implications for conservation planning under a warming climate (Keppel et al., 2012, 2015), especially where human land use has the potential to destroy or increase the number of "safe islands" for threatened species (Serra-Diaz, Scheller, Syphard, & Franklin, 2015). In spite of their potential conservation importance in a climate-change context, it is still largely unknown if the persistence of populations in microrefugia at their warm range margin is driven by a cold microclimate or some other factor (Vilà-Cabrera, Premoli, & Jump, 2019).

It has often been suggested that species at their warm range margin are limited by biotic interactions, such as competition, and not abiotic conditions (Austin, 1990; Brown, Stevens, & Kaufman, 1996; Normand et al., 2009). If so, frequent disturbance via removal of warm-adapted competitors would be one possible mechanism enabling the persistence at warm-edge margins (Gentili et al., 2015; Lenoir, Gégout, et al., 2010). Such microrefugia would not necessarily be colder than the surrounding landscape. Northern species at their warm edge might also survive at sites with locally harsher climate conditions where southern, more competitive species do not thrive, for example, in places with a shorter growing season (Hylander et al., 2015; Kollas, Körner, & Randin, 2014), later snow melt, lower winter

minimum temperature (Ashcroft, French, & Chisholm, 2011) or later spring frost (Kollas et al., 2014). A systematic review by Cahill et al. (2014) seems to suggest that even at their warm-range margins, species might often be directly limited by abiotic factors, for example, by heat or drought. Warm-edge populations might be locally favoured by low summer maximum temperatures, because they have reduced heat or drought tolerances, or high climate stability, because climate fluctuations increase the extinction risk for small edge populations (Ashcroft et al., 2012).

Regardless of the actual mechanism, the characteristics of the environments where rear-edge populations may persist are largely unknown. Various attempts have been made to locate potential microrefugia by delineating certain abiotic environments, using microclimate variables and topographic features (Ashcroft et al., 2012; Maclean, Suggitt, Wilson, Duffy, & Bennie, 2016), assessing also the vegetation structure (Schut et al., 2014), locating isolated rear-edge populations outside their main range (Niskanen, Luoto, Väre, & Heikkinen, 2016) or identifying locations where one or several cold-adapted species are predicted to persist under future warming scenarios (Baumgartner, Esperón-Rodríguez, & Beaumont, 2018; Meineri & Hylander, 2017). Investigations of microrefugia are often constrained by the spatial or temporal resolution of the available climate data and the inherent collinearity of climate variables. In recent years, advances in remote sensing and availability of affordable climate microsensors have allowed microclimate modelling at very small spatial and temporal scales and the development of high-resolution climate grids (Bramer et al., 2018). Based on such microclimate models, several studies suggest that topographically complex environments, that is, those with a high microclimate variation, can buffer climate-driven extinctions of both plants and insects (Serra-Diaz et al., 2015; Suggitt et al., 2018). Even in seemingly homogeneous steppes, vegetation structure can create thermal refugia on metre scales (Milling et al., 2018). Many microrefugia studies have been performed in mountain, tundra or other open environments, whereas the characteristics of lowland forest microrefugia are still poorly known. In highly managed forests, as along the southern margin of the boreal zone, potential microrefugia may be created or destroyed by forestry activities (e.g. clear cutting, thinning and planting of certain tree species) due to the relatively high influence of canopy cover, stand density and forest structure on near-ground temperatures (Greiser, Meineri, Luoto, Ehrlén, & Hylander, 2018; Jucker et al., 2018; Kovács, Tinya, & Ódor, 2017). However, there is limited knowledge about the role of forest management on microclimate and about the factors influencing survival of species at their warm range margins.

In this study, we aim to characterize climatic microrefugia inhabited by warm-edge populations of boreal understory species in central Sweden. We performed univariate and multivariate analyses on pooled data of 99 populations of 12 species, assuming a similarity across species in terms of microclimate preferences (Abeli et al., 2018; Keppel et al., 2012), since all species share the same boreal understory habitat and have a similar northern distribution with declining frequency in the focal study area (Figure 1). We were particularly interested in identifying similarities among species as such patterns would provide a way to develop more general tools and advice for

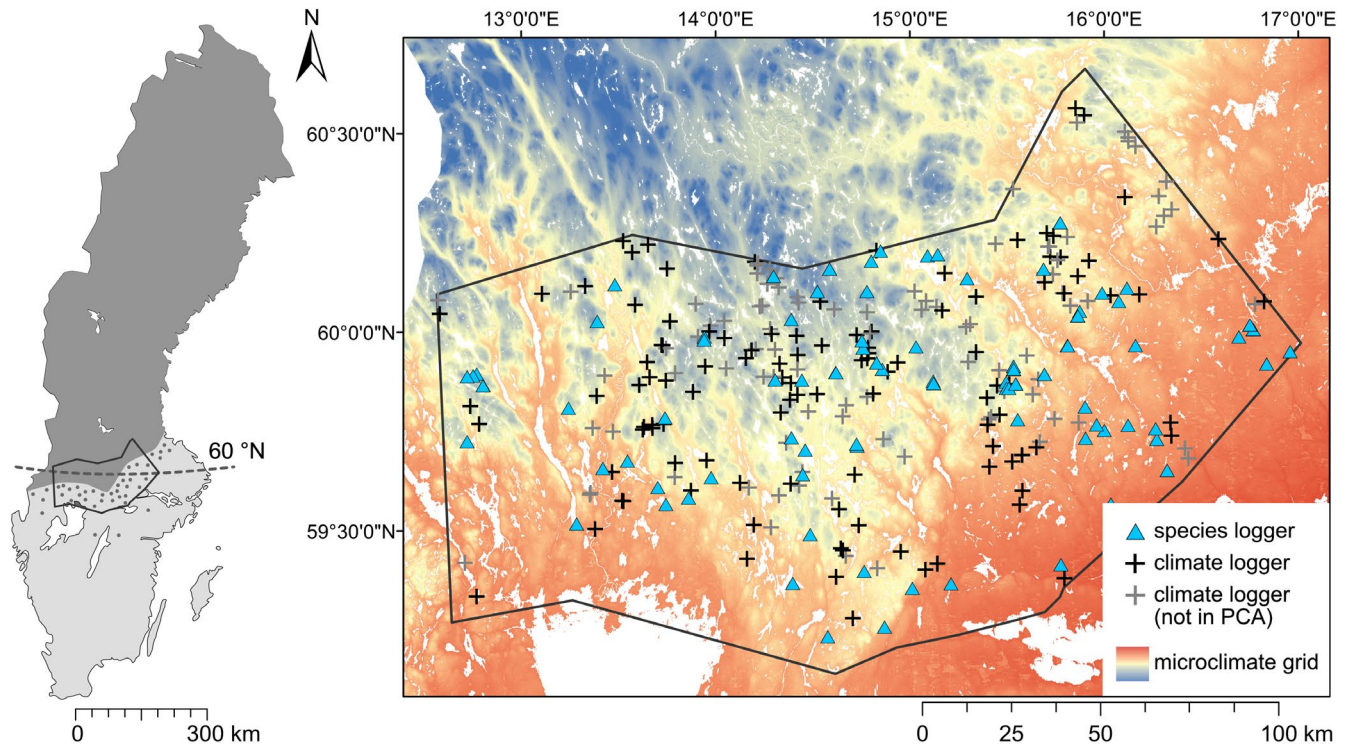


FIGURE 1 Left: Generalized distribution of the studied boreal understory species in Sweden showing in dark grey the main range and the southern range margin with isolated edge populations; Right: study area with 99 warm-edge populations of species with a northern distribution (Δ) and 203 sites representing the full range of microclimates in the area (+). Only locations, for which the full microclimate record was available, could be used in one of the principle component analyses (PCAs; Figure 3b) and are indicated in the map. Background climate grid from Meineri and Hylander (2017)

conservation planning and forest management. However, since the species vary in life form, substrate and specific forest habitat, they are also likely to differ in several respects, which is why we also test for interspecific differences.

We ask:

1. Do the microclimates inhabited by the rear-edge populations differ from the average microclimate in the landscape?
2. Do climate preferences differ among species?
3. Do forest and topography features differ between the microrefugia (places inhabited by rear-edge populations) and the average landscape?

By answering these questions, we also aim to provide a basis for concrete actions, by which forest management and conservation can attenuate climate change-driven biodiversity loss.

2 | MATERIALS AND METHODS

2.1 | Study area and species

Our study area was a managed boreal forest landscape in central Sweden (59°–61°N and 12.5°–17°E; Figure 1), covering large parts of the sharp transition zone ‘Limes Norrlandicus’ (Fransson, 1965),

where many northern and southern species have their low- or high-latitude range margin (Rydin, Snoeijis, & Diekmann, 1999; Sjörs et al., 1965). The area spans in total 24,000 km² of which ca. 65% is forested land. The canopy layer in the forests is dominated by spruce and pine with occasional deciduous elements, whereas ericaceous dwarfshrubs, mosses and lichens dominate the field layer. Forest management has a long history in Sweden and has removed almost all primary forests (Östlund, Zackrisson, & Axelsson, 1997). Since the early 20th century, clear-cutting has been the dominating management system (Nilsson & Wardle, 2005). The climate is cold temperate and humid (600–800 mm/year) with precipitation falling mostly during the summer; in winter the precipitation often falls as snow. Mean annual temperature ranges from 5°C in the south and southeast to 3°C in the north (SMHI, 2017).

To investigate whether northern forest understory species at their warm range margin are found in certain cold microclimates, we located 99 rear-edge populations of 12 species (Figure 1). In a first step, we created a list of forest understory species with vascular plants, mosses, liverworts and lichens (excluding epiphytic or crustose lichens), which disappear or decline clearly in central Sweden around 60°N (Table S1). The list was further narrowed down to species that were identifiable in field and had at least 10 reported occurrences in our study area (further details on species selection in Appendix A). The 12 species selected for the study represent different life forms, substrates and habitats, and include species growing on rock surfaces or soil and species preferring wet or mesic forests (Table S1; Figure 4). Occurrences were

downloaded from a citizen science database (<https://artportalen.se/>, all observations up to beginning of 2015). We selected specific locations of a chosen species to be as well distributed across the entire area as possible. However, sometimes locations of two different species were close to each other (min. distance = 13 m, seven population pairs were closer than 25 m, 12 population pairs were closer than 50 m). We included all species locations in the analysis as independent data points.

Within each of the 99 populations we installed a logger (micro-sensor, MaximIntegrated iButton, type DS1921G-F5 or DS1922L) at ca. 5–10 cm height that measured and recorded the temperature eight times per day (3:00, 6:00, 9:00, etc.) during 12 months, from 1 September 2015 to 31 August 2016. The logger was shielded from direct sunlight and rain by an inverted plastic cup taped to a wooden stick. Additionally to microclimate, we recorded canopy cover, basal area and the soil moisture class of each site, using vegetation of the field layer as an indicator of moisture. We also recorded the population size (nr. of individuals/tussocks or cover in dm²) and the coordinates of each population using a handheld GPS (Garmin 64s).

2.2 | The microclimate data

We used two types of microclimate data, map data and logger data, to compare conditions at sites where species occurred with conditions across the entire landscape.

The map data were drawn from high-resolution microclimate maps that were produced from 203 systematically placed loggers to capture the full range of possible microclimates in the landscape. We created maps of maximum and minimum temperature for each month, except for the mid-winter, by relating the logger data to a number of well-known climate-forcing factors available in gridded layers at 25 m resolution such as elevation, relative elevation, forest basal area, topographic wetness index, solar radiation and distance to waterbodies. We used general linear models, where all six environmental variables were retained in the final models (for more details, see Greiser et al., 2018). The logger data consisted of the 99 loggers at the species sites and the 203 landscape loggers that were used to create the microclimate maps.

While the landscape loggers were placed deliberately so that they capture the full range of possible microclimates, they do not necessarily reflect the frequencies of certain temperatures in the landscape. Thus, the estimated means of the climate variables derived cannot be compared with the means of the species logger data. With the map data, we can better estimate means, thereby test if populations are occurring non-randomly within the landscape, and if so how much the microclimate at sites with northern species occurrence differs from the landscape average. However, the map data are modelled and averaged over a 25 m grid cell and provide a less accurate estimation of variances since the most extreme values, that might be typical for microrefugia, are under-represented (for details, see Greiser et al., 2018). Finally, with the logger data set, we could investigate the effect of climate variables that were unavailable in a mapped form, for example,

winter temperatures and time of snow melt. We therefore decided to compare microrefugia occurrences and background data using these two complementary data sets.

First, for the map data we drew 10,000 random points from the maps and compared them with the cell values of the 99 species population sites. We used the following mapped microclimate variables: monthly averages of daily minimum and maximum temperatures from June to December 2015 and April to May 2016 (=18 variables, labelled ' T_{max1} ' for maximum temperature in January, ' T_{min4} ' for minimum temperature in April a.s.o.).

Secondly, we compared the measured microclimate data from the loggers that were assembled in field (landscape loggers and species loggers). The overlapping microclimate records of the landscape loggers and the species loggers comprised 12 months. We used the following microclimate variables: monthly averages of daily minimum and maximum temperatures from September 2015 to August 2016 ($T_{min9} \dots T_{max8}$), monthly average of daily variation (difference between daily T_{max} and T_{min}) for April, July and September (T_{var4} , T_{var7} , T_{var9}), the difference between minimum temperature of the coldest month and maximum temperature of the warmest months (annual range, corresponding to 'BIO7' in Fick & Hijmans, 2017), date of last snow melt (snow melt) and growing degree days (GDD) with a base of 5°C. The date of last snow melt was calculated from the fluctuation strength (SD) of daily maximum temperatures of three consecutive days. An SD of lower than 0.5 was interpreted as snow cover. Due to failed loggers, complete records of all microclimate variables were available for 110 of 203 comparison sites and for 88 of 99 species sites.

The first exploratory analyses were done using the full set of available microclimate variables. However, since climate variables are often strongly correlated, we focused in later parts of the analyses particularly on a handful of variables, which we hypothesized to play a role for climate microrefugia (Table S2). We expected species to occur at sites with colder summer maximum temperatures (T_{max6} , T_{max7} , T_{max8}) and more daily and seasonally stable microclimates (annual range), because they may not tolerate heat, drought or large temperature fluctuations. We also expected species to occur under conditions that exclude less tolerant southern competitors, for example, colder winter and spring minimum temperatures (T_{min1} , T_{min4}), and in places with fewer GDD and later snow melt dates (snow melt). Globally, minimum temperatures are rising faster than maximum temperatures (Hughes, 2000) and in Sweden, winter mean temperatures have experienced the largest absolute increase (www.smhi.se) compared to the other seasons; thus, winter conditions (T_{min1} , snow melt) could be particularly important for climate refugia (Ashcroft, 2010; Ashcroft, Chisholm, & French, 2009).

2.3 | Statistical analysis

2.3.1 | Microclimate characteristics

First, we tested the difference between the available microclimates (500 of 10,000 background points due to computation limitations) and

the occupied microclimates (99 population points) with a permutational multivariate analysis of variance (PERMANOVA, function *adonis()* from R package *vegan*; Oksanen et al., 2012), which is distribution free and can handle many collinear variables (Anderson, 2001). This analysis was performed on a Euclidean distance matrix of standardized (scaled and centred) microclimate data; tests of significance were performed using 999 unrestricted permutations. In order to identify, along which microclimate gradients the populations differ most from the available microclimates, we compared the standardized PERMANOVA coefficients. Coefficients were also back-transformed to absolute mean differences between the species and the random background points ($\text{std.coeff} \times SD \times 2$). We then quantified the significant differences (effect sizes) between the species locations and 10,000 random points for each single microclimate variable with two-sample *t* tests. Significance levels were Bonferroni-corrected to counteract the problem of multiple comparisons. This procedure corresponds to the standard procedure of ANOVA followed by a post hoc pairwise comparison. *t* Tests were run on untransformed data and *p* values were checked to be robust to lower sample sizes (1,000 or 100 instead of 10,000 background points).

With two complementary principle component analyses (PCAs), we visualized the largest microclimatic gradients in the landscape, the distribution and range of the available microclimatic space and where the populations are placed in this space. The first PCA was done on the map data (99 species location vs. 10,000 random background points describing the distribution of available microclimates), whereas the second PCA was done on the logger data (88 species locations vs. 110 climate loggers describing the full range of climates). All data were scaled and centred prior to ordination and the PCAs were performed with the *prcomp()* function from the R package *vegan*.

2.3.2 | Interspecific differences

Second, in order to test, if the occupied microclimates differ across species due to their different ecological requirements, we visualized the species in the second PCA and performed a PERMANOVA test only on the scaled and centred species logger data. For this analysis, we excluded species with fewer than six locations, leaving eight species. We used simple boxplots to show the differences across species for our focal microclimate variables ($T_{\text{max}8}$, $T_{\text{min}4}$, $T_{\text{min}1}$, *GDD*, annual range and snow melt).

2.3.3 | Non-climatic characteristics

Third, since the analyses described above indicated that microrefugia differ from the landscape average regarding certain microclimatic variables, we also wanted to identify what kind of habitats these sites are, that is, what other forest and landscape features were characteristic for them. As a site can be cold for many reasons, we investigated the features that, according to Greiser et al. (2018), are typically linked to low $T_{\text{max}8}$ and $T_{\text{max}10}$ (selected based

on the PERMANOVA result): forest basal area (vegetation shading), solar radiation in October (topographic shading), log-transformed relative elevation within 500 m (cold air pooling) and altitude (lapse rate). These features were tested for their differences between the species sites and 10,000 background points with two-sample *t* tests and a Bonferroni correction of the *p* values.

2.3.4 | Microrefugia potential map

Lastly, for the species with the microclimate niches that were consistently deviating from the landscape mean, we produced a high-resolution map of microrefugia potential. This map combines the two microclimatic features with the largest influence in the previous PERMANOVA analysis and which were available in a mapped form: low $T_{\text{max}8}$ and low $T_{\text{max}10}$. Both variables were normalized to range from zero to one, transformed to positive variables (i.e. the more the better for northern species microrefugia) and averaged for each 25 m grid cell. Thereby, we obtained a map with pixels ranging from 0 to 1, where 1 suggests a high microrefugia potential, that is, a high suitability for northern species. All analyses were done in R version 3.4.3 (R Core Team, 2017).

3 | RESULTS

3.1 | Microclimate characteristics

The microclimates (as a composition of 18 different variables) occupied by all the investigated northern species together differed significantly from the available average microclimates in the landscape (map data, PERMANOVA; $F_1 = 34.47$; $p = .001$). Northern species occurred at sites with lower maximum temperatures and slightly higher summer minimum temperatures. Maximum temperatures, especially in October and August, contributed most to the PERMANOVA difference (Figure 2). However, absolute temperature differences across sites are not as large in October as they are in the summer months. Therefore, all summer month maximum temperatures rank higher, when the PERMANOVA coefficients are back-transformed to absolute mean differences (Figure 2). These back-transformed coefficients correspond roughly to the effect sizes yielded by the univariate pairwise comparisons (*t* tests). Pairwise differences that were larger than 0.5°C were significant for minimum temperature in August (difference of 0.6°C) and all maximum temperatures except in November and December (Figure 2; Table S3; Figure S1). The absolute differences between the species mean and the average landscape mean for maximum temperatures ranged from 1.0°C in October to 2.7°C in August. Other significant effect sizes were negligible small, that is, below 0.5°C and considered biologically irrelevant with respect to the noise in the data (Table S3; Figure S1).

In the PCAs visualizing the range and distribution of microclimates in the landscape, the species sites versus the background points and climate logger sites, respectively, were shifted along both the first and the second PCA axis. The largest variation in both PCAs was found

along gradients of minimum and maximum temperatures during the warm months (Figure 3; Figures S2 and S3). Many of the variables forming the first principle component axis were highly correlated with

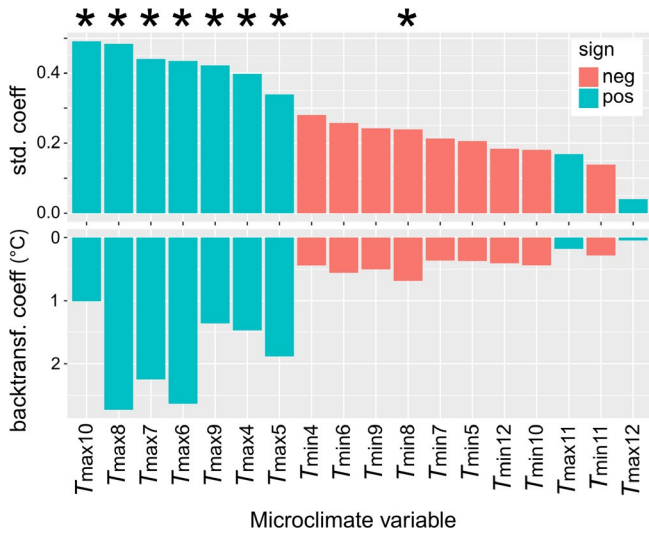


FIGURE 2 PERMANOVA (adonis) coefficients, map values. (Above) Standardized coefficients and (below) back-transformed coefficients corresponding to mean temperature differences between northern species locations and 500 random locations. Asterisks mark variables that were significant in the two-sample *t* tests with Bonferroni correction and that had an effect size larger than 0.5°C (Table S3). Sign = direction of coefficient: negative or positive, $T_{\max10}$ = maximum temperature in October, $T_{\min4}$ = minimum temperature in April, a.s.o.

each other (overlapping and parallel arrows in Figure 3). The PCA on the logger values equals largely the PCA on the map values, but includes additional microclimate variables, for example, daily and seasonal climate fluctuation (PC1), snow melt (PC2) and winter conditions (PC3; Figure S3). When displaying the first two PCA axes, the northern species are shifted towards cooler maximum temperatures, warmer minimum temperatures, lower daily and seasonal variation and later snow melt. There was no differentiation of the species along the third axis ($T_{\min1}$, $T_{\max1}$) of the PCA based on the logger values. Compared to the distribution of available microclimates, the species climate space comprises quite a few exceptional climates (blue points at the edge of the red point cloud, most pronounced in Figure 3b). There were many sites with microclimate combinations that were not captured by the climate logger data set, though these were deliberately sampled to cover as much variation as possible along the examined gradients.

3.2 | Differences among species

The species inhabited significantly different microclimates (PERMANOVA; $F_7 = 3.26$; $p = .001$; Figure 4; Figure S5). *Barbilophozia lycopodioides*, *Nephroma arctica* and *Lactuca alpina* had their multivariate centroids on the first two principal component axes at sites with later snow melt, colder summer maximum temperatures and high annual climate stability. *Carex loliacea* and *Sphagnum wulfianum* inhabited a larger range of microclimates and were more spread along the first two PCA axes. *Galium triflorum* differed as much from the average climate as *L. alpina*, *B. lycopodioides* and *N. arctica* but

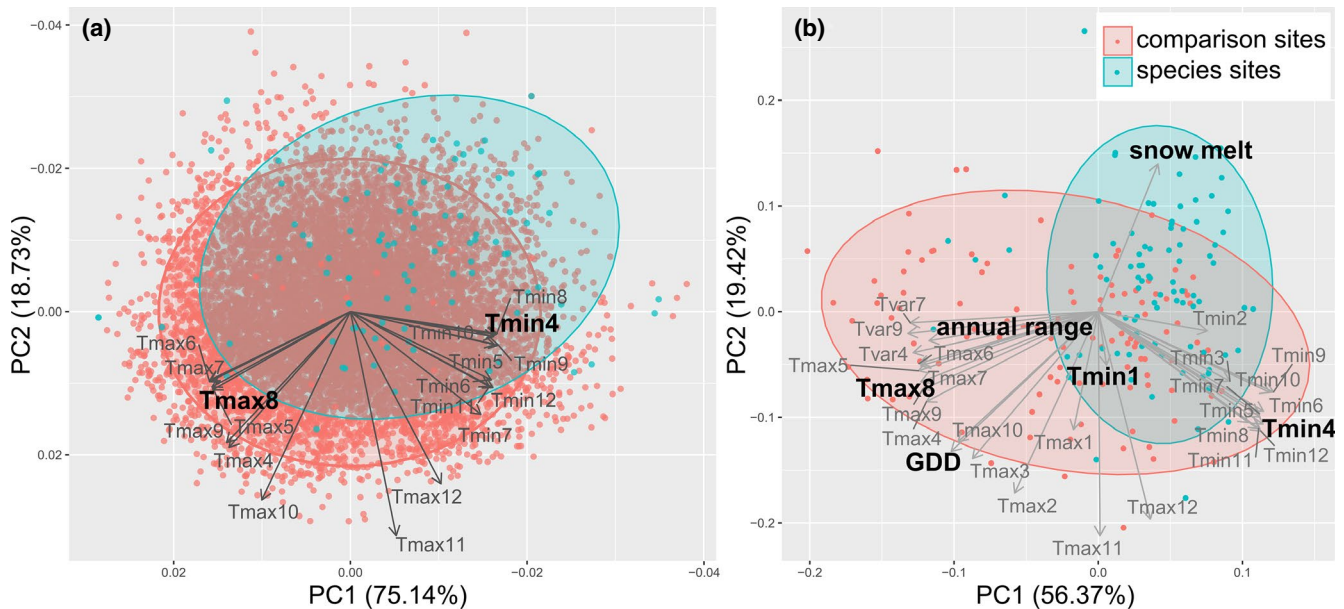


FIGURE 3 Principle component analysis (PCA) on a number of microclimate variables. Blue: 'microrefugia' hosting rear-edge populations; red: comparison sites (left: 10,000 random background points, right: 110 logger locations). Concentration ellipses are drawn around the 0.95 level of a multivariate *t*-distribution. Note that ellipses of the mean SE would be separated, but this way of displaying identifies the general distribution of the point cloud with most occurrences inside the ellipses. (a) PCA map values. The proportion of variance explained by PC1 and PC2 was 75% and 19% respectively. The other axes did not contribute substantially (<3% for PC3). (b) PCA logger values. The proportion of variance explained by PC1, PC2 and PC3 was 56%, 19% and 9% respectively

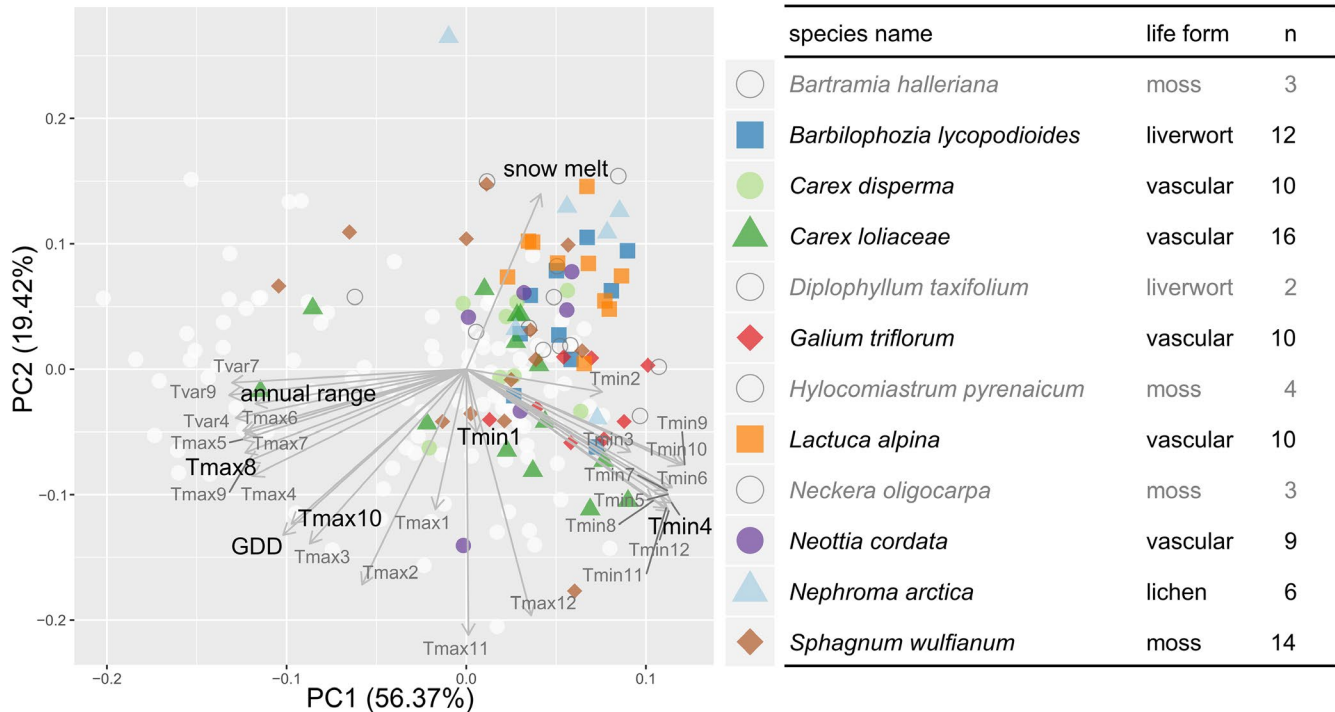


FIGURE 4 Same principle component analysis (PCA) as in Figure 3b, but displaying species with more than six observations (visited populations, n) in colours and the climate loggers in white. Species with fewer than six observations are symbolized with an empty circle in the PCA and marked grey in the table beside

inhabited distinct different microclimates with very cold mid-winter minimum temperatures, high summer minimum temperature, but early snow melt dates (Figure 4; Figure S5).

3.3 | Non-climatic characteristics

Northern species occurred on average on sites with higher forest basal area and lower solar radiation in October compared to the landscape average (Figure 5; Table 1; Figure S4). There was no overall pattern for altitude and relative elevation, but there were also substantial differences among species. For example, *L. alpina* and *B. lycopodioides* occurred on higher absolute and relative altitudes, whereas *Carex disperma*, *C. loliaceae*, *G. triflorum* and *Neottia cordata* occurred at lower sites (Figure S6).

Excluding clear cuts and very young forests had no effect on the main patterns identified in all the analyses above, only on effect sizes. For example, the average difference in August maximum temperature for the species locations and 10,000 background points was 2.4°C instead of 2.6°C (Appendix C).

4 | DISCUSSION

We aimed at characterizing microrefugia for boreal understory species in order to study the potential of forest management and conservation to slow down climate change-driven extinctions at species' rear edge. Using empirical data from 99 edge populations of 12 species

representing different taxonomic groups, we were able to show that sites hosting rear-edge populations were places with special microclimates (e.g. with cooler summer maximum temperatures) and special landscape features (topographically shaded places and denser forests) compared to the average surrounding landscape. The characterization of the microclimate niche was overall consistent between comparisons based on logger data and comparisons based on microclimate maps. Within the climate envelope occupied by the northern species, microclimatic niches differed among species with some species deviating more from the landscape average than others did. Overall, our results illustrate how it is possible to move from a very broad conception of microrefugia as occurring in areas with high microclimate complexity (Suggitt et al., 2018) to a more explicit characterization of these habitats. Such characterization provides a valuable tool for integrating microrefugia into landscape planning, adaptive forest management and biodiversity conservation. Below, we discuss some possible mechanisms underlying the observed climatic properties of microrefugia, the similarities and differences among species and possible actions for conservation and forest management to mitigate biodiversity loss.

4.1 | Northern species at their rear edge occur in distinct microclimates

Microrefugia, that is, places hosting warm-edge populations, were characterized by on average colder maximum temperatures (mostly in summer and autumn) and warmer summer minimum temperatures.

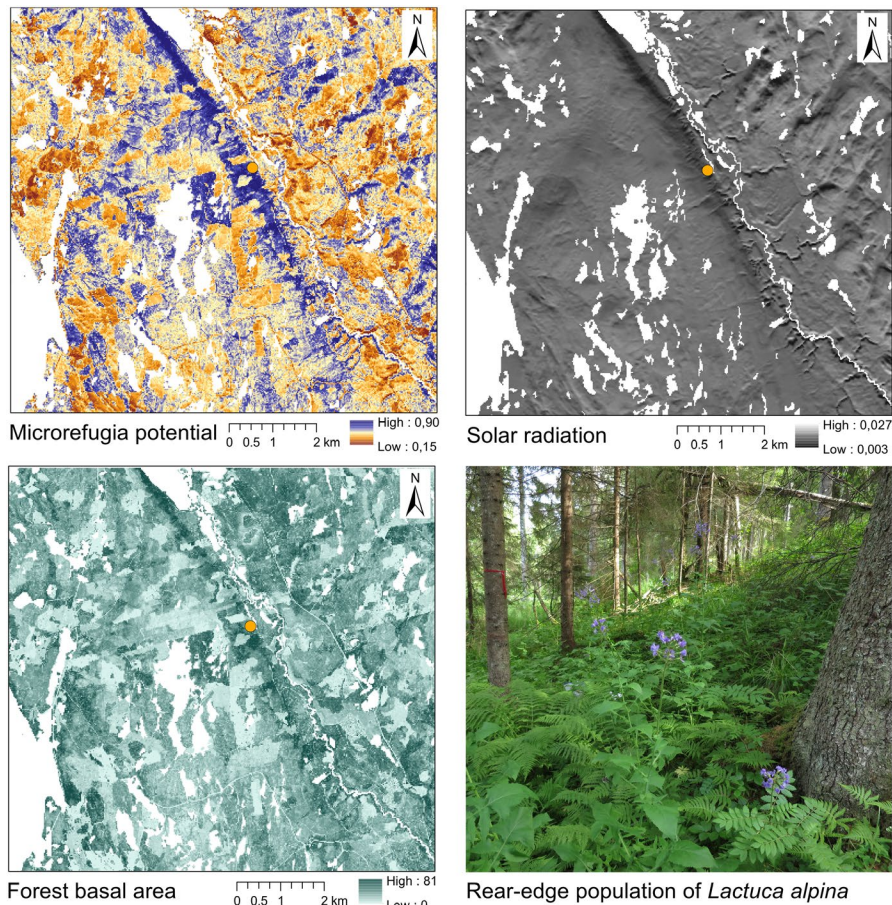


FIGURE 5 Section of the study area with a population of *Lactuca alpina* (orange dot in the maps). Top left: Microrefugia potential created by averaging maps of the two most important microclimate variables ($T_{\max 8}$, $T_{\max 10}$) after having normalized them to range between zero and one and after a transformation into 'positive' variables (the more, the better). High values mark sites with high microrefugia potential. The map is likely to be most useful for the species with largest difference from the landscape mean such as *L. alpina*, *Nephroma arctica* and *Barbilophozia lycopodioides*. Top right: Solar radiation in October (MW/m^2). Bottom left: Forest basal area (m^2/ha). Bottom right: Rear-edge population of *L. alpina* in field

Variable	tv	df	p	mean.clim	mean.spec	diff
Basal area [m^2/ha]	-6.805	99.518	<.001	19.41	28.02	8.61
(log) relative elevation [m]	2.179	99.385	.032	2.881	2.657	-0.224
Altitude [m]	-0.715	99.652	.476	180.218	186.783	6.565
Solar radiation October [MW/m^2]	5.164	98.717	<.001	0.014	0.012	-0.001

Note: p Values in bold symbolize significance at the .0125 level, which is the adjusted significance level after Bonferroni correction of multiple comparisons ($p/(\text{no. of tests})$). These landscape features were chosen since they are typically linked to low $T_{\max 8}$ and $T_{\max 10}$ (see Section 2).

The map data confirmed that means of maximum temperatures were lower in the microrefugia than on average in the landscape, and the logger data revealed that microrefugia also occur at the cold end of the maximum temperature gradients. The comparison between the two logger data sets further characterized the microrefugia sites as having higher daily and seasonal climate stability, lower GDD and later snow melt dates. The revealed patterns were not only the effect of clear cuts and young forests, though they extended the microclimate gradients and increased effect sizes. The identified climatic features largely confirm our hypotheses, but leave open the underlying mechanisms for these preferences (e.g. competition exclusion vs.

physiological tolerance). One possible cause of the observed pattern is that rear-edge populations occur in places with lower summer maximum temperatures, avoiding exposure to heat or drought. Another possibility is that southern competing species cannot complete their lifecycle in these places. A global review on upper and lower thermal tolerances of a wide range of taxa (plants, ectotherms and endotherms) suggests that the upper limits of species' fundamental thermal niches are often similar, while tolerances to cold temperatures vary between species (Araújo et al., 2013). Similar patterns have also been observed for the realized niche of alpine plants (Pellissier et al., 2013), suggesting that cold-adapted species can better cope with colder conditions

TABLE 1 Results of two-sample *t* test comparing a few important non-climatic site characteristics of 99 species locations ('spec') and 10,000 random points ('clim'). 'diff' is the difference between the means ('mean.spec'-'mean.clim')

than warm-adapted species, instead of actually suffering from higher temperatures. Therefore, a true upper physiological temperature limit might be less common than a true lower physiological limit. Bryophytes (mosses, liverworts) are generally better adapted to cold conditions than angiosperms (Furness & Grime, 1982; Glime, 2007) and our observed pattern might indicate preferences for colder microclimates and a lower tolerance for high temperatures (Mateo et al., 2016). Moreover, northern bryophytes and lichens may suffer from low air humidity during the growing season, which is tightly coupled to high maximum temperatures, implying that the observed distribution pattern might for some species be caused by humidity rather than temperature (Löbel, Mair, Lönnell, Schröder, & Snäll, 2018). Contrary to our expectations, we did not see a preference of warm-edge populations for sites with low winter minimum temperatures, maybe because the boreal forest floor is often covered by snow during the winter, pausing growth and reproduction for both northern and southern species (Vercauteren, Lyon, & Destouni, 2014). Instead, the studied populations showed a general tendency to occur on places with late snow melt dates, which might be linked to a decreased risk of drought during the early growing season.

Daytime microclimates in the summer are often strongly related to forest canopy cover, which not only buffers high maximum temperatures but also low minimum (night-time) temperatures, suggesting that the populations occupying sites with lower maximum temperatures in denser forests also experience more stable climates. Climate or habitat stability has been suggested to be one of the core features of refugia (Andrew & Warrener, 2017; Ashcroft et al., 2012; Keppel et al., 2015; Morelli et al., 2016). Since a continuous forest cover buffers large temperature fluctuations, boreal rear-edge populations may actually depend on low levels of disturbances in terms of management activities like thinning or clearing.

Above we have discussed several possible mechanisms explaining the microclimate features of microrefugia. Yet, correlations among climate variables made it hard to determine which of them that were most important for the persistence of marginal populations (e.g. the similar pattern for maximum temperatures in October and GDD, see parallel arrows in Figure 3b). This problem remains for any study based on observational data and can only partly be solved by greenhouse experiments or in situ temperature manipulations (De Frenne et al., 2015).

For a better understanding of what makes a site a microrefugium, we need further research on the mechanisms underlying the detected microclimate preferences. This could be achieved by demographic studies differentiating viable from non-viable edge populations and identifying physiological constraints on different life stages, comparisons of climate preferences of rear-edge populations versus central populations or transplant experiments across microclimatic gradients with and without competition. Studying the physiological constraints of competing southern species at their northern range margin could also provide valuable information about where to find microrefugia for northern species. In this study, we assumed that the relative temperature differences across sites remain the same across years. However, future research on microrefugia may also consider the temporal decoupling of local microclimates (Hylander et al., 2015; Lenoir et al.,

2017) and the identification of cold places that are also warming up in a slower pace than the regional climate.

4.2 | Similarities and differences among species

We selected species from different life forms and different forest types for our analyses because we wanted to find general patterns for boreal understory species, assuming they prefer similar microclimates at their southern range margin. We based this assumption on the species sharing a common habitat (boreal understory) and a similar range margin and thus a number of climatic features such as similarities in snow cover duration and growing season length. Our finding of an overall difference between the sites inhabited by northern species and the landscape average and range suggests such a similarity, and there was no clear distinction between taxonomic groups in terms of their climate niche. However, despite a low sample size at the species level, it is clear that several of them occupied distinctly different parts of the climate niche space. Species differed not only in the centre but also in the breadth of their occupied climate niche, adding to the overall variation within the pooled northern species cluster and to the overlap with the background points. One possible explanation for interspecific differences is that the species have other varying non-climatic habitat requirements (e.g. substrate, soil/litter pH, moisture levels). Thus, to further explore individual species' microclimatic niche and if they occur within the colder subset of a specific habitat (e.g. swamp forests) across a landscape, it could be valuable to do the comparisons by keeping these non-climatic factors constant. While acknowledging species-specific responses to climate change (Stewart, Lister, Barnes, & Dalén, 2010), effort should nevertheless also be put in identifying species groups with similar microrefugia requirements, in order to be able to protect as many boreal northern understory species as possible.

4.3 | Implications for conservation and forest management

The (micro)refugia concept has been studied and discussed around the globe, across taxa and ecosystems (Andrew & Warrener, 2017; Hannah et al., 2014; Kiedrzyński, Zielińska, Kiedrzyńska, & Rewicz, 2017; Niskanen et al., 2016; Osman et al., 2018; Scheffers, Edwards, Diesmos, Williams, & Evans, 2014; Schut et al., 2014; Terribile et al., 2012) and a considerable amount of speculation and expectation has been expressed on the carrying role of microrefugia to slow down ongoing climate-driven loss of species and genetic biodiversity (Abeli et al., 2018; Hampe & Petit, 2005; Keppel et al., 2012; Provan & Maggs, 2011). Much of the work has been theoretical, and more empirical studies, like ours, are needed to understand the characteristics of microrefugia, to make realistic predictions and to give adequate advice to conservation and management. In this study, we believe to have identified the most crucial microclimate and landscape features of microrefugia in boreal forests, a hitherto under-represented ecosystem in

microrefugia research. We also combined the features to a map of microrefugia potential, illustrating one way in which this kind of data can be translated into a tool for landscape planning (Figure 5; Figure S7). Areas with a high microrefugia potential could be further inventoried for the presence of certain target species and possibly prioritized for conservation or adapted forest management. A further ranking of the conservation value or “capacity” (Keppel et al., 2015; Keppel & Wardell-Johnson, 2015) of potential microrefugia can be based on additional criteria, for example, the presence and abundance of one or more northern species, the viability of local populations or the size of the area.

Even without the availability of microclimate maps, our results suggest that the simple intersection of high-resolution topography and forest density maps can aid in a rough but quick and easy ranking of sites across a larger landscape from a microrefugia perspective (Figure 5). In contrast to alpine species that normally retreat upward the mountains (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Lenoir, Marquet, Ruffray, & Brisse, 2010; Parmesan & Yohe, 2003; Randin et al., 2009), we did not find that the studied populations occur at higher altitudes. Instead, the typical microrefugium was characterized by a higher forest basal area and a lower exposure to sun in autumn and spring. In other words, these are topographically sheltered places (e.g. north-facing slopes, shady depressions and ravines) with old or dense forests (e.g. like in Lenoir et al., 2017). Therefore, in order to provide suitable habitats for species threatened by climate warming, a fairly simple strategy could be to maintain a continuous forest layer on north-facing slopes, in shady depressions and ravines and to keep or establish buffer zones of continuous forest around those habitats to minimize microclimatic edge effects (Didham & Lawton, 1999; Hylander, 2005). The practice of clear-cutting for regenerating forests, which has been the prevailing method since the 1950s in Sweden (Lundmark, Josefsson, & Östlund, 2013), is from a microclimate perspective a rather invasive measure and is likely to be detrimental to refugial populations of northern species. Given that boreal understory species vary a lot in their dispersal capacity (Cain, Damman, & Muir, 1998; Löbel, Snäll, & Rydin, 2006) and that it is unlikely for many species to colonize new (fragmented, isolated) habitat patches at their rear edge, priority may be given to maintaining old continuous forest patches that harbour already a number of northern species instead of relying on a spatially and temporally variable mosaic of stands with partly appropriate microclimates.

As forest productivity and stand density have generally increased in recent decades (Felton et al., 2017), a microclimate buffering of macroclimate warming effects on understory vegetation is conceivable, and has been suggested for temperate forests (De Frenne et al., 2013). However, a too dense canopy might be detrimental for understory species for other reasons such as low light levels, interception of rain and high litter fall (Barbier, Gosselin, & Balandier, 2008; Serçu et al., 2017). More research is needed to understand the combined historical effects of forest management (e.g. change in forest structure and composition) as well as differences in current management practices on forest floor microclimates and

biodiversity, irrespective of climate change trajectories (Chen et al., 1996; Östlund et al., 1997).

This study highlights the opportunities of responsible forest management to slow down climate-driven species local extinction, but also shows the risk of accelerated regional biodiversity loss under inconsiderate management. We further demonstrated how valuable the use of empirical biotic data (species occurrences) and abiotic data (microclimate) is to concretize the microrefugia concept in lowland forest ecosystems. We hope our work encourages future research on forest microrefugia and their integration into conservation and management strategies.

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DATA AVAILABILITY STATEMENT

Microclimate data are accessible at <https://doi.org/10.17043/greiser-2019-microclimate> and <https://doi.org/10.17043/greiser-2019-refugiaclimate>.

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SUPPORTING INFORMATION

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

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