RESEARCH ARTICLE

Warm range margin of boreal bryophytes and lichens not directly limited by temperatures

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Abstract

1. Species at their warm range margin are potentially threatened by higher temperatures, but may persist in microrefugia. Whether such microsites occur due to more suitable microclimate or due to lower biotic pressure from, for example competitive species, is still not fully resolved.

2. We examined whether boreal bryophytes and lichens show signs of direct climate limitation, that is whether they perform better in cold and/or humid microclimates at their warm range margin. We transplanted a moss, a liverwort and a lichen to 58 boreal forest sites with different microclimates at the species' southern range margin in central Sweden. Species were grown in garden soil patches to control the effects of competitive exclusion and soil quality. We followed the transplanted species over three growing seasons (2016–2018) and modelled growth and vitality for each species as a function of subcanopy temperature, soil moisture, air humidity and forest type. In 2018, we also recorded the cover of other plants having recolonized the garden soil patches and modelled this potential future competition with the same environmental variables plus litter.

3. Species performance increased with warmer temperatures, which was often conditional on high soil moisture, and at sites with more conifers. Soil moisture had a positive effect, especially on the moss in the last year 2018, when the growing season was exceptionally hot and dry. The lichen was mostly affected by gastropod grazing. Recolonization of other plants was also faster at warmer and moister sites. The results indicate that competition, herbivory, shading leaf litter and water scarcity might be more important than the direct effects of temperature for performance at the species' warm range margin.

4. *Synthesis.* In a transplant experiment with three boreal understorey species, we did not find signs of direct temperature limitation towards the south. Forest microrefugia, that is habitats where these species could persist regional warming, may instead be sites with fewer competitors and enemies, and with sufficient moisture and more conifers in the overstorey.

1 | INTRODUCTION

In a warming world, species have two options to avoid (local) extinction: adapting to novel climatic conditions or tracking their climate niche and shifting their ranges. Species range shifts are already occurring and are expected to continue in response to shifting climate conditions (Parmesan, 2006; Pecl et al., 2017; Thuiller et al., 2008). Yet, the effects of climate on range shifts can only be fully understood and predicted if we know the factors determining current range margins. The effect of climate on range margins can be direct, due to physiological tolerances and optima, or indirect, acting via other factors such as species interactions or soil quality (Pugnaire et al., 2019; Tomiolo et al., 2015). Extreme and rare climate events, like cold spells or severe droughts, may affect species range margins directly or indirectly, but are difficult to capture in studies using long-term average climate data or in short-term field experiments (van Bergen et al., 2020).

In a global warming context, we refer to the range margin towards the equator and lower elevations as the distributional 'rear edge' or 'warm edge'. Here, if abiotic conditions are otherwise favourable, species are often believed to be limited by biotic pressure, for example competition or natural enemies (figure 7 in Austin, 1990; Fisichelli et al., 2014). This prediction is made by the asymmetric abiotic stress level hypothesis (AASL, Normand et al., 2009) and more indirectly also by the stress-gradient hypothesis (SGH, Brooker & Callaghan, 1998; Brooker et al., 2008). However, also abiotic factors, like heat or drought, can directly limit species at their warm edge (Lesica & McCune, 2004; Soja et al., 2007). Species at their warm edge are potentially threatened by a warmer climate, but may escape regional warming in colder microclimates (Hampe & Jump, 2010; Hampe & Petit, 2005). These so-called 'microrefugia' are places with locally favourable conditions outside the main range of a species and which host marginal populations (Dobrowski, 2011; Hylander et al., 2015; Keppel et al., 2012; Rull, 2009). Microrefugia can be places with a colder or more humid microclimate that directly facilitate local persistence of rear-edge populations, or that indirectly favour cold-adapted species via excluding warm-adapted competitors or natural enemies. So far, there is insufficient knowledge of how microclimate variation might allow survival in microrefugia, which is particularly true for forest ecosystems.

In forests, the climate near the ground is shaped by the combined effects of landscape physiography (terrain) and tree canopy (Chen et al., 1996; De Frenne et al., 2021; Geiger et al., 2012; Greiser et al., 2018). Weather stations measure climate at ~1.5 m above the ground in an open environment, and the derived low-resolution gridded climate data are therefore of little use for studying the performance and distribution of forest understorey species (De Frenne & Verheyen, 2015). Under forest canopies, air humidity is often higher,

wind speed and insolation lower, maximum temperatures cooler and minimum temperatures warmer, than in adjacent open areas (Davis et al., 2019; De Frenne et al., 2019; Lenoir et al., 2017). Despite the potential of microrefugia to slow down climate-driven biodiversity loss and despite the potential of forest management to protect and even create favourable microclimates, little is known about forest microrefugia. A previous study showed that rear-edge populations of 12 boreal understorey species occur in cold places, including those with low maximum temperatures, less temperature fluctuations, low levels of growing degree days (GDD) and late snowmelt (Greiser et al., 2019). Yet, these patterns need to be tested experimentally to investigate if they reflect physiological preferences or if biotic pressure potentially forces rear-edge populations to retract to abiotically suboptimal habitats (Alexander et al., 2016; Hargreaves et al., 2014; Lee-Yaw et al., 2016).

Only recently, there has been a broadening of microclimate research to also consider soil moisture and air humidity (see e.g. Kemppinen et al., 2018, 2019; Le Roux et al., 2013), because future climate may pose additional drought stress on organisms due to changed precipitation patterns, which has led to the concept of 'hydrologic refugia' (McLaughlin et al., 2017). In addition, research shows that the capacity of forests to buffer temperature extremes increases with local water availability (Davis et al., 2019). Microrefugia requirements can be different for different species and more specific for poikilohydric organisms, for which water status varies passively with surrounding conditions. Such organisms, for example bryophytes and lichens, are likely to be much more sensitive to changes in humidity and moisture than other organisms due to their lack of mechanisms to regulate water uptake and loss.

In boreal forests, the ground-covering vegetation is often dominated by bryophytes (mosses, liverworts) and lichens (Esseen et al., 1997; Turetsky et al., 2012), which play important functional roles, for example, for carbon cycling, primary productivity (Asplund & Wardle, 2017; Lakatos, 2011; Nilsson & Wardle, 2005; Turetsky et al., 2012) and water retention (Betts et al., 1999; Flanagan et al., 1999; Hartard et al., 2008; van Zuijlen et al., 2020). Due to their poikilohydric nature and often tight coupling to understorey temperature, moisture and light levels, bryophytes and lichens are particularly influenced by changes in the microclimate and sensitive to habitat changes resulting from forest management. They are therefore often used as indicators for certain microclimates (Hylander, 2005; Hylander et al., 2002).

Both groups can survive desiccation, but that ability depends strongly on the species and the length of desiccation (Proctor et al., 2007). Therefore, extreme drought events can be lethal despite a general desiccation tolerance, and a suboptimal water balance may limit many species towards their warm range margin (Rogers, 1971). Under moist conditions, on the other hand, increasing temperatures

eventually decrease growth because photosynthetic assimilation cannot outbalance respiratory losses (Colesie et al., 2018). Thus, depending on the hydration status, high temperatures can cause distributional limits of bryophytes and lichens.

Due to their slow growth and low growth form, warm-edge populations of northern ground-dwelling bryophytes and lichens can be out-competed by species of the same or other taxonomic groups that are warm-adapted or more common and grow faster and larger (Löbel et al., 2018; e.g. *Vaccinium myrtillus*, *Deschampsia flexuosa*, *Hylocomium splendens*, *Dicranum scoparium* or *Rhytidiadelphus triquetrus*). Further relevant biotic stressors for northern bryophytes and lichens are dense light-blocking litter from broadleaved trees (Schmalholz & Granath, 2014) and grazing gastropods, for example *Arion fuscus* grazing on the lichen *Nephroma arcticum*. South of the boreal zone, gastropod density is higher, probably due to a higher proportion of broadleaved trees providing more moisture, food and shelter in the litter (Suominen et al., 2003). Therefore, gastropod grazing on lichens has even been suggested as a biotic distribution-limiting factor on regional scales (Asplund & Gauslaa, 2010), and even local scales on single tree trunks (Asplund et al., 2010).

1.1 | Aims

Here, we test the influence of microclimate (temperature, air humidity, soil moisture) on the performance of three boreal understorey species at their southern range margin to detect the potential mechanisms limiting their distribution, and to identify the characteristics of potential boreal microrefugia. We transplanted three northern species—a moss *Dicranum drummondii*, a liverwort *Barbilophozia lycopodioides* and a lichen *Nephroma arcticum*—at their southern range margin to 58 forest sites along microclimate gradients excluding effects of soil quality and competition, and followed their growth and vitality over three growing seasons. We tested the effect of both abiotic and biotic potentially limiting factors. The last growing season in 2018 was hit by a severe drought and we used this event to investigate how extreme weather affects the relative importance of temperature versus moisture for the performance of the transplanted edge populations. We expect the species to respond negatively to temperature and/or drought when climate is directly limiting them towards the south. On the other hand, we expect the species to respond positively or not at all to temperature and negatively to leaf litter or herbivory, when biotic stress is limiting them towards the south. This could be summarized into three hypotheses:

1. The species respond negatively to temperature, and this depends on water availability.
2. The species respond positively to air humidity and soil moisture, and these effects were stronger in the dry year 2018.
3. The species react negatively to biotic stress coming from either leaf litter or herbivory, which in turn can be influenced by climatic factors.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area is situated at the southern edge of the boreal forest in central Sweden around 60°N. Around this latitude, the southern boreal zone in Sweden is characterized by sharp changes in climate, soil and vegetation conditions (Figure 1). This transitional zone constitutes the warm and cold range margin of many northern and southern species respectively. Thus, it is particularly prone to be affected by climate change with potential effects on species composition via local extinctions and colonizations (Elmhagen et al., 2011).

The climate is humid, cold-temperate with cold winters, temperate summers and mean annual temperatures between 2 and 6°C (SMHI, 2017). Annual precipitation increases from east (600 mm) to west (800 mm), falls mostly in summer, and in the winter often as snow. The growing season extends roughly from April (May) to September (October) depending on local climate.

The area is dominated by coniferous forests with Scots pine *Pinus sylvestris* L. and Norway spruce *Picea abies* (L.) H. Karst. and scattered broadleaved elements in lower parts of the terrain. The forest floor is dominated by mosses, dwarf shrubs and lichens and in moist and nutrient-rich sites also by herbs (Rydin et al., 1999). The forest in Sweden is heavily managed with practices including clearing, planting and thinning. The main management scheme since the 1940s is clear-cutting (Nilsson & Wardle, 2005).
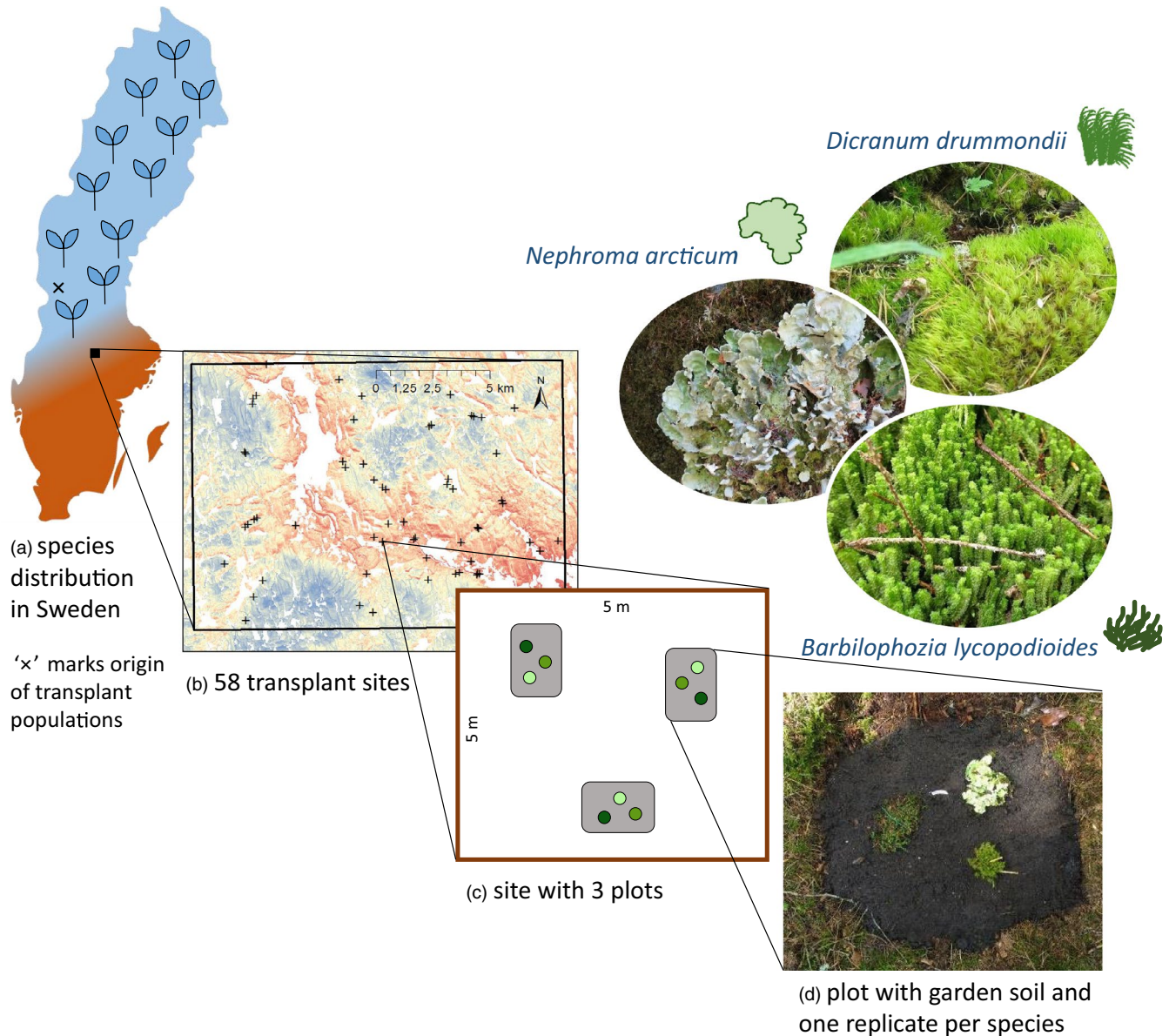
2.2 | Study species

The three study organisms are common ground-dwelling northern boreal understorey species, which strongly decline in abundance from north to south across the study area. Species were chosen to cover different growth forms and water uptake mechanisms and to capture variation in tolerances to high temperatures and drought. However, due to their relatively similar habitat requirements, distributions and poikilohydric lifestyle, we expected to find common patterns in their reactions to climate change at their southern range margin.

Barbilophozia lycopodioides (Wallr.) Loeske is a leafy low-growing liverwort common in spruce-dominated boreal forests. It often builds pure mats on humus derived from conifer needles and is more abundant on shaded slopes (Dahlberg et al., 2014; Damsholt & Pagh, 2009; Hallingbäck & Holmåsen, 2016).

Dicranum drummondii Müll. Hal. is a moss that is most frequent in pine-dominated forests with rocky ground and moraine with relatively dry and acidic conditions. Its upright shoots build loose homogenous tuffs, generally surrounded by the feather moss *Pleurozium schreberi*, other *Dicranum* species and different *Cladonia* species (Hedenäs & Bisang, 2004).

Nephroma arcticum (L.) Torss. is a large, foliose, mat-forming lichen growing up to several decimetres in diameter with up to 3 cm broad lobes. The tripartite lichen consists of a fungus, a green algae and nitrogen-fixing cyanobacteria, the latter making the lichen

FIGURE 1 Spatial study design and portraits of study species. (a) Map of Sweden with simplified distribution of study species and location of transplant area at their southern range margin. (b) Fifty-eight transplant sites with contrasting microclimates in a *c.* 16 × 16 km area. (c) At each site, three plots were established within 5 × 5 m, which had each one replicate cushion of three transplant species: *Dicranum drummondii* (moss), *Barbilophozia lycopodioides* (liverwort) and *Nephroma arcticum* (lichen). (d) Each plot was cleared from topsoil and vegetation and filled with standard garden soil

palatable for gastropods, which preferably graze on the nitrogen-rich parts (Asplund & Gauslaa, 2010). *N. arcticum* grows on bare soil, on moss carpets or on mossy rocks in semi-open coniferous forests and mountain birch forests; at the south of its range, it is restricted to humid places (Asplund & Gauslaa, 2010; Moberg & Hultengren, 2016).

2.3 | Transplantation

The transplant sites were distributed in a square of *c.* 16 × 16 km in the county of Västmanland and Dalarna (59°56′N, 15°30′E, 280 m

a.s.l.). We selected the sites in a way that covered gradients of microclimate and forest type using gridded environmental data at a 50-m resolution (details in Appendix A). Transplant material was collected in the north-western part of Dalarna county close to Sälen (61°09″N, 13°15″E 350 m a.s.l., *B. lycopodioides* and *D. drummondii*) and Idre (61°51″N, 12°43″E 452 m a.s.l., *N. arcticum*), between 17 and 20 May 2016 (Figure 1). For each species, all materials (*c.* 2 m²) were collected at a single location. Species were transported in plastic boxes and stored at a humid and shaded place until they were transplanted between 2 and 15 June 2016.

At each of the 58 sites, we established three transplantation plots of 80 × 50 cm scattered within a 5 × 5 m area. Before

transplantation, the topsoil was removed and replaced by nutrient-poor garden soil to exclude the effects of competition and variation in local soil conditions (c. 10-cm thick layer, in total 40 L of soil were distributed among the three plots). In each plot, we transplanted one cushion of each species of c. 0.5–1.0 dm^2 size with a minimum distance of 15 cm to plot edges and the other species cushions (Figure 1). The lichen and the liverwort were attached to the soil with a plastic-coated metal wire arch. The moss was cut to 10-cm long shoots and planted so deep into the soil that only green parts were above the ground. Two wooden sticks for marking growth were placed within and beside the moss cushion.

Right after transplantation, size-referenced photographs of the lichen and the liverwort were taken from above and height was marked at the measure stick for the moss (= initial size measurements). Because cushion size varies with their water content, we recorded transplant size in full hydration by spraying water until they were completely hydrated and took photographs and measurements a few minutes after hydration. After the growing season, we took photographs, measured growth and recorded vitality of each transplant. Vitality for all species was evaluated using a scale from 1 (no green tissue or leaves) to 7 (all shoots were healthy and green or 100% healthy tissue, Dynesius et al., 2008; Hylander et al., 2002). Before modelling, we transformed the vitality classes into the proportion of vital tissue by replacing class with the mean proportion of each class (see Appendix A). We also recorded grazing damage in the lichen using the following scale: (a) 0%–1% grazed, (b) 2%–6%, (c) 6%–15%, (d) 16%–30% and (e) 30%–50% (Figure S1; Benesperi & Tretiach, 2004), and back-transformed scores to mean percentage values for each category (e.g. category 1 = 0.5%, category 2 = 4% a.s.o.). Measuring and scoring took place in June 2016, October 2016, April 2017, October 2017, April 2018 and October 2018. As the species did not grow noticeably during the winter (Figures S3, S4, and S5), we only examined June–October (2016) and April–October (2017, 2018) transitions. Growth for the lichen and the liverwort was expressed as the proportional change in area from one measurement to the next (area$_{t+1}$/area$_t$). Area [cm^2] was estimated using the software ImageJ (version 1.51r) from the images after delineating manually the healthy shoots and tissue of each individual cushion. Growth for the moss was estimated by the change in height [mm] from one measurement to the next. In October 2016, we replaced some disappeared or destroyed cushions with new cushions from the same source (the final dataset included only few of these replaced cushions: one *D. drummondii*, six *N. arcticum* and two *B. lycopodioides*.

2.4 | Site variables

At each site, two microsensor loggers (MaximIntegrated iButton, type DS1923 or DS1921G-F5) were installed to measure temperature every 3 hr. The first logger was placed in an inverted plastic cup taped to a wooden stick at c. 5–10 cm above the ground (Figure S2).

The second logger was placed in a white PVC tube of c. 25 cm length that was attached horizontally to the next tree trunk at 1 m height in a north–south orientation (Figure S2, George et al., 2015). This logger also recorded relative air humidity (%). Both shields protected the logger from direct sunlight, rain and snow.

During both leaf-on season and leaf-off season, we took five canopy cover images per site with a standard digital camera (Canon Powershot S120) from 60 cm above the ground straight upward—one image above the ground logger and four images around it with c. 5 m distance from the central point. The images were converted to binary images before calculating the fraction of white pixels with the software ImageJ (version 1.51r). The average of all five pictures per site describes canopy openness and was used as an estimate of available light.

From on-site basal area measurements, we extracted the proportion of coniferous trees for each site (0%–100%). This variable was used as a covariate in the models because of the effect on the amount and quality of litter and on the light regime in the beginning and end of the growing season.

We extracted two complementary microclimate indices from the ground logger data for the growing season between the transplant measurements (in 2016: 15 June–30 September, in 2017 and 2018: 1 May–30 September)—the average of daily minimum temperatures (T_{min}) and GDD with a base of 5°C.

Both bryophytes and lichens are poikilohydric, yet both groups take up and make use of water in very different ways: many lichens can make use of water vapour and even suffer from too much liquid water, whereas many mosses need liquid water for growth (Lakatos, 2011). Therefore, we used two different variables describing water availability—soil moisture (soilmoist) and vapour pressure deficit (VPD). VPD has been shown to be an important predictor variable for bryophyte and lichen growth (Busby et al., 1978; Ellis, 2020; Stewart & Mallik, 2006). Volumetric soil moisture was measured across six dry days in September 2017 (5–7 and 15–17 September) with a moisture metre (DELTA-T DEVICES, SM300). To describe the dryness of the air at each site during the day, we calculated from the temperature and relative air humidity measurements of the 1-m logger a growing season average of daily maximum VPD (for more details on variable preparation, see Appendix A).

Finally, during the final measurement in October 2018, we recorded the proportions of each subplot that were covered by broadleaved and coniferous litter and by recolonizing vegetation, representing the estimates of disturbance and competition respectively.

All variables used in the models with their mean and range are summarized in Table 1 and climate variables for all 3 years are plotted in Figure S7. Some plots or sites were removed from the final analysis due to heavy disturbance from forest management, wild boars or wind-fallen trees. Each year we lost some of the originally 522 transplanted cushions (three cushions of three species at 58 sites), and only 327 cushions (60%) remained after 3 years. Final sample sizes for each species and year are provided in Figure 3.

TABLE 1 Predictors for growth and vitality models, mean and range for year 2017 (all predictors, except proportion of conifers and soil moisture, changed slightly across the 3 years)

Abbreviation	Variable	Unit	Mean	SD	Min	Max
GDD	Growing degree days	Unitless	1,107	109	934	1,375
T_{min}	Daily minimum temperature, averaged over growing season	°C	7.9	0.6	6.9	8.9
VPD	Vapour pressure deficit	kPa	0.71	0.08	0.56	0.85
Soilmoist	Soil moisture	Vol %	29	11	11	60
Grazing	Proportion of grazed tissue	%	3.7	5.7	0	24.0
Conif	Proportion of conifers	%	81	27	7	100

FIGURE 2 Growth distribution for all species and years. Growth for *Barbilophozia lycopodioides* and *Nephroma arcticum* is square-root transformed proportional change in area in cm^2 (numbers below 1 indicate shrinkage); growth for *Dicranum drummondii* is change in height in mm (numbers below 0 indicate shrinkage)
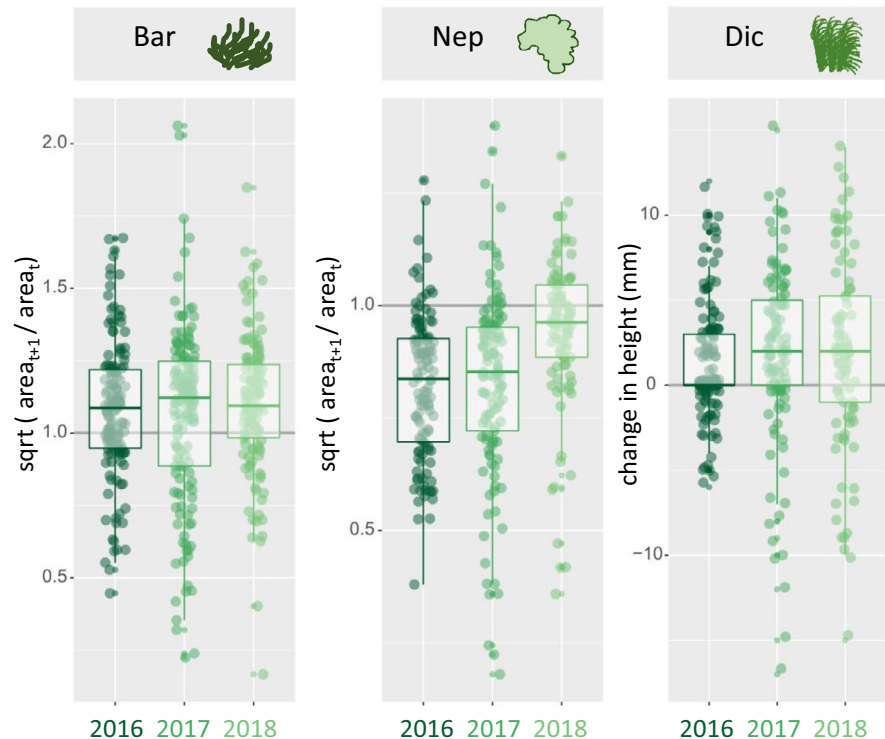

2.5 | Statistical analyses

All statistical analyses were done in R version 4.0.3 (R Core Team, 2020). First, for each species and each year, we modelled growth as a function of GDD, cold temperature (T_{min}), air dryness (VPD), soil moisture, proportion of conifers (conif) and grazing (only found on the lichen and included only in the lichen models), including site as a random intercept term in linear mixed effect models using the *lmer* function of the package LME4 (Bates et al., 2015). Additionally, we included the interactions between GDD and soil moisture and GDD and VPD. As a response variable, we used proportional growth for the lichen and the liverwort to account for the effect that big individuals also grow more. Before modelling, proportional growth was square-root transformed in order to meet the model assumptions of normality. For the moss, we only used absolute increase in shoot length, since all of them were cut to roughly the same length before transplanting.

Second, we modelled vitality (proportion of vital tissue) for each year and species including the same model structure and same set of predictors, but excluding grazing (since scores probably influenced each other in the field, i.e. a heavily grazed lichen would also get a low vitality score from visual inspection). Vitality was arcsine square-root transformed before modelling.

Third, we modelled recolonization (% cover of vegetation having recolonized the subplots in October 2018 when the experiment was finished), an estimate for potential future competition, as a function of the above-mentioned environmental variables (T_{min}, GDD, VPD, soilmoist, conif, GDD:soilmoist and GDD:VPD) and amount of deciduous litter (% cover in each plot).

Gaussian error and identity link function were used for all growth and vitality models (fitted by restricted maximum likelihood criteria (REML)), whereas recolonization (a proportion) was modelled with a beta error and logit link function using the package GLMMTMB (Brooks et al., 2017). Beta regressions allow only response values between 0 and 1, therefore we transformed the values according to $y = (y(n - 1) + 0.5)/n$, where n is the sample size (Smithson & Verkuilen, 2006).
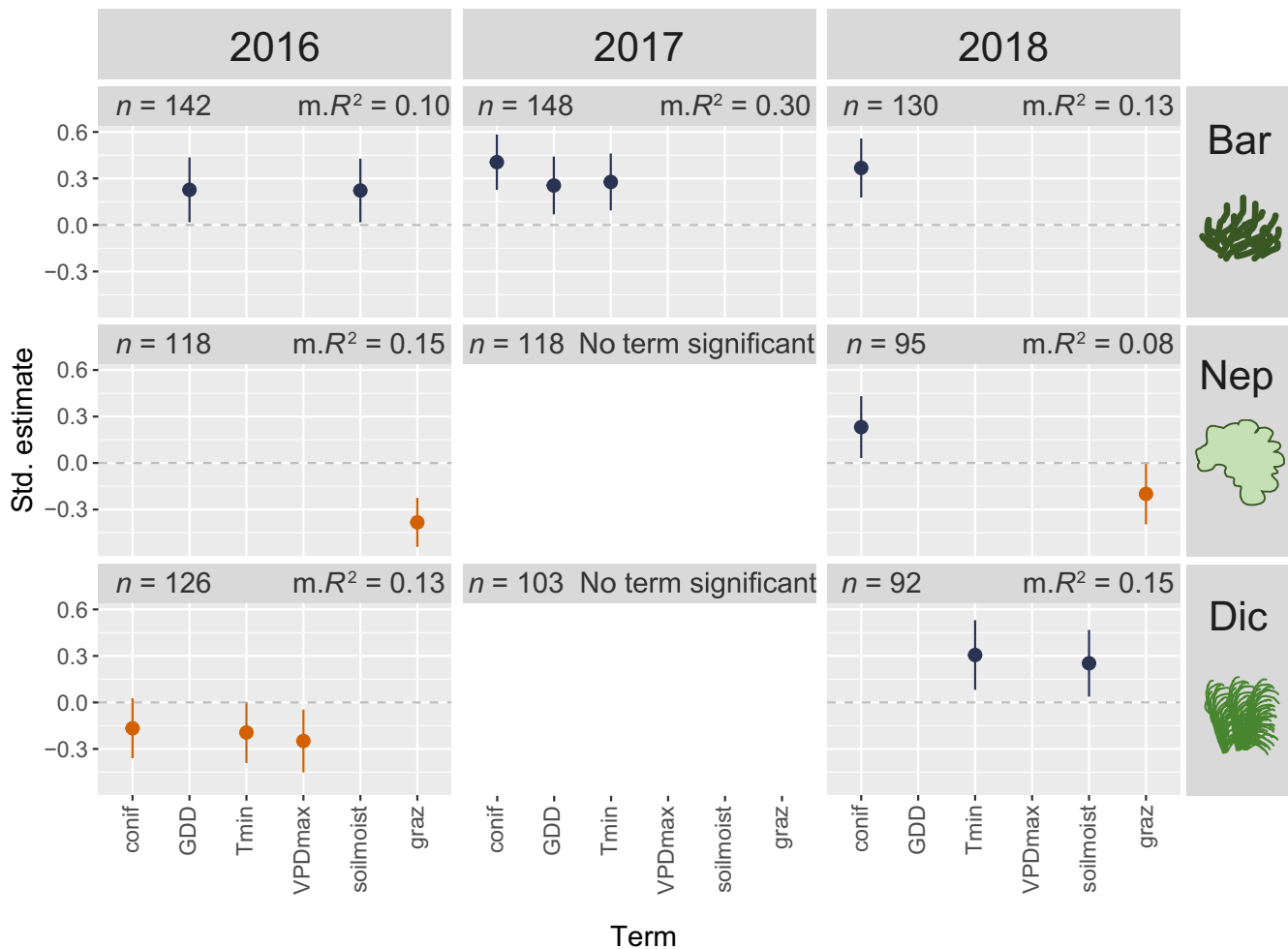
FIGURE 3 Standardized model coefficients and 95% confidence intervals for all variables kept in each growth model of three species (Bar = *Barbilophozia lycopodioides*, Nep = *Nephroma arcticum* and Dic = *Dicranum drummondii*) and 3 years (2016, 2017 and 2018) after model selection. Even response variables were standardized in order to be able to compare results across species and years. See Methods section for details. In 2017 and for *D. drummondii*, no variable was kept in the final model after model selection. Light red: negative coefficients, dark blue: positive coefficients. Sample size ('*n*') and marginal R^2 (m.R^2) for each model are plotted in each quadrant. Interaction terms are interpreted as following: If GDD:soilmoist is positive, GDD has a positive effect under high soil moisture. Conif, proportion of conifers; T_{min}, minimum temperature; GDD, growing degree days; soilmoist, soil moisture; VPD_{max}, maximum vapour pressure deficit; graz, proportion of tissue grazed by gastropods

We started with full models including all predictors and interactions and reduced the models using a backward stepwise selection based on a *p*-value threshold of 0.1. *p*-values of the fixed effects were extracted based on Satterthwaite degrees of freedom approximation using the package LMERTEST (Kuznetsova et al., 2017).

The final selected models were run again with standardized responses and explanatory variables in order to calculate standardized model coefficients and to compare them across species and years. Additionally, raw coefficients were multiplied with the range of each predictor variable to provide effect sizes translated to growth (in mm or proportion). We calculated the coefficient of determination ('Pseudo'-R^2 for GLMMs) for each model using the function r.squaredGLMM (Nakagawa & Schielzeth, 2013) of the R package MuMIN (Barton, 2017), and extracted both the marginal R^2 for fixed effects only and the conditional R^2, which includes both fixed and random effects. All predictors were checked for collinearity with the Pearson correlation coefficient (|r| <

0.7, Figure S6) and the variance inflation factor (no factor >3.1). Light (canopy openness during summer) was strongly correlated with GDD and VPD, and therefore not used in the analyses.

Model assumptions were checked by plotting residuals against fitted values, against each variable in the model and against each variable not in the model. For the growth models of *N. arcticum* in 2017 and 2018, the variance of the random effect approached zero, and we therefore excluded it and ran the models as a normal linear model with fixed effects only.

3 | RESULTS

The growing season weather in the years 2016 and 2017 was warm but not exceptional compared to the reference period 1961–1990 (Figure S7, SMHI, 2020), but 2018 was hit by a severe drought due

to a combination of less precipitation and warmer temperatures than normal during the growing season (SMHI, 2020). However, the extremely dry year 2018 did not create a general decline in growth across all transplant species, that is they grew at a similar rate in all years (Figure 2). While the mean growth of *B. lycopodioides* and *D. drummondii* in all years was positive, the average change in area of *N. arcticum* was negative (proportional growth <1, Figure 2).

The response of growth to temperature (GDD or T_{min}) was either lacking or positive and the effects were most consistent across years for *B. lycopodioides* (Figure 3; Table S1). Only *D. drummondii* in 2016 reacted negatively to warmer minimum temperatures. The drought index VPD had a negative effect on growth of *D. drummondii* in 2016. Soil moisture increased growth in *B. lycopodioides* (2016 and 2018) and *D. drummondii* (2018). We also found GDD–soil moisture interactions, where *D. drummondii* grew better under warmer conditions, especially when soil moisture was high, whereas *N. arcticum* grew better in warmer conditions when soil was drier (Figure 3; Table S1). The growth of *B. lycopodioides* and *N. arcticum* increased with increasing proportion of conifers in 2017 (only *B. lycopodioides*) and 2018. Gastropod grazing reduced the growth of *N. arcticum* in 2016 and 2018 (Figure 3, Table S1). Effect sizes for all significant variables in the model ranged from *c.* 2% to 16% change in size (for *B. lycopodioides* and *N. arcticum*) and from *c.* 3.5 to 7.7 mm change in height for *D. drummondii* (Figure S8).

The variance explained by the models was moderate for most models (marginal R^2 from 0.10 to 0.32, conditional R^2 from 0.21 to 0.52), but low for the *N. arcticum* model in 2017 (conditional and marginal R^2 0.02, Table S1). The variation explained by fixed effects only (marginal R^2) was often small, implying that much variation remained unexplained.

The models for growth and vitality showed similar patterns. In both models, soil moisture and proportion of conifers appeared regularly as significant positive effects. The vitality of *B. lycopodioides* increased with soil moisture in 2016, and with proportion of conifers in the other 2 years (Figure S9; Table S2). For *B. lycopodioides* in 2018, the positive effect of GDD was reduced when the air was dry (high VPD). The vitality of *D. drummondii* strongly increased with soil moisture in 2017 and 2018, whereas no effect could explain vitality in 2016. In 2018, the vitality of *N. arcticum* increased with the proportion of conifers and tended to increase with higher GDD and higher soil moisture, yet in 2017, none of the variables were maintained after model selection. In 2016, the maintained terms (GDD, soilmoist and their interaction) were not significant.

The recolonization of other plants was positively related to T_{min}, VPD and soil moisture, and negatively related to leaf litter cover in October 2018 (Figure S10, Table S3).

4 | DISCUSSION

Whether and how climate affects species distributions are long-standing questions in ecology and biogeography and becomes particularly pressing in times of rapid changes in climate and land use

(Parmesan, 2006; Travis, 2003). Incorporating climate on organism-relevant scales, that is microclimate, into correlative species distribution models has improved our understanding of climate as a driver of species distributional patterns (Lembrechts et al., 2018). Yet, experiments are still needed to test the relative importance of microclimate on local population performance and to test if microclimate acts as a direct or indirect driver. We tested the effect of microclimate, in terms of temperature and moisture, and biotic factors on the performance of boreal ground-dwelling bryophytes and lichens at their southern range margin. Species performed in general better in warmer microclimates, which was often conditional on water, indicating no direct temperature limitation but a possible drought limitation at their warm range margin. The most pronounced effects were those of biotic interactions, which suggests competition, herbivory and leaf litter—together with occasional drought stress—as limiting factors towards the south.

4.1 | Abiotic factors: Temperature and water

Despite that the species are found in relatively cold places in the landscape (Dahlberg et al., 2014; Greiser et al., 2019), we found that responses to temperature were either lacking or positive, indicating no direct temperature limitation at their warm range margin. A positive response of growth to temperature at the warm edge in situations without competition could indicate that species warmer range margins are instead mainly limited by higher intensity of competition or other biotic interactions including herbivory. This is in line with the AASL (Normand et al., 2009) and the SGH which predict increasing biotic pressure with decreasing abiotic stress, assuming in our case that warmer temperatures are generally favoured by the species (Brooker & Callaghan, 1998; Brooker et al., 2008).

On the other hand, in alignment with our second hypothesis, we found positive effects of air humidity (VPD) and soil moisture, especially for the moss, possibly due to its upright growth form with rhizoids, which can access and hold soil water more easily than the low mat-forming *B. lycopodioides* and *N. arcticum* (Stewart & Mallik, 2006). The effects of moisture on growth were also more frequent in the first year than in the second year, possibly due to stressful transplant effects, and in the last year, which was exceptionally dry and hot. This supports the hypothesis that extreme and rare events have the potential to affect range margins and that only multi-year experiments have the chance to capture a wide range of weather conditions (Camarero et al., 2015; Giesecke et al., 2010; Hoffmann et al., 2019; Lee-Yaw et al., 2016). The moss reacted negatively to warmer minimum temperatures in the first year, which is the only support we found for our first hypothesis on temperature limitation. However, even this can reflect a water limitation, since colder minimum temperatures during early morning hours increase dewfall, which is an important water source for both bryophytes and lichens (Proctor et al., 2007).

Most importantly, positive responses to temperature were often conditional on water (Figure 3; Figure S9), which has three

implications. First, due to temperature–moisture interactions, a net effect of temperature may sometimes not have been detected. Second, climate may still also directly limit the species towards the south, though not via temperatures but via a negative water balance during critical growing periods (Merinero et al., 2020). And third, we need more controlled ecophysiological laboratory experiments and carefully planned phenological field studies to disentangle the effects of temperature and moisture to know *when* during the day and during the year and under which temperature–moisture combinations the species actually grow or die. This understanding may in turn help to find more appropriate microclimate variables for correlative performance models like ours.

Caution must be used in interpreting the reactions to microclimate conditions—especially in the first year—as the transplanted cushions were placed on bare soil outside the protecting vegetation. This rather unnatural setting might have caused increased evapotranspiration and thus increased dependence on soil moisture. Likewise, increased air flow around the cushions might have decreased heat stress.

We cannot exclude that the observed patterns of temperature also were influenced by light availability at the forest floor, even if many forest floor species have low-light saturation points, since canopy openness was highly correlated with GDD (Pearson $r = 0.80$ for 2017 data, Figure S6) and could therefore not be included in the models. In fact, the tree canopy is the major driver of daytime understorey microclimate in this landscape (Greiser et al., 2018) and the effects of light and temperatures during the growing season can only be fully disentangled with warming treatments. However, we also found that species reacted positively to warmer night-time temperatures (T_{min}), which were not so related to canopy openness, supporting our main conclusion. Also, even if the positive effect of GDD is ascribable to an ultimate light limitation, we did not find support for a direct limitation by warm temperatures (under more open canopies) that could overwrite the positive response to light.

Although we followed the species over three growing seasons, of which one was extremely hot and dry, we acknowledge that there may be long-term effects of exposure to high temperatures that we did not capture in our 3-year experiment.

4.2 | Biotic factors: Herbivory and forest type

Compared to the abiotic factors (temperature and moisture), the biotic factors (grazing and proportion of conifers) had relatively large effects on the transplant performance. The positive effect of coniferous trees on the boreal species may be associated with the effects of litter (Schmalholz & Granath, 2014). Leaf litter from broadleaved trees is covering low-growing cryptogams more efficiently than needle litter, because it creates problematic full-shade conditions. We recorded cover and type of litter in 2018 and models where the variable 'proportion of conifers' was replaced by 'cover of leaf litter' (Pearson $r = -0.79$) looked very similar to the original models (though not better). This supports the hypothesis that the proportion of conifers vs. broadleaved trees has an impact on the transplanted species ultimately via the proportion of needle vs. leaf litter. Further, coniferous forests provide shady conditions all year-round and therefore limit evaporative water loss for the species. Also, more conifers (or fewer broadleaved trees) might imply less gastropods that prefer higher pH litter, as we also found a positive effect of conifers on the lichen (Asplund et al., 2018).

Grazing severity was the only significant variable in the 2016 model for the lichen and probably explains why many of the transplanted cushions not only grew little but in fact shrank in size (Figure 3). As southern herbivores may be a major limiting factor for northern species, the spatial distribution of natural enemies must be investigated further. Slugs are generally more common in the south and the most frequently found species that potentially feed on lichens (*Arion fuscus*, *Limax cinereoniger*, *Lehmannia marginata* and *Malacolimax tenellus*) decline in abundance north of the study area (participative citizen science database; https://artfakta.se/, accessed 2020-05-15), probably due to a decreasing proportion of broadleaved trees providing more moisture, food and shelter in the litter (Suominen et al., 2003). In our study, herbivory was not related to environmental variables (Table S4), but potential indirect effects of climate acting via biotic interactions need to be further investigated, also using experimental approaches.

By the end of the experiment, other plants had recolonized the transplant plots, especially at sites that did not become so cold, had higher soil moisture, higher VPD (drier air) and less deciduous litter cover. Although recolonizing plants probably did not have yet an effect on the species, they will likely have so in the long run, and we could show that even this type of biotic pressure is a function of warm microclimate. The same environmental factors driving our transplant performance seem to control also vegetation recolonization, supporting the idea that climate controls biotic interactions and relative competitiveness among species (Normand et al., 2009; Walter, 1979), and that the role of microclimate is indirect via biotic effects in general. However, the outcome of these competitive interactions across microclimate gradients needs to be tested explicitly in the future experiments that also manipulate important biotic drivers and thus can specifically approach interactions between biotic and abiotic factors.

The overall results indicate a suboptimal water balance and biotic stress, that is competition, herbivory and leaf litter, as limiting factors at the species current warm range margin. However, we found large variations in growth and vitality among the individual transplanted cushions (Figure 2) and could only explain a small proportion of it, likely due to pronounced heterogeneity at each site created by single trees affecting both temperatures, litter and rain throughfall.

4.3 | Range margins in managed landscapes

Earlier studies found that warm-edge populations or species with a more northern distribution in a given landscape often occur in relatively colder places (Ackerly et al., 2020; Dahlberg et al., 2020;

Greiser et al., 2019; Moracho et al., 2016; Slaton, 2015). In our study, which differed from observational studies examining the effects of climate both by using transplanted species and by eliminating competition, we were able to eliminate several alternative causes behind the observed distribution patterns. Colder microclimates are often moister and give the northern species a competition advantage against southern enemies. Microrefugia hosting warm-edge populations have been hypothesized to occur in cooler or more stable microclimates (Ashcroft et al., 2012; Dobrowski, 2011; Hylander et al., 2015). We showed that microrefugia probably have more dimensions than temperature, and that sufficient soil moisture and low evaporative stress (VPD) are important but still neglected features of microrefugia (Davis et al., 2019; Ellis, 2020; McLaughlin et al., 2017). Microrefugia for the studied boreal species in this landscape are probably located at cold coniferous sites not necessarily because of better overall growing conditions, but because competition, litter fall and herbivory are lower, yet growth is still possible.

Land use change and climate change are the two main drivers of changing global biodiversity patterns (Sala et al., 2000). Climate change is predicted to lead to both higher temperature and precipitation in Sweden, however, with a potential net decrease in regional water balance during the growing season, especially in the south (Eklund et al., 2015). Northern forest bryophytes and lichens at their southern range margin are therefore potentially threatened by two mechanisms. First, growth rates and survival may decrease due to prolonged and intensified desiccation periods, especially during the growing season. Second, rising competition levels by increasing or invading warm-adapted species and increased grazing pressure may lead to local extinctions and a deterioration of the warm range margin (Asplund & Gauslaa, 2010; Löbel et al., 2018).

At the same time, human land use (forestry) heavily modifies the microclimatic landscape in forests (Frey et al., 2016; Greiser et al., 2018). Clear-cuts can create hot islands, pull out moist air from adjacent forest patches (Baker et al., 2014; Laurance et al., 2002) and, together with drainage activities, reduce the water in the soil and thereby decrease the capacity of forests to buffer high temperature extremes (Davis et al., 2019; Von Arx et al., 2013).

We also showed that coniferous trees favour northern understorey species, likely via effects of litter structure and pH. This suggests that the species are strongly associated with a certain forest type (boreal conifer forest on poor acidic soils without fast-growing herbs) and that they may follow the general distribution and shift of the main overstorey tree species. Consequently, forest management carries a significant responsibility to favour locally the right tree species, to protect and create favourable microclimates and improve the water-holding capacity of the forest. For example, maintaining conifer-dominated stands in topographically shaded and moist places along the southern margin of the boreal zone can create potential microrefugia for our target species.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

B.W., C.G. and K.H. conceived the ideas and designed methodology; B.W., C.G. and S.M. collected the data; C.G. analysed the data and led the writing of the manuscript. All co-authors (J.E., M.L., E.M., S.M., B.W. and K.H.) contributed critically to the drafts and gave final approval for publication.

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DATA AVAILABILITY STATEMENT

The data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.qrfj6q5g8 (Greiser et al., 2021).

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