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Effects of past and present microclimates on northern and southern plant species in a managed forest landscape

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RESEARCH ARTICLE

Effects of past and present microclimates on northern and southern plant species in a managed forest landscape

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Abstract

Questions: Near-ground temperatures can vary substantially over relatively short distances, enabling species with different temperature preferences and geographical distributions to co-exist within a small area. In a forest landscape, the near-ground temperatures may change due to management activities that alter forest density. As a result of such management activities, current species distributions and performances might not only be affected by current microclimates, but also by past conditions due to time-lagged responses.

Location: Sweden.

Methods: We examined the effects of past and current microclimates on the distributions and performances of two northern, cold-favoured, and two southern, warm-favoured, plant species in 53 managed forest sites. Each pair was represented by one vascular plant and one bryophyte species. We used temperature logger data and predictions from microclimate models based on changes in basal area to relate patterns of occurrence, abundance, and reproduction to current and past microclimate.

Results: The two northern species were generally favoured by microclimates that were currently cold, characterised by later snowmelt and low accumulated heat over the growing season. In contrast, the two southern species were generally favoured by currently warm microclimates, characterised by high accumulated heat over the growing season. Species generally had higher abundance in sites with a preferred microclimate both in the past and present, and lower abundance than expected from current conditions, if the past microclimate had changed from warm to cold or vice versa, indicating time-lags in abundance patterns of the species.

Conclusions: Our results show a potential importance of past and present microclimate heterogeneity for the co-existence of species with different temperature preferences in the same landscape and highlight the possibility to manage microclimates to mitigate climate change impacts on forest biodiversity.

Ditte Marie Christiansen and Tanya Strydom shared first-author.

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KEYWORDS
abundance, boreal forest, climate, forest management, occurrence, presence-absence, regional co-existence, species responses, time-lags, understorey plants

1 | INTRODUCTION

Forest structure impacts temperatures experienced by species living near the ground (Scheffers et al., 2014; Greiser et al., 2018; Greiser, Ehrlén, et al., 2020). Over only a couple of meters, there can be several degrees difference, and such small-scale differences have been shown to influence community compositions, species distributions as well as individual performances (De Frenne et al., 2013; Graae et al., 2018; Oldfather & Ackerly, 2018; Stark & Fridley, 2022). Managed forests go through multiple management activities during stand development (Gold et al., 2006) resulting in dynamic understory microclimates. When a forest stand grows denser or gets thinned, the microclimate in the understorey changes (Zellweger et al., 2020; De Frenne et al., 2021). Such changes in microclimate might be fast compared to the responses of understorey species leading to legacy effects (Zellweger et al., 2020). Given lags in understorey plant species responses to changes in local climate, current distributions and performances across landscapes reflect variation in both past and present microclimates (Lenoir et al., 2022). Yet, our knowledge of how past conditions impact the current performance of understorey species is limited, not least for highly dynamic, managed forest landscapes (Christiansen et al., 2022).

Small-scale spatial variation in climate enables species with different climate preferences to co-exist within the same region (Hylander et al., 2022). In the northern hemisphere, plant species at their southern range margin tend to occur at colder microclimates than the average microclimate of the surrounding landscape (Greiser, Ehrlén, et al., 2020). Such places are characterised by later snow melt in spring, lower heat sums during the growing season and less diurnal variation in temperatures compared to the surrounding landscape (Ashcroft et al., 2012; Lenoir et al., 2017; Greiser, Ehrlén, et al., 2020). Plant species with a warmer temperature preference growing at the northern, cold part of their range instead tend to be found in warmer microclimates, characterised by earlier spring, higher heat sums and longer growing seasons (Hannah et al., 2014; Kollas et al., 2014; Lembrechts et al., 2017; Ackerly et al., 2020). The effects of different aspects of cold and warm microclimates might also depend on the life history, growth form and phenology of a species (Dahlberg et al., 2020; Greiser, Ehrlén, et al., 2020).

Changes in forest structure are expected to impact the northern (assumedly cold-favoured) and southern (warm-favoured) species within a community differently due to differences in plant species microclimate preferences (De Frenne et al., 2013). When a forest is thinned, the buffering layer of the canopy decreases, more light penetrate to the ground and summer maximum temperatures in the understorey can increase by several degrees (Greiser et al., 2018). This often leads to an increase in warm-favoured species, decrease in cold-favoured species, or both (Stevens et al., 2015; Zellweger et al., 2020; Christiansen et al., 2022). In forest stands that grow denser, on the other hand, summer maximum temperatures decrease (Greiser et al., 2018), and northern, more cold-favoured species might colonize and increase in abundance (Christiansen et al., 2022). However, these responses might often be slow, and the full effects will only occur a considerable time after a thinning or clearing event (Hylander & Weibull, 2012; Hylander & Ehrlén, 2013; Naaf & Kolk, 2015).

Responses to microclimate changes might first be detectable as effects on individual performance, then as changes in population abundance, and finally as changes in distributions. Individual performance, e.g. in terms of reproduction, is usually strongly linked to optimal climate conditions of the species, as species need sufficient resources to form reproductive organs (Ehrlén & Van Groenendael, 2001; Rydgren & Økland, 2003). If the climate becomes unsuitable, individuals might allocate less resources to flowering or spore production to maintain growth and survival (Ehrlén & Van Groenendael, 2001; Lindell et al., 2021). Eventually, such changes in individual performance will lead to abundance changes. However, it can take considerable time before altered environmental conditions affect also survival and growth, creating a time-lag between the environmental change and changes in abundance in long-lived species (Ehrlén & Morris, 2015). Moreover, even populations decreasing in size can be present for a long time before they go extinct (Kuussaari et al., 2009; Hylander & Ehrlén, 2013). Including multiple measures of species responses, such as occurrence, abundance, and reproduction, thus allow us to better identify and quantify effects of changes in microclimate on species' performances.

In this study, we examined how current and past microclimate influence reproduction, abundance, and occurrence of two northern, cold-favoured and two southern, warm-favoured plant species growing in a region in Central Sweden. Each pair was represented by one vascular plant and one bryophyte. All four species occur in the study region in central Sweden. We inventoried 53 plots in forest stands varying in current as well as past microclimate. We measured the current microclimate with temperature loggers. We modelled past microclimate using the microclimate models from Greiser et al. (2018), in combination with information of forest density 14 years prior to the study. Half of the sites had been thinned 12–14 years prior to the study and were expected to have experienced a colder microclimate before the thinning than under current conditions. The other half had grown denser during the same period, and were therefore expected to have had a warmer microclimate in the past. We hypothesize that:

1. Northern and southern species are favoured in cold and warm sites, respectively, and can therefore coexist in regions where microclimatic variation is large over small spatial scales.
2. Current distributions and performances are not only determined by the current microclimate, but there are also effects of past microclimate.

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2 | METHODS

2.1 | Study area and site selection

The study area was situated in a transition zone called "*Limes norrlandicus*" between the northern boreal forests and the southern boreo-nemoral forests in Sweden. Both north and south of this border the forests are dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), with birch *Betula* spp. and aspen *Populus tremula* having scattered occurrences. However, a range of other broad leaved trees (e.g. pedunculate oak *Quercus robur*) and many other ground-dwelling species have either their southern or northern range limits in this region (Fransson, 1965). Differences in microclimate across the landscape could therefore have a large impact on species composition. We selected sites with varying microclimates, using the publicly available microclimate maps of monthly maximum and minimum temperatures from Greiser et al. (2018). We used two different maps to select sites varying in growing season length. Maximum temperature in April was chosen as a proxy for the start of the growing season, and minimum temperature in September was chosen to represent the end of the growing season. The microclimate maps are at a 25-m resolution, but we wanted to select 50 × 50 m plots and a buffer surrounding each plot with as little microclimate variation within each plot as possible. We therefore aggregated the resolution of the maps from 25 to 100 m using the mean value. To ensure a homogenous microclimate within each plot, we then chose grid cells that had standard deviations of maximum 0.2°C in maximum April and minimum September temperature variation from the original 16 adjacent 25 m grid cells. From these grid cells, we selected comparable forest stands (spruce-dominated and mesic forests) but with different current microclimates (see details in Appendix S1).

To examine the possible effects of past microclimate changes, we stratified our sites further based on changes in forest density between year 2005 and 2018 and information of management activities. Thinned sites were selected if the thinning activities had been conducted during the years 2005–2007 (i.e. 12–14 years prior the study) to ensure enough time for the plants to respond to the new warmer microclimate, and to ensure that the sites were still warmer than prior to the thinning event, i.e. that they had a lower density in 2018 than in 2005. Included sites with a higher density in 2018 than in 2005 had grown denser without any thinning activities. The final number of selected sites was 53, including 27 sites that had grown denser and 26 sites that had been thinned (Figure 1).

2.2 | Species data

We established a 50 × 50 m plot at each of the 53 sites, in which we inventoried the vascular plant communities from the end of June to the end of July 2018, and bryophyte communities in October 2018. From the inventories, we selected four understorey species that were frequent; two northern, cold-favoured, (one herb and one liverwort) and two southern, warm-favoured, species (one grass and one moss). All four are common understorey species in boreal forests, but with declining trends towards either the north or the south of the study area (Figure 1, Appendix S2). *Barbilophozia lycopodioides* (occurring at 13 of the study sites) is a ground-dwelling liverwort found in spruce-dominated forests and declines sharply in abundance south of the transition zone (Rydin

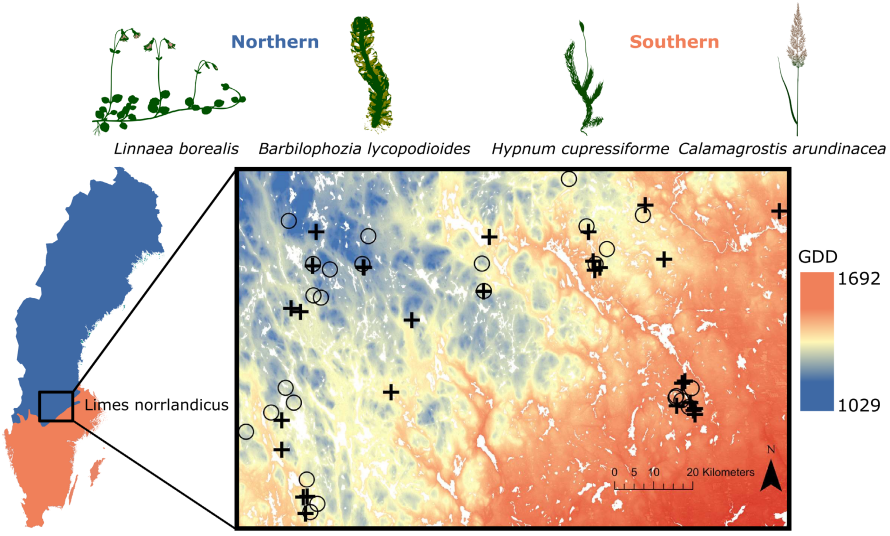

FIGURE 1 Study region, site locations and study species. Map of Sweden showing the study area situated in the transition between the northern boreal zone (blue) and the southern boreo-nemoral zone (red) (*Limes norrlandicus*). The + marks sites in forest stands that had grown denser from 2005 to 2018, and ○ marks the sites that were thinned 2005–2007, and therefore still had a lower forest density in 2018 than in 2005. Colours in the study area map show growing degree days (GDD) from Meineri and Hylander (2017), with blue denoting low GDD values and red denoting high GDD values. Above the maps, the four study species are depicted. For specific locations of the four species, see Figure S1.

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et al., 1999; Damsholt, 2009). *Linnaea borealis* (39 sites) is a northern herb growing in conifer forests (Mossberg & Stenberg, 2010). It is also found south of the study area, but with a lower regional abundance (Rydin et al., 1999). The moss *Hypnum cupressiforme* (29 sites) and the grass *Calamagrostis arundinacea* (42 sites) have southern distributions in Sweden (Mossberg & Stenberg, 2010; Hedenäs et al., 2014).

During July 2019, we recorded presence-absence, abundance, and reproduction for each of the four species. For the two vascular plants, abundance and reproduction was estimated in a 25×25 m plot central of the 50×50 m plot. Within the 25×25 m plot a randomly picked numbered flag was put up for each 1 m^2 in which the species was present. For a maximum of 20 of the lowest numbered flags, a 1×1 m grid consisting of 100 cells of 1 dm^2 was then used to count number of dm^2 with at least one rooted individual. Abundance was estimated as the number of dm^2 with at least one rooted individual present. If the species was present in more than 20 m^2 grids, abundance was estimated by calculating the mean number of dm^2 for the 20 grids multiplied with the total number of square metres with the species present. Reproduction was estimated as number of dm^2 with flowering individuals, and following the same procedure as described above for abundance for populations where the species was present in more than twenty 1 m^2-plots. For the two bryophyte species, we measured abundance and reproduction for the 50×50 m plot by slowly walking transects and counting number of dm^2 with the species present and number of dm^2 with spore-producing individuals. Spore-producing individuals were only recorded for the southern moss since the sporophytes in the northern liverwort are visible only for a very short time.

2.3 | Environmental data

During the period when the vascular plant community was inventoried (July 2018), we placed two microclimate loggers (Lascar USB-2) in the centre of each plot to monitor the microclimate every hour. One logger was placed at the centre of the plot under the moss vegetation in a plastic zip bag to monitor the local ground surface temperatures. A second logger was placed in a 25 cm long white plastic tube horizontally on the north-facing side of the nearest tree to the centre of the plot at 1 m height to monitor air temperature. The two loggers recorded for 1 year and were collected the following summer in July 2019.

To examine how the study species were affected by microclimate, we calculated two microclimate variables from the logger data, representing heat sums during the growing season and last snow melt day, respectively. There are many climate variables that could have effects on species performance. However, recent studies have shown that heat sums and last snow melt day are important drivers of distribution patterns of plant species with different temperature preferences in the boreal understorey (Greiser, Ehrlén, et al., 2020; Greiser, Hylander, et al., 2020). As the temperature loggers were set up in July 2018 and taken down in July 2019, the logger data covered parts of two different growing periods. We therefore calculated growing degree days (GDD) during the growing season across the two seasons, using the mean for the overlapping days. The loggers measuring temperatures at 1 m height was used to calculate GDD during the growing season for each site. Growing season was defined as the consecutive period of mean daily temperatures above 5 degrees. For this period, GDD was calculated as the sum of mean daily temperatures above 5 degrees. The logger under the moss vegetation was used to calculate last snowmelt day, i.e. the first day of spring 2019 after the last period of three consecutive days of maximum daily temperatures varying less than 0.5°C, and with maximum daily temperatures below 3°C (Greiser, Ehrlén, et al., 2020). Due to logger failure, we needed to impute GDD values for four sites using linear regressions (see details in Appendix S3).

To account for current light availability, we took five canopy photos ca. 20 cm above the ground at each site with a digital compact camera and wide angle lenses (Canon PowerShot S120, 5.2 mm). Each 50×50 m plot was divided into four quadrants, and photos were taken from the centre of the 50×50 m plot and from the centre of each of the quadrants. Canopy gap, hereafter called light, was then estimated as the mean of the percentage of pixels not covered by canopy after binarizing from the five photos using the program ImageJ (Schneider et al., 2012). Lastly, we counted the number of boulders in the 50×50 m plot because they are important substrates for *H. cupressiforme*.

To predict past microclimate, we used logger temperature data and explanatory variables from Greiser et al. (2018). Logger data used in Greiser et al. (2018) cover the period May 2015 – September 2016 and include more than 200 loggers spread across a larger area overlapping with our study area and with a significant variation in forest density and topography. Using the logger data from Greiser et al. (2018), we calculated GDD in 2016 using the same method as for the current GDD values described above. We then created a model for GDD in 2016 using explanatory variables from Greiser et al. (2018) consisting of basal area in 2016, altitude, solar radiation, relative elevation, distance to Lake Vänern and distance to nearest waterbody (adjusted R^2 value = 0.51, Appendix S4, and see Greiser et al., 2018). To predict values for past GDD in 2005 (before any thinning treatment) for each of our focal sites we then replaced basal area in 2016 with basal area in 2005 from the forest company using the calibrated model. Basal area in 2016 and 2005 were both estimated using a relascope. We did not include regional climate in the model, as the area is relatively small for significant differences in regional climate as well as changes in regional climate between sites. We chose to not predict past snowmelt dates, as the variation explained by the snowmelt model was very low.

2.4 | Statistical analyses

All statistical analyses were done in R version 4.0.5 (R Core Team, 2021). To examine the effect of current microclimate, we modelled probability of occurrence, abundance (number of dm^2 per

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plot with the species present) and probability of flowering or spore-production for each species as functions of snowmelt date, growing degree days (GDD) and we included light to account for any covariation with microclimate. Number of boulders were included as a covariate in models for the southern moss, *H. cupressiforme*.

Probability of occurrence was modelled as a logistic regression with a binomial error distribution and a logit-link function, except for *B. lycopodioides* where the complementary log–log link function was used to account for the skewed proportion of a low number of presence points and a high number of absence points. We modelled abundances at sites where the species was present using a log-link function assuming a Poisson distribution. To account for overdispersion, a random intercept per observation (site) was included (Harrison, 2014). Due to the low number of records of *B. lycopodioides* (13), we ran two abundance models, one with snowmelt and one with GDD and used AICc to select the best model. Due to low number of sites with reproducing individuals, reproduction for all species was modelled as presence-absence at the sites where the species was present, using a binomial distribution with a logit-link function.

To examine whether information of past microclimate influenced the responses of the four species, we ran the models described above, also including the predicted past GDD. To test whether the models including past GDD were better than those with only current conditions, we compared the AICc of models showing a significant relationship between a species response and past GDD values with those models excluding past GDD. The abundance model of the northern liverwort did not converge when including both current GDD, past GDD and light. We therefore first ran the abundance model with only current GDD and compared it with a model including current and past GDD (both models excluding light).

Models were fitted using generalized linear models or generalized linear mixed models with the functions *glm()* and *glmer()* from the *lme4* package (Bates et al., 2015). All predictors were scaled to unit variance and mean-centered prior to analysis. Model diagnostics were assessed using the *DHARMa* package (Hartig, 2021). Likelihood ratio test was used for statistical significance of predictor variables with the function *Anova()* from the *car* package for the occurrence and reproduction models (Fox & Weisberg, 2019), and *drop1()* from the *MuMin* package for the abundance models (Bartón, 2020). To visualise the marginal effects of significant predictors, we used the function *ggpredict()* in the *ggeffects* package (Lüdecke, 2018) and partial residual points were extracted with the function *remef()* in the *remef* package (Hohenstein & Kliegl, 2022).

3 | RESULTS

3.1 | Effects of current microclimate

Current microclimate conditions varied substantially across the sites, GDD from 1231 to 1680, and snowmelt date from day 77 to 106. In most cases when microclimate had an effect on occurrence, abundance or reproduction, the study species were influenced in the way expected based on their geographical distribution, i.e., northern species were often favoured by later snowmelt, and southern species by higher levels of GDD (Figure 2, Appendix S5). Occurrence of the two northern species, and abundance of the northern herb, *L. borealis*, significantly increased in sites with later snowmelt (Figures 2 and 3a). Abundance of the northern liverwort, *B. lycopodioides*, increased with decreasing GDD (Figure 3c). Flowering was positively affected by later snowmelt in the northern herb. The southern moss, *H. cupressiforme*, was more often present at sites with higher levels of GDD (Figure 3d). The abundance of the southern grass *C. arundinacea* increased with increasing GDD (Figure 3b).

3.2 | Effects of past microclimate

Past GDD significantly affected abundance of three of the four species (Figure 4, Appendix S6). The northern liverwort was negatively affected by both current as well as past GDD (Figure 4a). The southern grass was positively affected by past GDD (Figure 4b). When past GDD values were included in the abundance model of the southern moss, it was negatively affected by current GDD, but positively affected by past GDD (Figure 4c). This means that the highest abundance was in sites with a warm past microclimate and where the forest since had grown denser and thereby had a colder current microclimate.

4 | DISCUSSION

We examined the responses of northern and southern boreal understorey plant species to current and past microclimates. Overall, when microclimate had an effect, the observed patterns agreed with the expected. Northern species responded positively to cold microclimates and southern species responded positively to warm microclimates. Past microclimate, in terms of GDD, had significant effects on the abundance of three out of four species. Our findings suggest that in a heterogeneous microclimate landscape, co-occurring northern and southern plant species are distributed and perform in accordance with their temperature preference as inferred from their wider geographical distribution (Dahlberg et al., 2020). They also suggest that time-lags in the response of species to forest management and altered microclimate are important.

4.1 | Effects of current microclimate

Abundance and probability of occurrence of the two northern species were often higher in colder microclimates, whereas they were generally lower for the two southern species in those sites. This is consistent with the idea that in a landscape, species with different geographical distributions are often found in places where the microclimates most resemble the conditions across their

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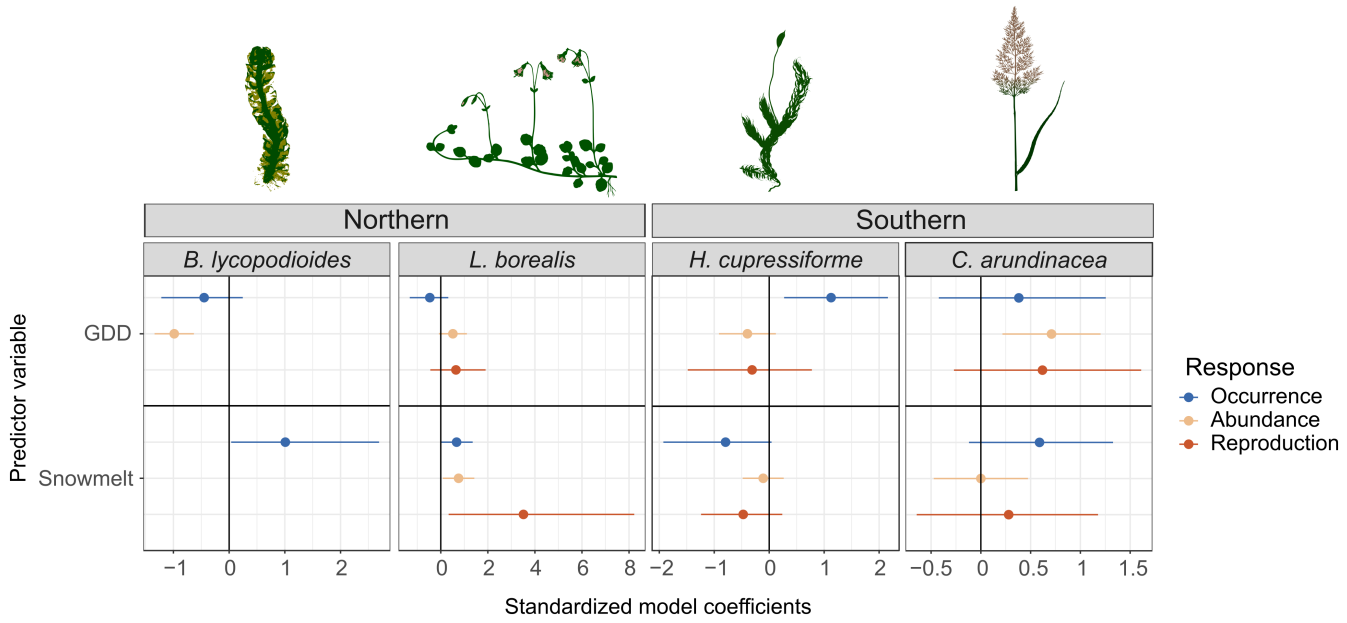

FIGURE 2 Standardized model coefficients of log-odds and log-incidence rate ratios with 95% confidence interval bands from models of the relationships between the four species responses and growing degree days (GDD) and snowmelt day, respectively.

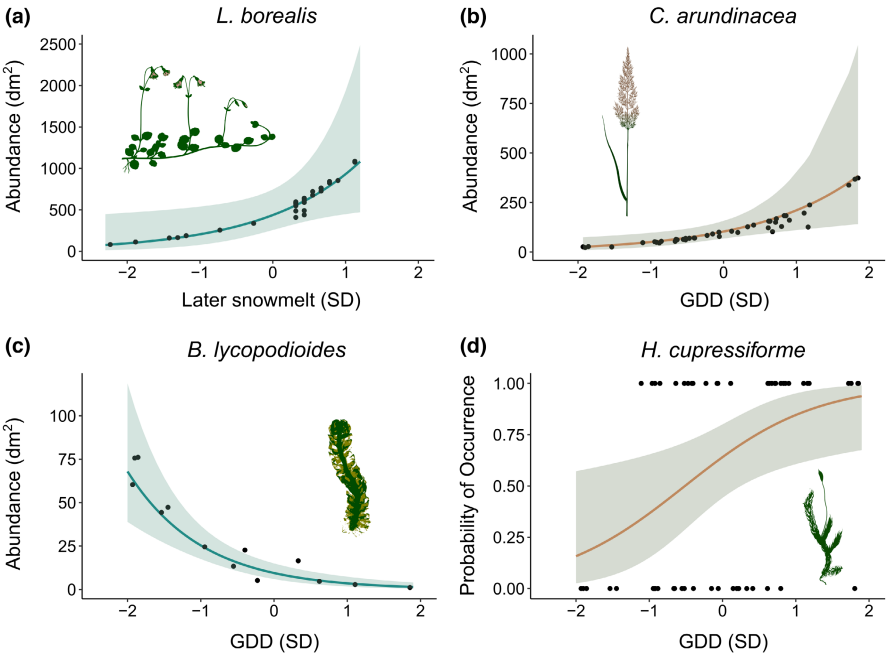

FIGURE 3 Partial regression plots of relationship between snowmelt or GDD on abundance or probability of occurrence for the two northern plant species (a) *L. borealis* and (c) *B. lycopodioides* , and the two southern plant species (b) *C. arundinacea* and (d) *H. cupressiforme*. Lines represent the predicted marginal effects of the respective microclimate variable, with blue lines representing northern species and brown lines representing southern species. Shaded areas represent the 95th confidence interval. For abundance, points are partial residual points. Predictors are shown in units of standard deviations away from the mean.

distribution range (Ackerly et al., 2020; Greiser, Ehrlén, et al., 2020; Hylander et al., 2022). Consequently, heterogeneous microclimate landscapes, resulting from topographic heterogeneity and forest density variation, can harbour species with different climate niches (Ackerly et al., 2010; Graae et al., 2018). In our study, the northern, cold-favoured, species were positively affected by later snow melt and negatively affected by higher accumulated heat during the growing season (GDD). One possible reason why northern species might be favoured in cold microclimates is that they experience less physiological stress due to lower maximum temperatures (Greiser, Ehrlén, et al., 2020). Besides lower maximum temperature, sites with later snowmelt also secure more water in the soil further into the growing season (Blankinship et al., 2014; Zhang et al., 2019). An additional potential reason for northern species performing better and occurring more often in cold microclimates is that competition from southern species is less intense (Löbel et al., 2018; Paquette & Hargreaves, 2021). The lower competition might in turn be due to a lower tolerance of southern species to lower levels of accumulated heat over the growing season and shorter growing seasons (Normand et al., 2009). Bryophytes transplanted to their southern range margin also performed better in warm than cold temperatures in plots without any competing vegetation (Greiser et al., 2021), supporting the notion that poorer performance at the warm range margin in nature might be caused by more intense competition rather

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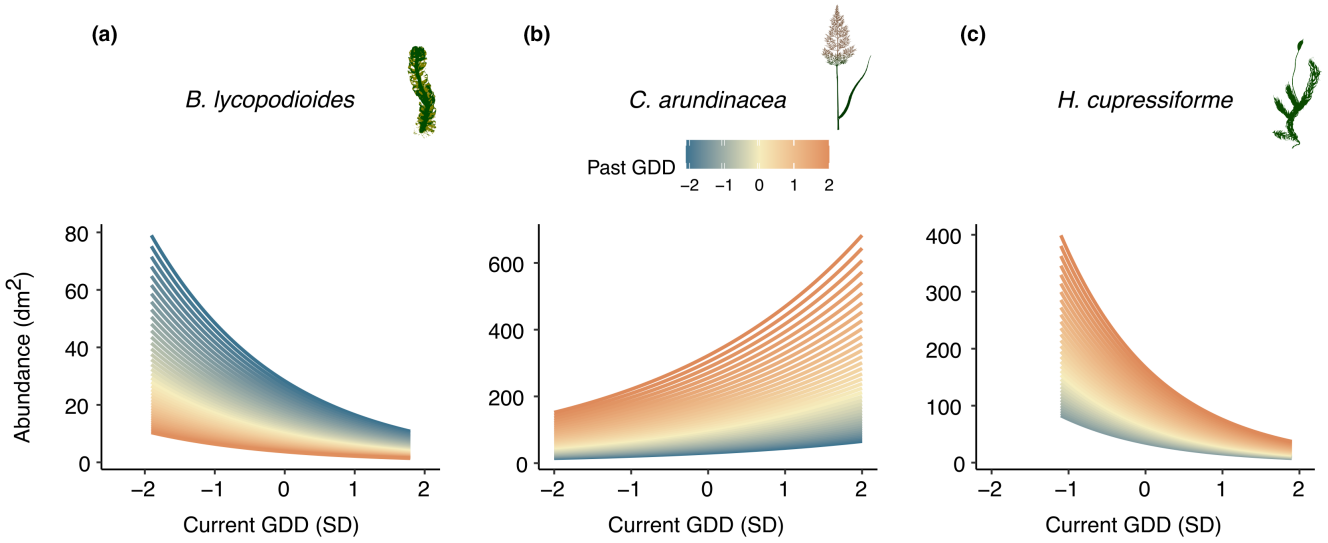

FIGURE 4 Predicted marginal effects of current and past GDD on abundance of (a) the northern liverwort (*B. lycopodioides*), (b) the southern grass (*C. arundinacea*) and (c) the southern moss (*H. cupressiforme*). Colored lines show past GDD values, with blue denoting sites that were colder in the past, and orange sites that were warmer in the past. X-axis shows current values of GDD. Units of both current and past GDD are shown in standard deviations away from the mean.

than being the direct effects of climate. The positive effect of later snowmelt and lower GDD on northern plant species in our study might therefore be a combination of direct and indirect effects in terms of relaxation of physiological stress and reduced competition (Heegaard & Vandvik, 2004; Zhang et al., 2019; Greiser et al., 2021; Paquette & Hargreaves, 2021).

The two southern, warm-favoured, species were positively affected by GDD and did not respond to variation in snowmelt. Southern species are often found to perform better at sites with an early spring, and thus longer growing seasons and higher levels of accumulated heat (Normand et al., 2009; Lenz et al., 2013; Greiser, Hylander, et al., 2020). High levels of GDD decrease development time, thereby increasing time for accumulation of resources to the next season as well as the time for reproduction (Morin et al., 2008; Ehrlén & Valdés, 2020; Lindell et al., 2021). Increased accumulated heat should therefore give southern and relatively fast-growing species a competitive advantage compared to more northern and slow-growing species (Löbel et al., 2018). That snowmelt did not affect the performance of the southern species might be because accumulated heat during the growing season is more important than the timing of snowmelt.

We expected a relatively strong relationship between frequency of flowering and spore-production and current microclimate. Yet, it was only for the northern herb, *L. borealis*, that we found a positive correlation between later snowmelt and probability of flowering. Possibly this was caused by the ability of snow to protect the plant and its flower buds from damaging spring frost events (Inouye, 2008; Iler et al., 2019; Pardee et al., 2019). It is also possible that water availability coupled to later snowmelt (Iler et al., 2019) improved the plants resource acquisition necessary for producing flowers. The absent relationship between flowering and microclimate for the southern grass might be due to use of stored resources from previous growing seasons as is common for perennial species. For the southern moss, air humidity might be a more important driver of spore production than temperature (Rydgren et al., 2006).

4.2 | Effects of past microclimate

Past microclimate in terms of GDD influenced the current abundance of three species. As hypothesized, sites that were continuously cold or warm had higher abundances of northern and southern species, respectively, than sites that had experienced different conditions in the past. We focused on effects of changes in microclimate, although management activities can induce change in other factors such as humidity and light that could have effects on understory species responses (Govaert, Vangansbeke, Blondeel, De Lombaerde, et al., 2021; Greiser et al., 2021). We chose sites with similar moisture levels and included current light levels in the analyses to ensure that the observed effects of microclimate are not only due to these other factors. However, to fully separate the effects of light and temperature and their interactive effects requires experimental studies (Blondeel et al., 2020; De Frenne et al., 2015; Govaert, Vangansbeke, Blondeel, Steppe, et al., 2021). Effects of changes in temperature and other factors could also act indirectly through changes in competitive interactions, herbivory and interactions with soil biota (Pagès et al., 2003; Rasmussen et al., 2020; Greiser et al., 2021). The effects of past microclimate observed in this study might therefore be a combination of both direct and indirect effects of past temperatures as well as past light conditions and their interactive effects.

Lags in plant responses to climate change have been documented in several studies (Bertrand et al., 2011; Dullinger et al., 2012; Talluto et al., 2017; Rumpf et al., 2019). Still, many predictions of

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species responses to either micro- or macroclimate warming assume equilibrium between current species patterns and current climatic conditions (Dormann et al., 2012; Alexander et al., 2017; Lee-Yaw et al., 2022). If species are not in equilibrium with current conditions, but exhibit legacy effects of past conditions, it hampers our ability to infer how species will respond to climate change from current patterns of abundances and distributions (Svenning & Sandel, 2013).

We found effects of past microclimate on abundance, but not on occurrence. This might be because local extinction and colonization processes are slower than changes in performance and abundance (Vellend et al., 2006; Svenning & Sandel, 2013; Lehtilä et al., 2016). Many long-lived vascular plants decrease in abundance as a response to changes in forest density and microclimate but can persist under unfavourable conditions over a considerable period, and might therefore be able to bridge the gap between unfavourable and favourable conditions (Eriksson, 1996; Graae et al., 2018). Responses of abundance, although relatively slow, might thus be fast enough to respond to conditions earlier in the management cycle, while responses of distributions might be so slow that they integrate effects over more than one management cycle. Persistence despite temporarily unfavourable conditions might therefore be possible in managed forest stands if alterations between favourable and unfavourable microclimates, caused by cycles of thinning activities and periods of growing denser again, often occur over shorter time intervals than local extinctions. Short-lived species might on the other hand be more likely to go locally extinct if they are sensitive to unfavourable conditions in dynamic managed forests, as they are likely to respond more rapidly to impaired conditions (Löbel et al., 2021). In highly dynamic managed forest landscapes, the observed understorey community composition at a specific point in time is likely to always be more or less in disequilibrium with the current environment. Old-growth forests also experience natural disturbance dynamics resulting in spatiotemporal variation in microclimate. However, unlike the disturbance regime of managed forests with spatially regular and temporally short rotation system, old-growth forest landscapes often include substantial areas with stable and cooler microclimates over long timespans (Kim et al., 2022; Xu et al., 2022). Nevertheless, it is essential to account for past conditions and previous disturbances in both managed and natural dynamic forest systems when analysing current patterns of distributions and performances of plant species in the understorey (Lenoir et al., 2022).

5 | CONCLUSION

Our results support the notion that geographic distributions over large spatial scales can inform us about where in a focal landscape different species are present and abundant (Dahlberg et al., 2020). This pattern, if proven to be general, implies that characterising and preserving gradients of warm and cold microclimates across landscapes constitutes a valuable tool to mitigate effects of climate change on forest biodiversity (Hylander et al., 2022). Our results also show that time-lags in species responses to climate and land-use changes might sometimes be important. An important implication of such time-lags is that the relationship between current species distributions and abundances and environmental conditions is more complicated than often assumed, and that predictions of responses to recent environmental change will need to account for time-lagged responses (Svenning & Sandel, 2013). We therefore encourage future research efforts to also incorporate past conditions when examining responses to climate change, especially when studying highly dynamic landscapes, such as managed forests, and when studying long-lived species which are likely to respond slowly.

AUTHOR CONTRIBUTIONS

DMC, CG, JE, and KH designed the study. TS, RM and DMC conducted the fieldwork. DMC and TS analysed the data. DMC wrote the first draft with support from CG, JE, and KH. All authors contributed to the final version of the manuscript.

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DATA AVAILABILITY STATEMENT

Data used for the analyses can be found in the Figshare repository: https://doi.org/10.6084/m9.figshare.23544609.v2

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SUPPORTING INFORMATION

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

Appendix S1. Additional details on site selection.

Appendix S2. Maps of occurrences of the four study species.

Appendix S3. Imputing current GDD values.

Appendix S4. Prediction of past GDD values.

Appendix S5. Effects of current microclimate on occurrence, abundance and reproduction of the four species.

Appendix S6. Effects of past microclimate on the four species.

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