

RESEARCH ARTICLE

Changes in forest structure drive temperature preferences of boreal understorey plant communities

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Abstract

1. The local climate in forest understories can deviate substantially from ambient conditions. Moreover, forest microclimates are often characterized by cyclic changes driven by management activities such as clear-cutting and subsequent planting. To understand how and why understorey plant communities change, both ambient climate change and temporal variation in forest structure have to be considered.
2. We used inventories from 11,436 productive forest sites in Sweden repeated every 10th year 1993–2017 to examine how variation in forest structure influences changes in the average value of minimum and maximum temperature preferences of all species in a community, that is, community temperature indices (CTIs). We then evaluated to what extent these changes were driven by local extinctions and colonizations, respectively, and to what extent the difference in CTI value between two inventories was related to changes in forest density and in macroclimate. Lastly, we tested whether effects on CTI change by these two drivers were modified by topography, soil moisture and tree species composition.
3. CTI values of the understorey plant communities increased after clear-cutting, and decreased during periods when the forest grew denser. During the period immediately after clear-cutting, changes were predominately driven by colonizations of species with a preference for higher temperatures. During the forest regeneration phase, both colonizations by species preferring lower temperatures and local extinctions of species preferring higher temperatures increased. The change in understorey CTI over 10-year periods was explained more by changes in forest density, than by changes in macroclimate. Soil moisture, topography and forest tree species composition modified to some extent the effects of changes in forest density and in macroclimate on understorey CTI values.
4. *Synthesis.* Via stand manipulation, forest management impacts the effects of regional climate on understorey plant communities. This implies that forest management by creating denser stands locally even can counterbalance the effects

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of regional changes in climate. Consequently, interpretations of changes in the mean temperature preference of species in forest understorey communities should take forest management regimes into account.

KEYWORDS

boreal forests, chronosequence, climate change, community temperature index, forest management, microclimate, temperature niche, understorey plants

1 | INTRODUCTION

Dense forest canopy and sheltering topography create forest microclimates that can be several degrees colder than outside the forest on a hot summer day (Ashcroft & Gollan, 2012; De Frenne et al., 2019; Greiser et al., 2018). Due to the capacity of the forest canopy to buffer temperature extremes and severe droughts, forests can act as microrefugia for plants and animals in landscapes of otherwise unfavourable regional climate conditions (Frey et al., 2016; Greiser et al., 2020; Scheffers et al., 2014). The buffering effect of forests increases with increasing regional temperatures (De Lombaerde et al., 2021). This indicates that the importance of forests for maintaining populations of species disfavoured by high temperatures is likely to increase during contemporary climate warming (De Frenne et al., 2019). Still, our knowledge of how forest microclimate impacts the response of understorey communities to climate warming is limited (De Frenne et al., 2013; Zellweger et al., 2020). This is especially true for forest ecosystems with large scale anthropogenic or natural disturbance dynamics (Richard et al., 2021).

In many forest ecosystems, the canopy cover undergoes frequent and dramatic changes. Forest fires, storms and pest outbreaks (Gauthier et al., 2015; Kuuluvainen & Aakala, 2011) create large spatial and temporal variation in the understorey microclimate that in turn affect the composition of the understorey communities. In many managed forest systems, forest structure changes with cycles of clear-cutting, planting and thinning (Gold et al., 2006). A decrease in stand density after clear-cutting is expected to reduce local climate buffering and cause a shift in understorey communities towards a larger proportion of warm-favoured species (Stevens et al., 2015; Zellweger et al., 2020). On the other hand, current forest management regimes that include replanting after clear-cutting result in higher densities than natural regeneration after disturbances (Ackzell, 1993), likely reducing ground temperatures and favouring cold-favoured species. As a result of clear-cutting, planting and thinning cycles, we expect that microclimate and temperature preference of the understorey community varies in both magnitude and direction with time (Richard et al., 2021).

Community dynamics are structured by colonization, extinction and changes in abundance of individual species. If only presence/absence data exist the mean temperature preference of species in the community will increase or decrease as species go extinct or colonize in response to changes in microclimate. Forest plants vary in their ability to colonize and avoid extinctions (Vellend et al., 2006). For example, many bryophytes are known to exhibit relatively high

rates of extinction after disturbances (Vanha-Majamaa et al., 2017), whereas some long-lived perennial plants are known for relatively slow rates of both colonization and extinction (Lehtilä et al., 2016; Vellend et al., 2006). So far, the relative contribution of extinction and colonization processes to understorey community responses to changing climate during management cycles is poorly known.

Irrespective of the relative contribution of colonizations and extinctions, current climate change is expected to lead to warmer mean temperature preferences of plant communities, so-called thermophilization (Zellweger et al., 2020). However, several studies have found that forest understorey communities have responded less to climate warming than expected given species temperature preferences (Bertrand et al., 2011; Harrison et al., 2010; Savage & Vellend, 2015). Such smaller than expected responses might be due to the buffering effect forests have on the local microclimate (De Frenne et al., 2013; Guo et al., 2018; Zellweger et al., 2020). This mechanism is expected to be particularly pronounced in managed forests with strong variation in canopy cover over time.

Besides forest structure, several other climate-forcing factors may modify the forest understorey response to climate warming. For example, plants in sites with a less exposed topography might respond less to changes in forest density or macroclimate compared to plants in exposed sites (Åström et al., 2007; Graae et al., 2018), and high soil moisture might buffer high temperatures and reduce community change after canopy opening (Ashcroft & Gollan, 2013; Davis et al., 2019). However, the extent to which these factors modify the responses of the understorey communities to macroclimate changes or management-driven changes in forest density is still largely unexplored.

The aim of this study is to explore how variation in temperature buffering of the forests and changes in macroclimate affect the mean temperature preference of species in the understorey plant communities. A metric often used to quantify the response of communities to climate change is the community temperature index (CTI), which is the average value of species-specific temperature preferences across all occurring species in a community (Devictor et al., 2012; Richard et al., 2021; Zellweger et al., 2020). Based on species-specific temperature preferences inferred from distribution patterns, we calculated CTI of maximum (CTI_{max}) and CTI of minimum (CTI_{min}) temperatures for understorey plant communities in 11,436 Swedish temperate–boreal permanent forest plots that were inventoried two to three times during the period 1993–2017. We then examined how these values changed between two consecutive inventories 10 years apart, and addressed the following questions:

1. How does the mean temperature preference, in terms of CTI_{max} and CTI_{min} , change with time since clear-cutting in the understorey plant communities?
2. To what extent are changes in the mean temperature preference of species in the understorey plant communities caused by local extinction versus colonization events?
3. What is the impact of changes in forest density and macroclimate on the mean temperature preference of species in the understorey plant communities?
4. To what extent are the effects of changes in forest density and macroclimate on the mean temperature preferences of species in the understorey plant communities modified by tree species composition, topography and soil moisture?

As plants experience climate locally, we predict that forest understorey plant communities will respond to management-induced changes in microclimate. Because maximum temperatures are often lower inside forests than outside (De Frenne et al., 2019), we predict that understorey CTI of maximum temperature will increase after clear-cutting and decrease when the forest grows dense. As minimum temperatures are often higher inside forests than outside (De Frenne et al., 2019), we predict the opposite pattern for understorey CTI of minimum temperature. We predict that both colonization and extinction caused by changed conditions will make substantial contributions to changes in CTI values. Over the investigated 10-year time steps, we predict that forest density is a stronger driver of change in CTI values of the communities than macroclimate (Greiser et al., 2018; Zellweger et al., 2020). Last, we predict that responses of CTI values to changes in macroclimate and forest density are modified by topographical position, soil moisture and tree species composition.

2 | MATERIALS AND METHODS

2.1 | Study area

Sweden extends over 14 degrees of latitude, and annual mean temperatures in the normal period 1961–1990 ranged from -3 to 8°C (Persson, 2015). The southern part of Sweden is in the temperate biome and northern parts belong to the boreal and sub-alpine biomes. Annual mean temperatures increased by approximately one degree from 1993 to 2017, and all study years except two had a higher annual mean temperature than the mean during 1961–1990 (higher annual mean ranging from 0.28 to 2.26°C ; www.smhi.se, Persson, 2015).

Productive forest lands cover 58% of the total area of Sweden. Almost all productive forests are managed. The management practices have changed dramatically during the 20th century, with the introduction of harvesting by clear-cutting in the 1940s and planting in the 1960s (Lundmark et al., 2013; Östlund et al., 1997). The present forest landscape consists of mosaics of even-aged stands of all ages from newly clear-cut to mature stands, with the 0–40-year-age class

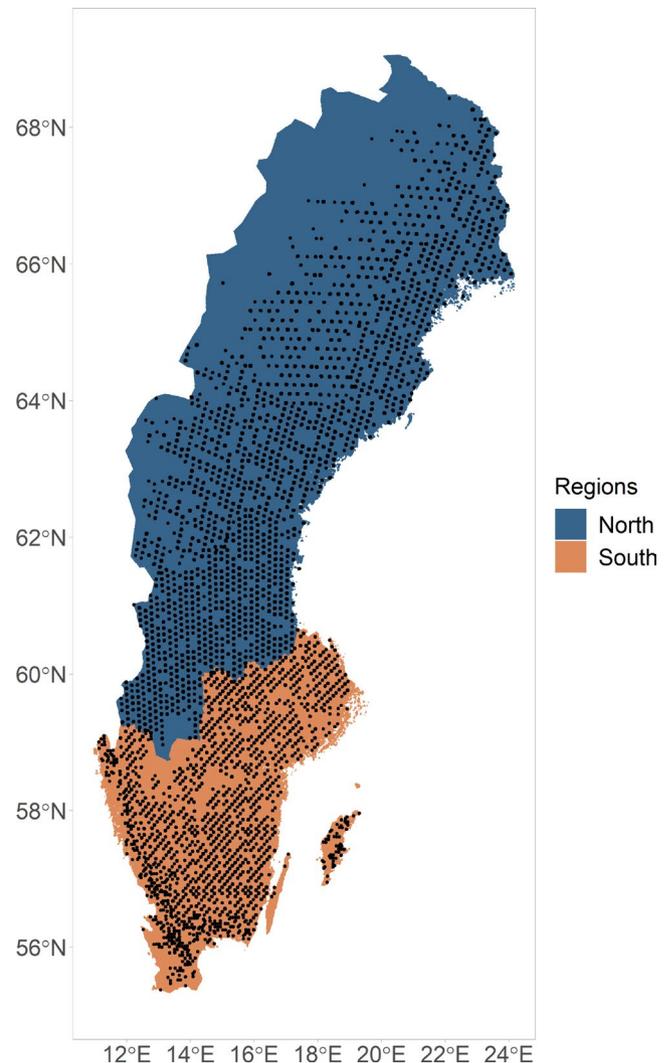


FIGURE 1 Map of Sweden showing the location of the permanent community plots of the National Forest Inventory (NFI) included in the analyses on top of the regions used for data partitioning

being most frequent (Nilsson et al., 2019). Forests are clear-cut at the age of 70–120 years, depending on productivity. There are multiple thinning cycles between planting and clear-cutting (Roberge et al., 2020), with the first thinning usually happening at the age of 25–55 years (Agestam, 2015). The dominant tree species are Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*, together covering 80% of the forest area.

2.2 | Data

We used 11,436 permanent plots of the national inventory of Sweden's productive forests (NFI; Figure 1). The NFI was initially established in 1929 to monitor the productivity of the Swedish forests in terms of timber production. Permanent plots were established from 1983 to monitor several forest ecosystem services, including understorey plant diversity (Fridman et al., 2014). During our study

period 1993–2017, understorey plants were inventoried in 14,384 permanent plots of 100 m² in cycles of 10 years (c. 1100 plots per year, with years of inventories differing between plots). For each plot, forest structure variables such as basal area (m²/ha), stand age and tree species composition were inventoried in an area of 300 m² (Fridman, 2016; Fridman et al., 2014). For our study, we used only plots that were located within productive forests, and excluded 1880 plots containing a mixture of land uses. Plots with a forest age above 150 years were also excluded, as these were not the focus of our study due to their effectively unmanaged status. Quantifying community changes required a minimum of two inventories across the study period, and plots with only a single visit (427) were excluded from the analysis. The final dataset included 11,436 plots, where 6076 plots had been inventoried twice and 5360 plots three times. A transition was defined as community changes from the first inventory to the second inventory, and the dataset included 16,796 transitions in total.

The presence of understorey plant species was registered from a list of 270 vascular plant, bryophyte and lichen species or species groups, of which we omitted some species groups due to the inclusion of two common species with different temperature preferences (see Table S1). Our aim was to examine the effects of changes in forest density and in macroclimate on the mean temperature preference of species in the understorey plant communities. In order to account for the fact that the understorey communities may also respond to changes in nutrient and light availability, that might change in parallel with temperature during forest development, Ellenberg nitrogen and light values were extracted for all species where they were available (Hill et al., 1999, 2007; Wirth, 2010). Ellenberg values are indicator scores on ordinal scales that position plants in Central Europe along gradients of environmental variables, and have been widely used in ecological studies (cf. Hedwall & Brunet, 2016; Perring et al., 2018; Tonteri et al., 2016). Nine species were missing Ellenberg values and were excluded from the analyses. The final dataset included 211 taxa (hereafter called 'species'), including 199 vascular plants, nine bryophytes and three lichens.

The northern and southern parts of Sweden differ in plant species pools, forest productivity, management regimes and land use history (Roberge et al., 2020). Following Hedwall and Brunet (2016), we explored patterns separately for northern-central Sweden (the boreal zone), and southern Sweden (the nemoral and hemiboreal zones; Figure 1).

2.3 | Changes in CTI values

To link changes in the composition of understorey communities to temperature, we used the community temperature index (CTI; Richard et al., 2021; Savage & Vellend, 2015; Zellweger et al., 2020). CTI reflects the composition of warm- and cold-favoured species in a community, and is therefore expected to change with a changing climate. We calculated two CTIs for each plot and inventory; CTI for maximum (CTI_{max}) and CTI for minimum (CTI_{min}) temperature. To do

this, we first calculated the species-specific maximum and minimum temperature preferences. We used globally collected occurrence points from Global Biodiversity Information Facility (GBIF) and bioclimate variables of maximum temperature during the warmest month and minimum temperature during the coldest month from CHELSA (averaged over the years 1979–2013, Karger et al., 2017). Duplicate records where the species were found at the same coordinates in multiple years were removed. For each species, the climate values at each occurrence point were extracted and temperature preferences were calculated by averaging the climate values from all occurrence points for maximum and minimum temperatures respectively. An advantage of inferring species-specific temperature preferences from occurrence databases like GBIF is that several different climate variables can be extracted. However, the GBIF database contains spatial biases in reporting of species, which might influence the absolute values. Since our aim was to examine changes in CTI values of communities between inventories rather than absolute values, we considered the approach appropriate.

For each plot and inventory, CTI values of maximum and minimum temperature were calculated by averaging the inferred temperature preference values of all species present. The change in CTI values between two inventories separated by 10 years, was then calculated by subtracting the value of the first inventory from the value of the second inventory. A positive value thus implied that the community at the second inventory was composed of species that occupy geographic ranges with higher average temperatures, and vice versa.

2.4 | Calculations of drivers of change in CTI

To analyse the impact of changes in forest density and macroclimate on changes in CTI values, we calculated the difference in macroclimate and in forest density between two consecutive inventories. We also calculated a number of covariates that we hypothesized would modify the effects of forest density and macroclimate on changes in CTI values. From the NFI, we used total basal area (m²/ha) as a measure of forest density, and calculated forest density change by subtracting the basal area of the first inventory from the basal area of the second inventory. We used TerraClimate (Abatzoglou et al., 2018) to estimate changes in macroclimate because information was available for all years, but CHELSA to calculate species-specific temperature preferences because it has a finer spatial resolution. At a 4 km resolution, maximum temperature of the warmest month and minimum temperature of the coldest month were extracted for each plot and inventory. We used a 5-year average of the macroclimate temperatures calculated from the year of the inventory and the 4 years preceding it, as the macroclimate temperature of the inventory. To estimate the change in macroclimate between inventories, the average minimum and maximum macroclimate temperature of the first inventory was subtracted from the average of the second inventory respectively.

For each plot, we extracted and calculated elevation, log-transformed relative elevation, soil moisture, slope, aspect and the

proportions of spruce and pine at the second inventory. Slope and aspect were combined into one measure of topographical northness, by multiplying the sine of slope with the cosine of aspect (Amatulli et al., 2018). Finally, the community means of Ellenberg nitrogen and light values of all species present at the second inventory were calculated. Calculations and motivations for the inclusion of each of these covariates can be found in Table S2.

2.5 | Statistical analyses

All statistical analyses were done in R version 3.6.3 (R Core Team, 2020). All models were run separately for CTI_{max} and CTI_{min} , and for each region. All models were fitted with the functions *gam* and *gamm* from the package *MGCV* (Wood, 2004). In all models, we included a two-dimensional spherical spline term based on the geographic coordinates of the plots in order to account for any spatial autocorrelation (Wood, 2006). All predictors were scaled across regions to unit variance and mean centred prior to analysis. All reported *p*-values are based on Wald tests (type III). For overview of variables and details on model structures, see Table S3.

To describe the general changes in CTI values, forest density and macroclimate across our entire study period 1993–2017, we used Gaussian intercept-only models. χ^2 tests were used to test the significance of the mean change. The average changes are reported as the mean with 95% confidence interval. The average changes of forest density and macroclimate are reported in Figure S2.

To examine how changes in CTI values varied with stand development after clear-cutting (Question 1), we used a chronosequence approach (Foster & Tilman, 2000), also known as space-for-time substitution. We used generalized additive models with change in CTI between two inventories as response variable and stand age at the second inventory as explanatory variable. We incorporated a cubic spline term with knots for every year (150) to follow the pattern of changes along the gradient of stand age as close as possible. For the predictions of changes in CTI values, the two-dimensional spherical spline term was held constant at the mean geographic position of the plots. We illustrated the pattern by highlighting periods of stand age where the mean predicted values of the change in CTI and the 95% confidence interval were above or below zero for a period of minimum 10 years.

To describe the relative contribution of extinctions and colonizations to the overall changes in CTI (Question 2), we calculated their respective contributions to changes in CTI (see Equation S1). For both extinctions and colonizations, positive values indicate that the species that went extinct or colonized between two consecutive inventories contributed to an increase in the CTI, and negative values indicate that species contributed to a decrease. We used these estimated values as response variables and stand age at the second inventory as explanatory variable to analyse how the relative contribution of local extinctions and colonizations to the overall changes in CTI was related to stand age. We implemented the same model and prediction structure used to examine changes in CTI in relation to stand age as described above for question 1.

Finally, we estimated the impact of changes in forest density and in macroclimate on understorey CTI values (Question 3), and investigated if such impacts were modified by topography, soil moisture and forest composition (Question 4). CTI values from the second inventory were used as response in a Gaussian linear mixed model with changes in forest density and macroclimate between two consecutive inventories as linear predictors. We included covariates of proportions of spruce and pine trees at the second inventory, soil moisture, topographical northness, relative elevation and absolute elevation to account for the effects of these landscape variables on the CTI values between plots. Moreover, to test if topography, soil moisture or forest tree species composition modify the effects of changes in forest density or in macroclimate, we included the interactions between changes in forest density and macroclimate, and landscape covariates. To account for possible covariation between the CTI values and community means of nitrogen and light, community means of Ellenberg nitrogen and light values from the second inventory were included. Finally, the CTI value of the respective temperature index from the first inventory was included as a covariate to account for the initial condition. Besides spatial autocorrelation, plot ID was included as a random intercept to account for possible effects of temporal autocorrelation. For results on covariates, see Figure S4 and Table S6.

3 | RESULTS

Changes in CTI_{max} between inventories in the north ranged from -0.35 to 0.4°C (1st and 99th percentile; mean \pm 95% CI = -0.003 ± 0.0028 , $p = 0.028$), while changes in the south ranged from -0.42 to 0.52°C (mean \pm 95% CI = 0.02 ± 0.0043 , $p < 0.001$). Changes in CTI_{min} ranged from -0.95 to 0.98°C (mean \pm 95% CI = 0.004 ± 0.004 , $p = 0.34$) in the northern region, and from -1 to 1.23°C (mean \pm 95% CI = 0.06 ± 0.01 , $p < 0.001$) in the southern region.

3.1 | Changes in CTI values of understorey plant communities with stand age

Both CTI_{max} and CTI_{min} increased during the first phase after clear-cutting, then decreased, and finally stabilized around zero (Figure 2; Table S4). Changes in CTI_{max} and CTI_{min} were time-lagged during the first phase of stand development, with increases in CTI peaking at 4.5–6 years after clear-cutting. CTI values increased most during the first phase, and the length of the second phase with decreasing CTI values was shortest for minimum temperature in the southern region (from 15 to 27 years), and longest for maximum temperature in the northern region (from 15 to 47 years). Hereafter followed a relatively stable phase with only small increases in CTI values in the southern region (Figure 2b,d) and no increases in the northern region (Figure 2a,c).

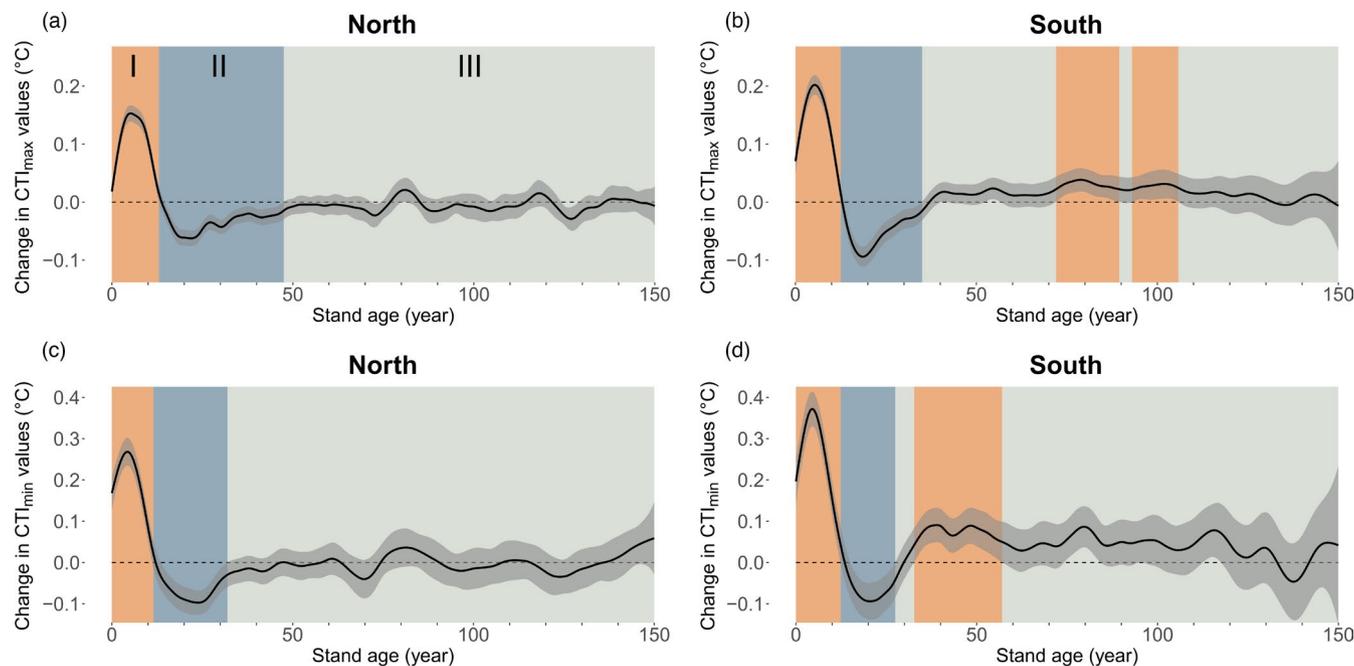


FIGURE 2 Predicted mean changes in CTI_{max} (a, b) and CTI_{min} (c, d) between inventories of 10 years with 95% confidence interval in relation to stand age. Orange and blue colours highlight periods of stand age where changes in CTI values were significantly different from zero during a period of at least 10 years. Orange denotes periods of increases in CTI values, and blue denotes periods of decreases in CTI values. Grey colour denotes periods of stand age where change in CTI values was not significantly different from zero for at least 10 years. Numbers on Figure 2a refer to highlighted phases of stand age, where first phase after clear-cutting shows general increases in CTI values, followed by second phase with general decreases, and lastly a longer and relatively stable third phase

3.2 | Changes in CTI caused by local extinction versus colonization events

Both colonizations and extinctions contributed to the increase in CTI values during the first phase of stand development, but the contribution of colonizations was on average larger than that of extinctions (Figure 3; Table S5). During the second phase, the decrease in CTI values was driven equally by colonizations and extinctions (Figure 3). For the southern region, for which there were periods of increases in CTI values during the third phase, colonizations contributed to increases in both CTI_{max} and CTI_{min} , while extinctions counteracted the increase in CTI_{max} , but contributed to the increase in CTI_{min} .

3.3 | Impact of changes in forest density and in macroclimate on CTI

Increased forest density had a strong negative effect on CTI values in both regions. The effect of changes in forest density on CTI values was greater than the effect of changes in macroclimate (Figure 4, see also Figure S4; Table S6). As forests grew denser, both CTI_{max} and CTI_{min} decreased. Across all forest types, forest density had a negative effect on CTI values (Figure 4). Macroclimate change had no effect on differences in CTI_{max} between two inventories. However, there was a positive effect on CTI_{min} in the northern region (Figure 4).

3.4 | The effect modification of local landscape components

In the southern region, the negative effect of forest density on CTI_{max} was stronger for forests with higher proportions of spruce ($\beta = -0.005$, $p < 0.001$, Figure 5a), and weaker for high proportions of pine ($\beta = 0.004$, $p = 0.042$, Figure 4). Likewise, high proportions of pine weakened the response of CTI_{min} in the northern region to forest density ($\beta = 0.016$, $p < 0.001$). In the southern region, the effects of macroclimate change on CTI_{min} were positive in sites with low soil moisture levels but negative on sites with high soil moisture ($\beta = -0.014$, $p = 0.008$, Figure 5b). In the southern region, there was also an interaction between macroclimate change and elevation, with positive effects on CTI_{min} on low elevation sites but negative on high elevation sites ($\beta = -0.019$, $p = 0.049$; Figure 4).

4 | DISCUSSION

Using a large dataset of re-inventoried plots across the Swedish managed forest landscape, we showed that forest management over the investigated time-scales is more important than macroclimate in driving changes in CTIs of the forest understorey vegetation. Removal of the forest canopy, which is assumed to lead to increases in near-ground maximum temperatures, resulted in increases in CTI values, and was followed by decreases during the early forest

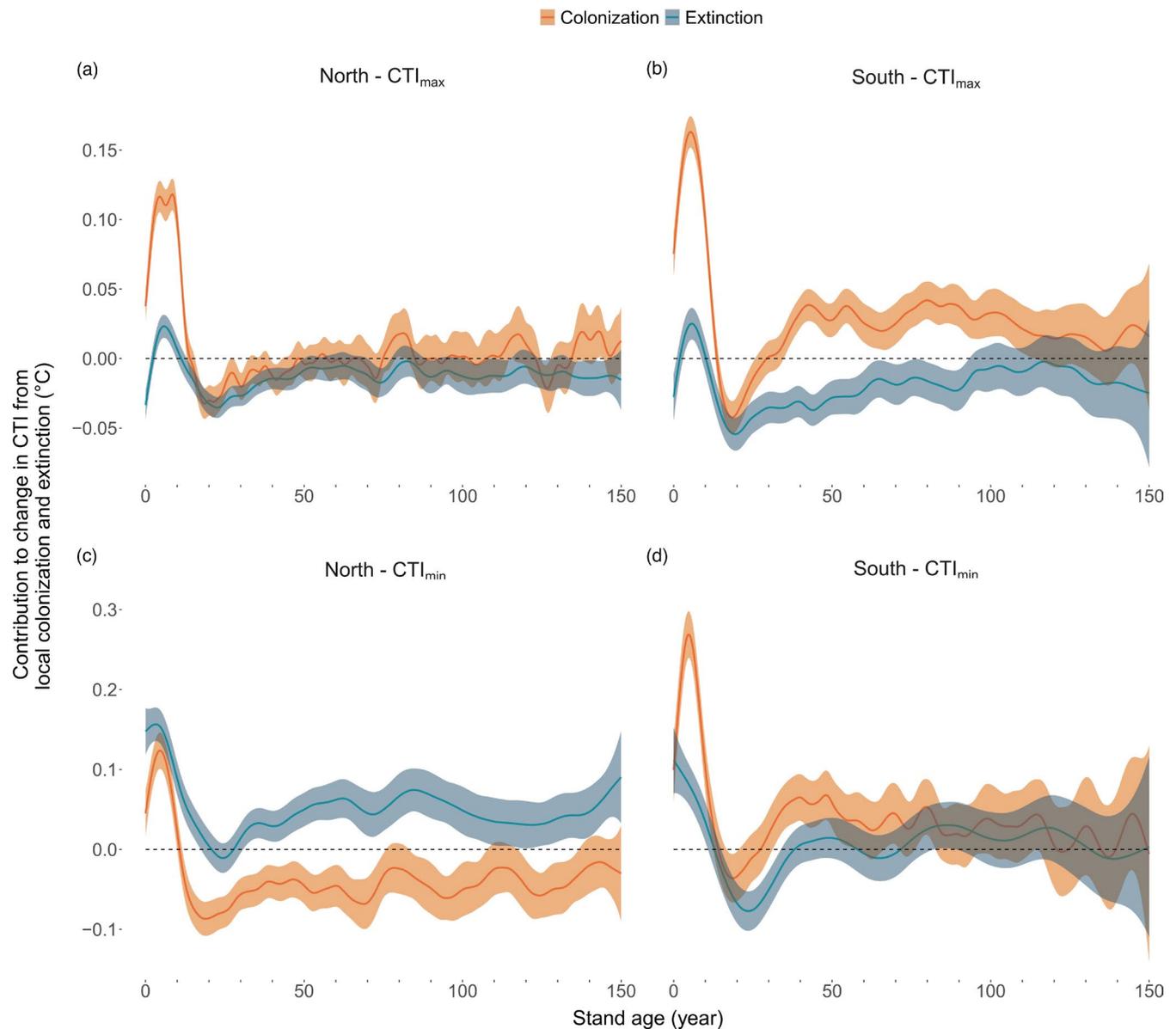


FIGURE 3 Contribution of local colonizations and extinctions to changes in CTI values between two inventories in relation to stand age. Orange colour denotes colonizations, where a positive value represents a situation where the colonizing species had warmer temperature preferences compared with the original community (persisting species between two consecutive inventories and extinctions together), and thus contribute to an increase in CTI value. Blue colour denotes extinctions, where a positive value means that the species that went extinct between two inventories on average had colder temperature preferences compared with the persisting species and thus that the extinctions in such a case contributed to an increase in the CTI value

succession phase. These changes were mainly driven by colonizations in the immediate period after clear-cut, followed by equal contributions of colonizations and local extinctions to a decrease in CTI values as the forest grew denser. Forest density changes had strong and consistent effects on both CTI_{max} and CTI_{min} values, while effects of macroclimate change were detectable only on CTI_{min} . Lastly, the effects of changes in forest density and in macroclimate were partly modified by topography, soil moisture and forest composition. We conclude that on decadal time-scales temperature preferences of understory plant communities in managed forests primarily respond to changes in forest structure, with only small impacts of macroclimate.

4.1 | Changes in understory CTI in relation to stand development

The CTI values of the understory communities fluctuated over different phases of stand development, but with a similar pattern across regions and temperature indices. While previous studies have shown that species richness of understory communities change nonlinearly with stand development (Bergstedt & Milberg, 2001; Jules et al., 2008), our results suggest that changes in community composition reflect the expected fluctuations in local microclimate conditions with stand development (Richard et al., 2021; Zellweger et al., 2020). Consistent with that decreases in forest density result

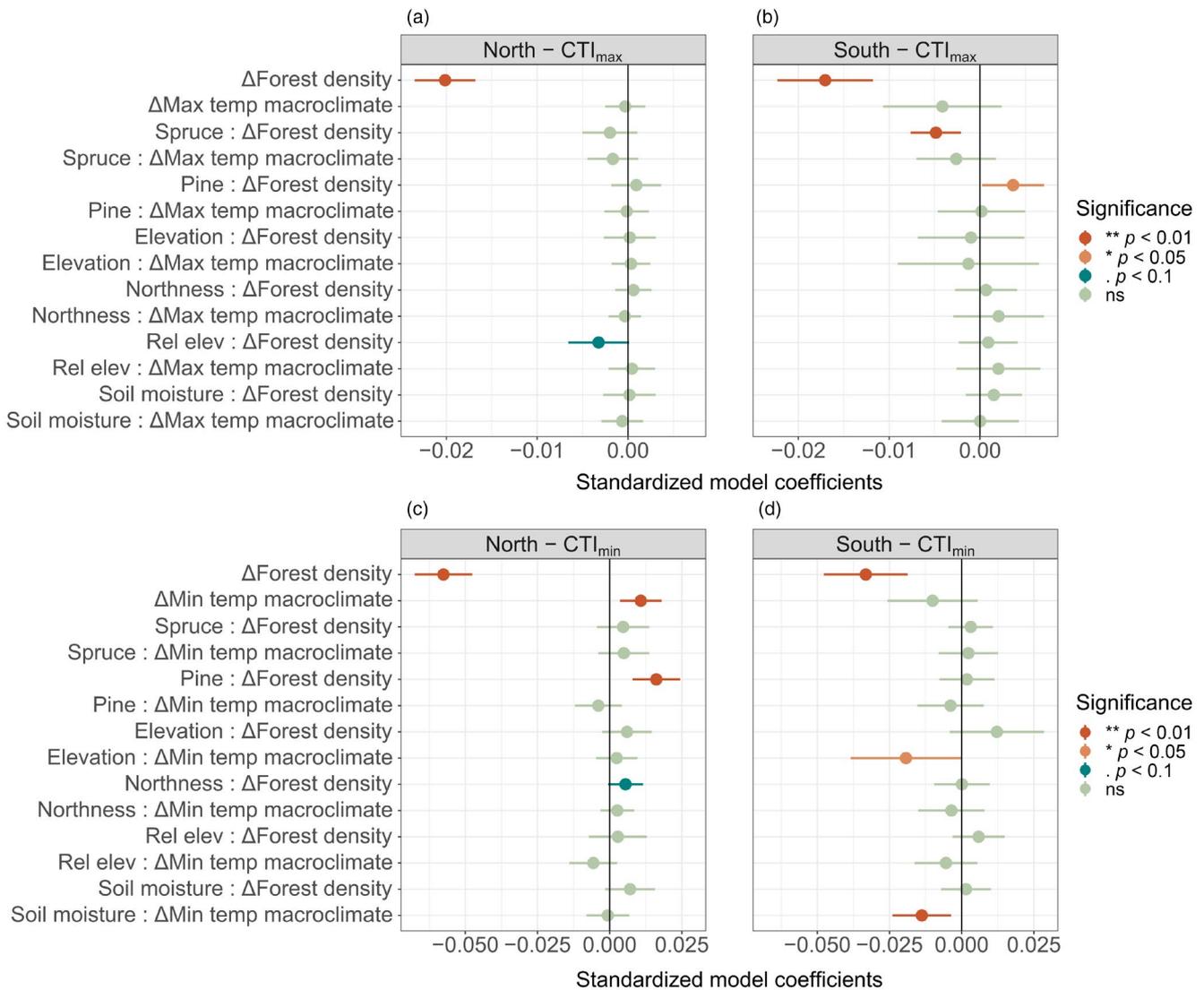


FIGURE 4 Standardized model coefficients for forest density change (Δ Forest density) and macroclimate change (Δ Max temp macroclimate and Δ Min temp macroclimate respectively) together with interactions with landscape covariates on change in CTI_{max} and CTI_{min} between two inventories of 10 years in the northern and southern regions (see also Figure S4 and Table S6, Supporting Information for full model output)

in higher maximum temperatures (Greiser et al., 2018), our results showed large increases in CTI values in the period immediately after clear-cut (Carlson et al., 2020; Liechty et al., 1992). The largest increases in CTI values occurred 4–6 years after clear-cutting, which is in agreement with a previous study that found increases in the presence of species with higher temperature preferences in the understorey community 5 years after reduction in forest density (Stevens et al., 2015). Other studies have found increases in understorey CTI up to several decades after disturbance in natural forests (De Frenne et al., 2013; Zellweger et al., 2020). The rapid decrease in the CTI values that we recorded during the second phase is likely caused by planting, leading to a rapid closure of the canopy (Ackzell, 1993) and cooler microclimate (Greiser et al., 2018). The observed decrease in CTI values with increasing forest density shows that understorey communities do not exhibit a directional thermophilization process, but fluctuate with the forest microclimate. Since thinning events

occur multiple times during stand development in managed forests (Roberge et al., 2020), thinning activities might be the main reason why the decrease in understorey CTI ceases at mid stand ages (Richard et al., 2021). The reason why increases in CTI values were detected in the later phases of stand development in the southern region but not in the northern, might be that forest productivity is higher and management cycles shorter in the southern region, leading to thinning activities that are more synchronized with respect to stand age (Roberge et al., 2020).

4.2 | Contribution of colonization and extinction processes to changes in CTI

Both colonization and local extinction processes contributed to the change in CTI values, but in the immediate period after clear-cutting,

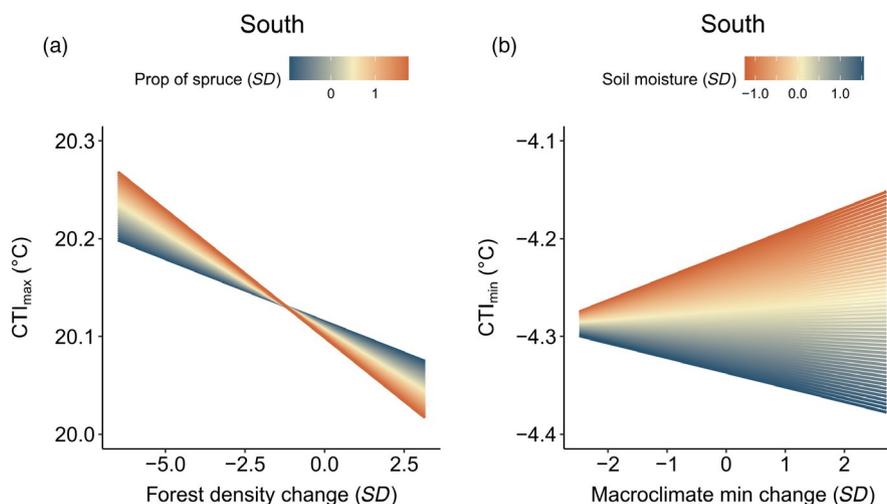


FIGURE 5 (a) Predictions of the effect of the interaction between proportion of spruce and change in forest density on CTI_{max} in the southern region between two inventories. (b) Predictions of the effect of the interaction between soil moisture and changes in macroclimate minimum temperature on CTI_{min} in the southern region between two inventories. The effects of proportion of spruce and soil moisture are shown for values between 10th and 90th quantile of their range. Units on x-axes are in standard deviations (SD). Mean centring was back-transformed for forest density change and macroclimate change, 0 indicating no change

colonizations made the largest contribution. Besides the drastic microclimate change, mechanical disturbances connected to clear-cutting affect the community by removing vegetation and opening up soils for colonization of well-dispersed pioneers (Closset-Kopp et al., 2019; Hédél & Chudomelová, 2020; Vanha-Majamaa et al., 2017). Colonizations could also occur from seedbanks or nearby remnants of grassland species, as many forests, especially in southern Sweden, had a more open canopy structure due to livestock grazing before timber production became the dominant activity (Milberg et al., 2019). Overall, local extinctions contributed slightly less to changes in CTI values than colonizations, especially in the period immediately after clear-cutting. This is likely because extinctions occur only with a time-lag after environmental changes (Hylander & Weibull, 2012; Vellend et al., 2006). However, some cold-favoured species went locally extinct after the forest canopy decreased, and warm-favoured species disappeared when the forest grew denser, consistent with the idea that extinctions were due to the expected microclimate changes. All in all, our results suggest that both extinction and colonization processes are important to study in order to understand changes in temperature preferences of understorey communities across time and space.

4.3 | Forest density drives changes in understorey CTI

Over the investigated time periods, forest density changes had strong effects on CTI values of the understorey communities, whereas effects of macroclimate were smaller. This is consistent with a recent study concluding that, across Europe, changes in forest structure are more important than macroclimate in explaining changes in temperature preferences of understorey communities (Zellweger et al., 2020). The reason for this is that the forest canopy

has a strong temperature buffering effect (De Frenne et al., 2019; Greiser et al., 2018), leading to the understorey community experiencing a climate inside the forest that deviates significantly from the climate outside the forest (De Frenne et al., 2021; Greiser et al., 2020). A cooler climate inside dense forests may sustain populations of cold-favoured species even under contemporary climate change (De Frenne et al., 2013; Zellweger et al., 2020). On the other hand, decreasing forest density due to clear-cutting or thinning activities could lead to even more rapid increases in understorey temperatures (Richard et al., 2021). The effects of changes in forestry and macroclimate on forest understorey communities examined in this study were on a decadal time-scale. Over such time periods, forest density changes are often monotonically declining or increasing, while changes in macroclimate are likely to be smaller and less consistent. However, over longer periods of time, the relative importance of changes in forest density and macroclimate might be different, since forestry will be cyclical while the macroclimate is predicted to change directionally. On the other hand, mean forest densities could also change consistently across the whole landscape over longer time periods, for example, due to changed management practices, as has been the case in Swedish forests over the last century (Hedwall et al., 2019; Lindbladh et al., 2014). The change in temperature preferences of understorey communities over longer temporal scales will therefore probably still to a large extent depend on forest management (De Frenne et al., 2013, 2021; Richard et al., 2021; Zellweger et al., 2020).

Both CTI_{max} and CTI_{min} values increased with a decreasing forest density. For CTI_{min} values, this is contradictory to our prediction that a decrease in forest density would result in lower CTI_{min} values as a consequence of more extreme minimum winter air temperatures in boreal systems (De Frenne et al., 2019; Greiser et al., 2018). A possible explanation for our result is that a decrease in forest density causes

both an increase in summer maximum temperature and a decrease in winter minimum temperature (Greiser et al., 2018). Most species have positively correlated temperature preferences for maximum and minimum temperatures across their larger distributions (Dahlberg et al., 2020). This implies that after a change in forest density, species need to respond either to the change in maximum or minimum air temperature. Our results suggest that they mainly respond to changes in forest density according to their maximum temperature preference (see also Dahlberg et al., 2020). One reason for this might be that vegetation is a weaker driver of variation in minimum temperatures than it is for maximum temperatures (Greiser et al., 2018; Zellweger et al., 2019). Another possibility is that in boreal systems, temperature differences during the winter across gradients in forest density are relatively small, as understorey plants are often under snow cover and are dormant (Rasmus et al., 2011). In contrast, a cooling of the macroclimate between two inventories indeed resulted in a decrease in CTI_{min} . A potential explanation for the different responses is that for macroclimate changes, we expect a positive correlation between maximum and minimum air temperatures, opposite to the negative correlation expected for forest density changes.

4.4 | Weak modification effects of local landscape components

Responses of the understorey communities to changes in forest density or macroclimate could be influenced by landscape features such as topography, soil moisture and forest composition (Ashcroft & Gollan, 2013; Davis et al., 2019; Petersson et al., 2019). However, in our study the modifying effects of local landscape components were overall weak and inconsistent across temperature indices and regions. One possible reason for this might be that the effects of these factors vary across stand age. For example, species compositions of bryophytes vary more between north- and south-facing slopes in early stages of stand development compared with late successional stages (Åström et al., 2007). Potential three-way interactions between forest density change, landscape covariates and stand age could therefore be valuable for future research.

We included covariates of community means of Ellenberg light as well as nitrogen indicator values as species preferences for temperature, light and nutrients might be correlated. Forest management activities might also not only increase microclimate temperatures by increasing warm and dry air, but also light and nutrient availability (De Frenne et al., 2021). Accounting also for these potential covarying community responses suggest that changes in the temperature preferences of the understorey communities in response to forest disturbances are at least partly independent of changes in light and nitrogen preferences.

5 | CONCLUSIONS

It has been predicted that species with higher temperature preferences will shift northwards in the boreal region due to climate

warming (Villén-Peréz et al., 2020). While this might be true at large spatial and temporal scales, we show that forest structure plays an important role for changes in forest understorey communities on short to intermediate time-scales. This implies that increased buffering of forest microclimate temperatures due to increased forest densities, as advocated by the forest industry, might mitigate the effects of contemporary climate warming on understorey communities (De Lombaerde et al., 2021; Hylander et al., 2021; Richard et al., 2021; Zellweger et al., 2020). However, at the same time the common management regime in boreal regions with cycles of clear-cutting, endangers the capacity of forest stands to serve as refugia for thermal-sensitive species (Greiser et al., 2020; Richard et al., 2021). Due to the large impact that temporal variation in forest density has on forest understorey species, it is critical that observed changes in temperature preferences of forest biodiversity are interpreted in the context of forest structure and natural or anthropogenic-caused disturbances.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

D.M.C., L.L.I., J.E. and K.H. contributed equally in conceiving the ideas and designing methodology; D.M.C. acquired the data with support from K.H.; D.M.C. analysed the data with support from L.L.I. and K.H.; D.M.C. led the writing of the first draft with support from K.H. All authors contributed critically to the drafts and gave final approval for publication.

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DATA AVAILABILITY STATEMENT

All data, except geographical coordinates, are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.q573n5tjk> (Christiansen et al., 2021).

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