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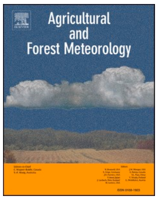

From broadleaves to conifers: The effect of tree composition and density on understory microclimate across latitudes

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ABSTRACT

Forest canopies buffer the macroclimate and thus play an important role in mitigating climate-warming impacts on forest ecosystems. Despite the importance of the tree layer for understory microclimate buffering, our knowledge about the effects of forest structure, composition and their interactions with macroclimate is limited, especially in mixtures of conifers and broadleaves. Here we studied five mixed forest stands along a 1800 km latitudinal gradient covering a 7°C span in mean annual temperature. In each of these forests we established 40 plots (200 in total), in which air and soil temperatures were measured continuously for at least one year. The plots were located across gradients of forest density and broadleaved proportions (i.e. from open to closed canopies, and from 100% conifer to 100% broadleaved tree dominance). Air minimum, mean and maximum temperature offsets (i.e. difference between macroclimate and microclimate) and soil mean temperature offsets were calculated for the coldest and warmest months. Forest structure, and especially forest density, was the key determinant of understory temperatures. However, the absolute and relative importance of the proportion of broadleaves and forest density differed largely between response variables. Forest density ranged from being independent of, to interacting with, tree species composition. The effect of these two variables was independent of the macroclimate along our latitudinal gradient. Temperature, precipitation, snow depth and wind outside forests affected understory temperature buffering. Finally, we found that the scale at which the overstory affects soil microclimate approximated 6-7 m, whereas for air microclimate this was at least 10 m. These findings have implications for biodiversity conservation and forest management in a changing climate, as they facilitate the projection of understory temperatures in scenarios where both forest structure and macroclimate are dynamic. This is especially relevant given the global importance of ongoing forest conversion from conifers to broadleaves, and vice versa.

1. Introduction

Temperature is an important driver of biodiversity at different scales. For instance, it affects the development of animals (Gillooly and Dodson, 2000) and plants (Porter and Delecolle, 1988), phenology (Zohner and Renner, 2014; MacCannell and Staples, 2021), reproductive success (Monasterio et al., 2013) and behavior (Caraco et al., 1990; Angiulli et al., 2020). These responses to temperature, in turn, influence species interactions (Kordas et al., 2011) and shape species diversity (Condamine et al., 2012; Zhou et al., 2016), composition (Macek et al., 2019) and distribution (Woodward, 1988; Repasky, 1991), which ultimately affects ecosystem functioning (García et al., 2018). Since pre-industrial

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times, the world has warmed 1.1°C on average with some areas, such as Europe, warming up considerably faster (IPCC, 2021). This temperature rise is causing largely negative effects on biodiversity (Arneth et al., 2020) and ecosystems (Ito et al., 2020). With global warming, species are expected to shift their native distribution ranges pole-wards (Thomas, 2010), or to higher altitudes (Frei et al., 2010), towards cooler, more suitable environments. Therefore, as a response to warming, species community composition can change, favoring warm-affinity species over cold-affinity species, leading to a process known as “thermophilization” (De Frenne et al., 2013).

Temperatures and other meteorological variables can be distinctive for very different spatial scales, from large regional scales to just a few centimeters. Variations in temperature and other meteorological variables found within a small or restricted area (centimeters to meters) that differ considerably from the macroclimatic conditions in a given geographical region are referred to as “microclimate” (De Frenne et al., 2021). Microclimatic conditions can shape the physiology, presence, distribution and development of species (e.g. Ulrey et al., 2016). For instance, local soil temperature and moisture conditions are important for seed germination and seedling establishment (Egley, 1995; Greenwood et al., 2015), as well as for plant growth, both directly and via their effect on nutrient availability (Paul et al., 2002; Onwuka, 2018). Similarly, development, occurrence and habitat selection of saproxylic beetles is influenced by microclimatic conditions in dead wood found in forests (Lindman et al., 2022). These microclimatic conditions can be affected both by understory plant cover (Pierson and Wight, 1991) and the forest overstory (Paul et al., 2002; De Frenne et al., 2019).

Trees are able to modulate the microclimate of their surroundings near the forest floor (De Frenne et al., 2019). For example, forest canopies buffer ambient temperatures (i.e. decrease high temperatures and increase low temperatures), creating microclimatic conditions that affect understory vegetation and ecosystem processes (De Frenne et al., 2013; Xu et al., 2022). Under forest canopies, maximum and mean temperatures are generally cooler than the macroclimate, whereas minimum temperatures are warmer compared to more open habitats (De Frenne et al., 2019). Therefore, forests can act as climatic microrefugia, allowing the presence of species that could not survive under the ambient macroclimate, and thereby slow down or mitigate the thermophilization of understory communities (De Frenne et al., 2013; Zellweger et al., 2020). In the microrefugia of boreal forests, cold-adapted plants are favored by lower summer and autumn maximum temperatures, late snow melt and higher climatic stability (Greiser et al., 2020). As temperature is considered the main driver of spring phenology in temperate and boreal ecosystems (Kramer et al., 2000), these microrefugia may be of utmost importance to mitigating the effects of phenological mismatches caused by climate change.

In many countries, the past widespread prioritization of conifer monocultures within production forests is being challenged by growing awareness of the potential benefits for biodiversity and ecosystem services derived from diversifying silviculture to include practices that better match natural forest disturbance regimes and tree species composition (Bauhus et al., 2017; Felton et al., 2020; Berglund and Kuuluvainen, 2021). This often involves the replacement of conifers with broadleaved tree species, as motivated by the need to adapt forests to climate change (Löf et al., 2012), current and future pathogen attacks (Thom et al., 2017), biodiversity conservation (Felton et al., 2010), and decreased soil acidification (Oostra et al., 2006). However, the microclimate implications from replacing the overstory species from conifer to broadleaves are still largely unclear (but see Ellison et al., 2005).

Understanding the relationship between forest structure (e.g. the interaction between forest density and composition) and macroclimate temperature is essential in adapting forests and forest management to climate change and for mitigating the impacts of rising temperatures on understory communities. Forest structural complexity is a key determinant of understory microclimates and structural differences among forest stands (e.g. as caused by management practices or stand age) that may explain differences in microclimatic conditions (Kovács et al., 2017; Ehbrecht et al., 2019; Lindenmayer et al., 2022). For instance, forests with denser canopies are better able to buffer macroclimate warming during the growing season (De Frenne et al., 2013). However, high forest densities may hamper biodiversity by reducing light availability (Hedwall et al., 2019b). Increasing spatial heterogeneity in forest structure (and thus in light availability) is a preferable option to increasing forest density, as it can increase microclimate variability (Kovács et al., 2017; Menge et al., 2023). Greiser et al. (2020) showed that the boreal forest patches in which cold-adapted understory species occur have higher basal area values and lower amount of incoming radiation reaching the understory layer in spring and autumn, and are thereby acting as microrefugia. Besides forest density, tree species composition can also affect macroclimate buffering in forests (Zhang et al., 2022). For example, higher tree species diversity in the overstory can create a more diverse set of microclimates, with unique microhabitats that can enhance understory biodiversity (Cavard et al., 2011) and even reduce human thermal stress (Gillerot et al., 2022).

In forests managed for wood production, stand density and tree species composition is largely governed by silvicultural activities. Therefore, forest management decisions can affect forest microclimate dynamics and hence forest efficacy as microclimatic refugia. This not only occurs when choosing the overstory species mixture and stand density, but also through thinning, harvesting or causing other disturbances that increase forest canopy openness. For instance, after a clearcut, thermophilization of the understory plant community regularly takes place (Stevens et al., 2015; Christiansen et al., 2022), as there are only a few trees left to buffer extreme temperatures. Subsequently, when forest regeneration progresses and the overstory becomes dense enough to buffer macroclimatic temperatures, the proportion of cold-adapted species may increase again (Christiansen et al., 2022).

Despite the recognized importance of the tree layer for understory microclimate, our knowledge about the interacting effects of forest density, tree species composition, tree spatial arrangement, temperature variation, and season remains limited. Here we used a large-scale natural experiment along a 1800 km latitudinal gradient to evaluate the absolute and relative importance of the proportion of broadleaved trees and forest density for understory temperature. We used 200 plots with temperature measurements in five mixed forests along a macroclimatic gradient spanning *ca.* 7°C difference in mean annual temperature, with forest density and tree species composition (broadleaves-conifer) gradients within each of these forests. Specifically, we proposed the following hypotheses: (1) Forest density and the proportion of broadleaves interact in their microclimatic buffering effects (i.e. the buffering effect from conifers is stronger than that one from broadleaves at a given density), (2) The effect of forest density and the share of broadleaves on the understory microclimate is independent of latitudinal temperature differences in macroclimate, (3) Meteorological variables outside the forest, such as the macroclimate temperature, precipitation and wind affect the amount of climate buffering. Additionally (4), we hypothesized that it is possible to quantify the area of influence at which trees affect soil and air microclimate buffering, and thus the scale to be considered when managing forests for macroclimate buffering.

2. Material and methods

2.1. Study sites and experimental setup

To increase the generality of our findings and to test whether the understory temperature buffering effect varies depending on macroclimate, five mixed forest areas (further referred to as “sites”) were selected along a latitudinal gradient from 49° N to 64° N in North-Western Europe. These sites all had a large within-site variation in tree species composition and forest density, small altitudinal differences and relatively homogeneous soil conditions. Three sites were located in Sweden: spanning the north (NS), mid (MS) and south (SS) of the country. Additional sites were located in western Germany (G) and eastern Belgium (B). These last two sites, albeit close in proximity, presented rather different macroclimates (Fig. 1A, Table 1).

The forests in G, SS, MS and NS had similar overstory species composition: the dominant conifer species was Norway spruce (*Picea abies* H. Karst), and the dominant broadleaved species was birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.). The overstory species composition in B differed to some extent, with oaks (*Quercus robur* L. and *Q. petraea* (Matt.) Liebl.) as the most abundant broadleaved species. All forest stands at the study sites originate from natural or artificial regeneration of conifers and broadleaves following clear-cutting or salvage harvesting after windthrow. We selected these species in our mixtures as representatives of tree species with different characteristics: Norway spruce as an evergreen, late-successional, shade-tolerant species, birch (and to some extent oak) as a deciduous, early successional, shade-intolerant species (Niinemets and Valladares, 2006). We believe that our results can also be valid for other tree species in these groups. In addition to spruce, birch and oak, other tree species were found to a lesser extent (< 4% of each stand basal area across all plots; Table 1). A shrub layer was generally lacking in all forest stands.

In all sites except B, we established 40 ten-meter radius plots. In site B, as trees were larger and tree separation higher, a 20 m radius was used instead. Plots were located along gradients of forest density and tree species composition, i.e. ranging from evergreen conifer to deciduous broadleaf dominance and from open to closed canopy, to maximize variability across these two overstory variables (Fig. 1C). In the center of each plot, two HOBO Pendant® MX Water Temperature Data Loggers (Onset Computer Corp., Bourne, MA, USA) were placed (80 in total per site): one recording air temperature at *ca.* 1.2 m height and the other recording temperature in the top soil layer (0–5 cm). No soil loggers were installed in site B due to frequent wild boar rooting at this site. Soil loggers were placed inside hermetic plastic jars to protect them from direct contact with the soil. Additionally, air loggers were protected by a well-ventilated plastic radiation shield (Fig. 1B). Both air and soil temperature measurements were taken every 15 min.

2.2. Overstory measurements

For all trees within a 10 m radius (20 m in site B) from the temperature loggers, we recorded the species identity, diameter at breast height (DBH), and the distance and azimuth angle (circular degrees, with north as 0° and south as 180°) to the logger. These data were used to calculate the total basal area (i.e. forest density) per plot, as well as the percent basal area of broadleaved trees per plot (i.e. proportion of broadleaves from here on). To determine at which distance from the data logger overstory tree species composition and basal area best accounted for microclimate measurements, all tree species composition (i.e. proportion of broadleaves) and basal area measurements were calculated at different radii between 4 m and 10 m (4 m and 20 m in B), meter by meter.

Hemispherical pictures were taken in each plot in summer to calculate canopy cover, using a Nikon 5300 camera with a fish-eye lens and tripod. All pictures were taken from above the air temperature logger, at an approximate height of 1.75 m. Pictures were then processed and analyzed in R as in ter Steege (2018). The blue channel in the RGB channel was selected due to its high absorption by chlorophyl in green leaves, resulting in a high contrast between the sky and tree foliage (Brusa and Bunker, 2014). Black and white images were created using a threshold of 0.55, from which canopy openness was calculated.

Besides basal area, canopy cover was also used as another proxy for forest density. The reason for this was twofold. Whereas basal area is a widely used metric in forestry and is used in decision support systems, canopy openness is more ecologically relevant, and in some cases outperforms basal area when predicting forest understory microclimate (Zellweger et al., 2019; Meeussen et al., 2021). Moreover, canopy cover data might be a more easily accessible explanatory variable due to remote sensing and open data policies. In our study, these two variables were correlated with an r = -0.44.

2.3. Microclimate and macroclimate temperature data

Microclimate temperature data recorded by our loggers during the warmest (July) and coldest (January) month were selected between 2020 and 2021 for each plot in each site (Table S1). For each plot, daily

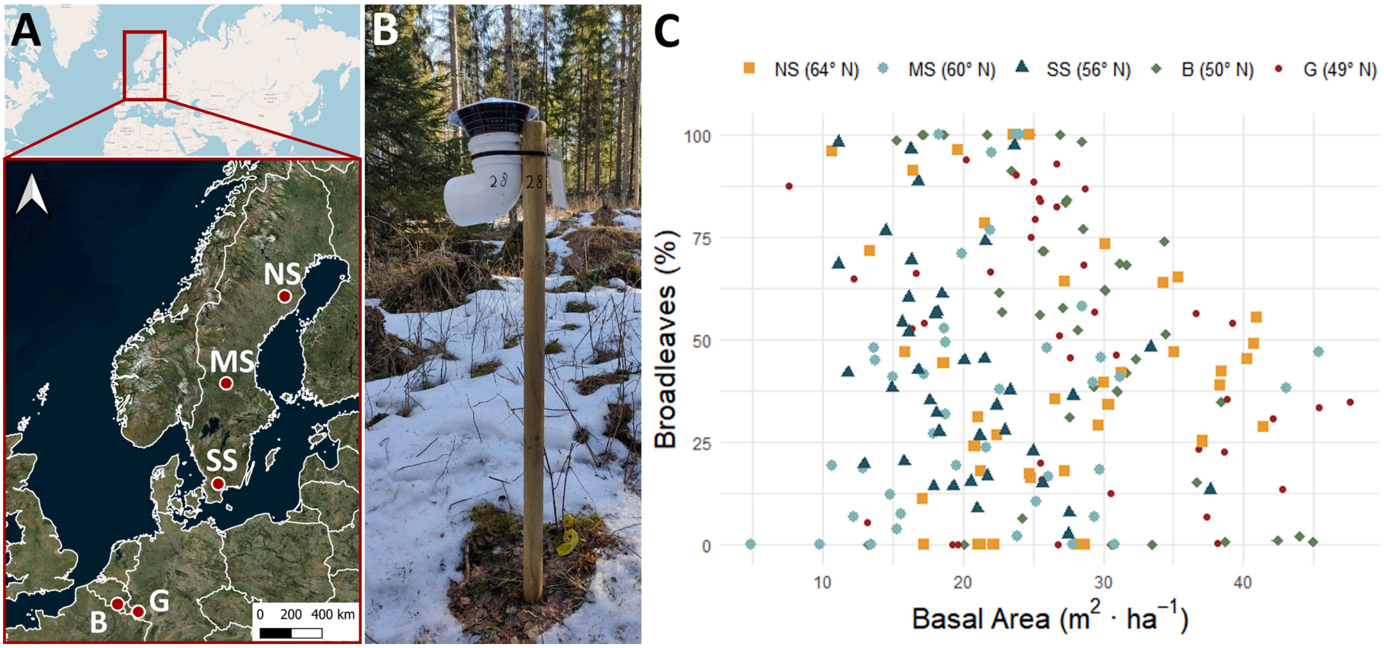

Fig. 1. A. Geographical location of forest stands used across Europe to discern how understory microclimate is affected by tree species composition and density. Stands were located in North Sweden (NS), Mid Sweden (MS), South Sweden (SS), Germany (G) and Belgium (B). **B.** Radiation shield used for air temperature loggers. **C.** Forest density estimated by basal area ($m^2 \cdot ha^{-1}$) and share (% of basal area) of broadleaved trees in 200 plots from the 5 sites (40 in each) included in the study.

Table 1

Description of the five forest sites across a 1800 km latitudinal gradient in which microclimate was measured. Tree species composition values represent the mean basal area ($m^2 \cdot ha^{-1}$) per species across all plots within site. Annual mean temperature and annual mean precipitation were extracted from the WorldClim version 2.1 climate data for 1970–2000 (Fick and Hijmans, 2017). Negative values for the elevational difference to the weather station indicate that the weather station was higher than the forest stands, and vice versa.

		Northern Sweden (NS)	Mid Sweden (MS)	Southern Sweden (SS)	Germany (G)	Belgium (B)
	Location	64°18′ N, 19°44′ E	60°50′ N, 14°40′ E	56°17′ N, 13°58′ E	49°36′ N, 7°01′ E	50°02′ N, 5°13′ E
	Mean annual temperature (°C)	1.50°C	4.52°C	6.79°C	7.51°C	8.58°C
	Total annual precipitation (mm)	599 mm	589 mm	738 mm	1029 mm	961 mm
	Distance to used weather station	~ 6 km	~ 15 km	~ 1 km	~ 17 km	~ 13 km
	Elevational difference to used weather station	35 m	-39 m	9 m	-33 m	-161 m
	Average tree diameter ± SD (cm)	16.7 ± 6.3	16.1 ± 5.3	12.9 ± 4.6	13.9 ± 6.4	35.7 ± 14.0
	Stem density (trees ha^{-1})	1061.56	946.17	1356.0	1522.17	248.57
	Average basal area ($m^2 \cdot ha^{-1}$)	26.8	21.6	19.9	27.9	28.7
Conifer species	*Picea abies*	14.8 $m^2 \cdot ha^{-1}$ (55.2%)	13.5 $m^2 \cdot ha^{-1}$ (62.4%)	12.1 $m^2 \cdot ha^{-1}$ (60.7%)	13.7 $m^2 \cdot ha^{-1}$ (48.8%)	14.6 $m^2 \cdot ha^{-1}$ (50.8%)
	Pinus sylvestris	1.0 $m^2 \cdot ha^{-1}$ (3.8%)	0.1 $m^2 \cdot ha^{-1}$ (0.6%)	-	<0.1 $m^2 \cdot ha^{-1}$ (0.3%)	-
	Pseudotsuga menziesii	-	-	-	0.2 $m^2 \cdot ha^{-1}$ (0.7%)	0.5 $m^2 \cdot ha^{-1}$ (1.8%)
	Larix spp.	-	-	-	1.1 $m^2 \cdot ha^{-1}$ (3.8%)	-
	Picea sitchensis	-	-	-	0.4 $m^2 \cdot ha^{-1}$ (1.5 %)	-
Broadleaf species	*Betula pubescens/pendula*	11.0 $m^2 \cdot ha^{-1}$ (41.0%)	8.0 $m^2 \cdot ha^{-1}$ (36.9%)	7.1 $m^2 \cdot ha^{-1}$ (35.6%)	11.4 $m^2 \cdot ha^{-1}$ (40.7%)	<0.1 $m^2 \cdot ha^{-1}$ (0.2%)
	Alnus incana/glutinosa	-	-	0.4 $m^2 \cdot ha^{-1}$ (1.9%)	<0.1 $m^2 \cdot ha^{-1}$ (0.1%)	-
	Fagus sylvatica	-	-	-	0.3 $m^2 \cdot ha^{-1}$ (1.1%)	0.3 $m^2 \cdot ha^{-1}$ (1.0%)
	Carpinus betulus	-	-	<0.1 $m^2 \cdot ha^{-1}$ (0.2%)	<0.1 $m^2 \cdot ha^{-1}$ (0.2%)	<0.1 $m^2 \cdot ha^{-1}$ (0.1%)
	Sambucus spp.	-	-	-	<0.1 $m^2 \cdot ha^{-1}$ (0.2%)	-
	Quercus robur/petraea	-	-	0.3 $m^2 \cdot ha^{-1}$ (1.7%)	0.3 $m^2 \cdot ha^{-1}$ (1.1%)	13.2 $m^2 \cdot ha^{-1}$ (46.0%)
	Sorbus spp.	-	-	-	0.4 $m^2 \cdot ha^{-1}$ (1.5%)	<0.1 $m^2 \cdot ha^{-1}$ (0.1%)
	Salix spp.	-	<0.1 $m^2 \cdot ha^{-1}$ (0.1%)	-	-	-

mean air and soil temperature were calculated. Additionally, daily maximum and minimum temperatures were calculated exclusively for air loggers, as we expected little variation in the daily soil temperature due to the additional insulating effect of the topsoil, litter layer and understory vegetation. In fact, the soil minimum and maximum temperatures were highly correlated with mean temperature. For loggers with less than 10% of data missing, absent values were filled with the mean of the temperatures recorded by the rest of the loggers from the same site for the respective period. Loggers missing more than 10% of data were removed from analyses (Table S1). Subsequently, daily temperature offsets (i.e. difference between macroclimate and microclimate) were calculated based on temperatures extracted from three different sources: the closest available weather stations to each site, the ERA5-Land climatic model (Hersbach et al., 2020) downloaded for reanalysis from the Copernicus Climate Data Source (cds.climate.copernicus.eu), and ERA5 data downloaded through the 'mcera5' R package (Klinges et al., 2022). The 'mcera5' R package applies an inverse distance weighting calculation and diurnal temperature range corrections (see Klinges et al. (2022) for details). Daily maximum and minimum temperatures for all these macroclimatic data sets were inferred from hourly mean temperature data. Temperature offsets were calculated by subtracting the macroclimate temperature from the microclimate temperature, so that negative offset values showed days in which the forest temperature was lower than the macroclimate, and positive values days in which temperature was higher. For a comparison of the air temperature offset values for each of the macroclimate temperature sources see Fig. S2. In the results, we refer to offsets calculated from nearby weather station data, as they followed microclimatic trends better than ERA5 and 'mcera5' data (Fig. S1). Results for offsets calculated with other macroclimatic sources can be found in the supplementary material, Table S3 and Figs. S6–9. Soil temperature offsets were calculated only from ERA5 data downloaded from the Copernicus Climate Data Source, as macroclimate soil temperature was not available from the other sources. Additionally, three meteorological variables were downloaded from the ERA5 climatic model and used as explanatory variables: wind gust, snow depth and precipitation. The maximum wind gust value per day was calculated. For snow depth data, values were averaged to obtain daily means. For precipitation, hourly data was summed to obtain daily values. Previous averaged macroclimatic temperature (PAT) and previous averaged precipitation (PAP), i.e. temperature and precipitation of the past 5 days, were calculated as a 5-day rolling mean. These two variables were always calculated from the same macroclimate data source as the response variable of each model, except for the models that used temperature offsets calculated from weather station data, as precipitation data were not available from all weather stations. In these cases, the previous precipitation was calculated from the ERA5 data instead.

2.4. Data analyses

To account for non-linearity and allow flexible response shapes, Generalized Additive Mixed Models (GAMMs) were used to model the effects of local forest structure and macroclimate on temperature offsets. A GAMM is a generalization of a Generalized Linear Mixed Model in which the assumption of a linear relationship between predictors and the response variable (on the scale of the link function) is relaxed. Daily mean, minimum and maximum offsets for air temperature and daily mean offsets for soil temperature were used as response variables. Forest density (i.e. canopy openness or basal area) and the proportion of broadleaves were used as predictors in Linear Mixed Models (LMM), both interactively and non-interactively for comparison with the GAMMs. In the GAMMs, these two predictors were used within a bidimensional smoother term, with and without interaction with site, or as separate smoother terms. All models were run with either canopy openness or basal area as proxies for forest density and for both the warmest (July) and coldest (January) months. To account for temporal autocorrelation, all models included date in a uni-dimensional smoother term. Finally, plots nested within site were used as a random intercept effect. Model selection was based on the Akaike's Information Criterion (AIC). Once the best smoother configuration was found, wind, PAT and PAP were added as covariates to the air models, and PAT and snow depth were added as covariates to the soil models, as these variables were assumed to affect the temperature offsets. See Table S2 for an overview of all the covariate and smoother term combinations used in the models and Table S3 for the models' details.

To assess the scale at which the overstory affects air and soil temperature offsets, GAMMs were run with basal area and proportion of broadleaves calculated at plot sizes of different radii. These two metrics were calculated at all possible combinations of radii between 4 and 10 m. Additionally, GAMMs with exclusively basal area or proportion of broadleaves were also run for each of these radii. This was only assessed for mean daily air and soil temperature. These models were run using basal area and proportion of broadleaves in a bidimensional smoother, and with date as a unidimensional smoother. In the cases where either basal area or the proportion of broadleaves were used alone, a unidimensional smoother was used instead. No covariates were used in these models. In site B, trees were measured within a 20 m radii and therefore, this site was analyzed independently from the other sites, including all data combinations from 4 to 20 m. A minimum radius of 4 m was selected in all sites based on the available data, as smaller radii resulted in a significant reduction of the total number of plots with trees. The GAMMs and LMMs were run using the 'gamm4' R package (Wood and Scheipl, 2020) in R version 4.2.2 (R Core Team, 2022). Refer to Tables S8 and S9 for further clarification of this analysis.

When reporting results we use the term "buffering" in relation to forest microclimates that operate within a narrower average range than macroclimate regardless of season (De Frenne et al., 2021). As such, a larger buffering capacity for maximum temperatures would involve cooler forest temperatures than the macroclimate, whereas a larger buffering capacity for minimum temperatures would involve warmer forest temperatures than the macroclimate.

2.5. Data and code availability

The data supporting this study are available upon request, and the code used for analyses is found at https://github.com/JDiazCalafat/ForestMicroclimate_Brodleaves_and_Density. For better reproduction of our results, we recommend using the R package "checkpoint" (Ooi et al., 2022) set to November 2022. This allows one to use the same version of the R packages that were applied when analyzing our data.

3. Results

3.1. Model selection

According to the AIC values, GAMMs outperformed LMMs (Table S3), indicating that non-linear models are needed to describe the effects of forest density and percentage of broadleaves (Table S3). Depending on the response variable and the season, either basal area or canopy openness produced the models with lowest AIC, yet differences in explained deviance were generally small (Table S3).

Generally, models with separate smoothers for forest density and percentage of broadleaves had a higher AIC than bidimensional smoothers, indicating an interactive effect of these two variables. Models without any site interaction had lower AICs than models where the effects of the overstory were allowed to vary between sites, which indicates that the effects of the overstory are consistent along our macroclimatic gradient. The only exception to this was for the mean air temperature models in the warmest month in which basal area was used as a proxy for forest density. In these, a bidimensional smoother with site interaction produced smaller AIC values. When canopy openness was used as a proxy for forest density, a bidimensional smoother with no site interaction was the best option in all cases, except in the coldest month for soil temperature models, in which separate unidimensional smoothers worked better (Table S3). The optimal models to predict the maximum, mean and minimum air and mean soil temperature can be found in Table 2. Output from the models can be found in Tables S4–S7.

Overall, differences between the AIC and R^2_{adj} values of the models with bidimensional smoothers without site interaction, and those with two separate individual smoothers, were rather small and thus we cannot assume that there were strong interactions between forest density and the proportion of broadleaves.

3.2. Air minimum temperature offset

Minimum air temperature offsets became larger with increasing basal area (i.e. they became smaller with decreasing canopy openness) in both the warmest and the coldest months. In other words, in both months, increasing basal area led to higher minimum air temperatures relative to the temperature outside the forest. The effect of the percentage of broadleaves, however, was different depending on the season: minimum temperature offsets became larger with a higher proportion of broadleaves in the warmest month (i.e. broadleaves held back longwave radiation released from the ground and understory plants more effectively than conifers), and became smaller in the coldest month (i.e. since broadleaves do not have leaves in winter, the energy loss from longwave radiation released from the ground was larger with an increasing proportion of broadleaves; Fig. 2A & B; Fig. S5A & B). Therefore, although forest minimum temperatures were always higher than those of the macroclimate ambient temperature, the maximum buffering capacity of the forest was obtained when both forest density and the proportion of broadleaves were high (in the warmest month) or when forest density was high and proportion of broadleaves low (in the coldest month, as broadleaves had no leaves). The amplitude of offsets predicted by our models within our double forest gradient was similar: 0.8°C for the warmest month and 0.7°C in the coldest month when assessing minimum temperature offsets through basal area and 0.5°C for the warmest month and 0.7°C in the coldest month when assessing temperature offsets with canopy openness.

3.3. Air mean temperature offset

Increasing forest density made mean air temperature offsets larger in both the warmest and in the coldest month (although with a relatively small effect, see below), making the forest cooler in summer and warmer in winter. Increasing the percentage of broadleaves made mean temperature offsets generally larger in the warmest month, while there was no clear effect in the coldest month. Therefore, the maximum buffering capacity of the forest with respect to mean air temperature was achieved when forest density was high in the coldest month and when both forest density and the proportion of broadleaves were intermediate or high in the warmest month (Fig. 2C & D; Fig. S5C & D). The effect of forest density on microclimate was consistently larger than that of the proportion of broadleaves. The amplitude of mean air temperature offsets predicted by the models was always higher in the warmest month than in the coldest month: in the warmest month it was 0.6°C both when considering basal area and canopy openness, and in the coldest month it was 0.3°C in the basal area models and 0.4°C in the canopy openness models. Therefore, despite our use of hemispherical pictures during the summer to calculate canopy openness, the predicted offset amplitudes during the coldest month were similar to those in the models where basal area was used.

Table 2

Models predicting the daily maximum, mean and minimum air and mean soil temperature offsets through forest and climate variables. An offset is the difference in temperature between the microclimate and the macroclimate (i.e. microclimate - macroclimate). Only the models with the lowest AIC values are shown. Air temperature offsets were calculated from nearby weather stations as macroclimatic data sources. Soil temperature offsets were calculated form ERA5 data. Wind and snow data was extracted from ERA5 data. Previous averaged precipitation in the last five days (PAP) was extracted with the 'mcera5' R package. Previous averaged temperature in the last five days (PAT) was calculated from weather station data (i.e. same macroclimate temperature source used for the offsets). Note that all models were conducted with a bidimensional smoother term including forest density (i.e. either basal area (BA) or canopy openness (CO)) and the percentage of basal area occupied by broadleaves. AIC values and R^2_{adj} are shown for the same models using basal area or canopy openness as a proxy for forest density. All models accounted for temporal autocorrelation.

				Basal area		Canopy openness	
Logger location	Response variable	Covariates	Period	R^2_{adj}	AIC	R^2_{adj}	AIC
Air	Min temp offset	site + wind + PAT + PAP	Coldest month	0.67	16482	0.67	16491
			Warmest month	0.48	17452	0.48	17477
Air	Mean temp offset	site + wind + PAT + PAP	Coldest month	0.64	13403	0.64	13395
			Warmest month	0.52	9658	0.53	9655
Air	Max temp offset	site + wind + PAT + PAP	Coldest month	0.60	13124	0.59	13141
			Warmest month	0.61	15168	0.60	15179
Soil	Mean temp offset	site + snow + PAT	Coldest month	0.53	13018	0.53	13028
		site + PAT	Warmest month	0.71	11191	0.71	11200

3.4. Air maximum temperature offset

Maximum air temperature offsets in the coldest month were affected mainly by species composition and to a lesser extent by forest density. The amplitude of this effect was overall rather small, though, of approximately 0.15°C (Fig. 2E; Fig. S5E). However, in the warmest month there was a linear response to density and a weak or absent response to proportion of broadleaves. Increasing forest density made maximum air temperature offsets larger (i.e. increased the cooling effect). In this month, the amplitude of the offsets predicted by our models was about 3°C (Fig. 2F; Fig. S5F). The buffering effect of maximum temperatures in the warmest month was maximal in high density plots largely independent of the proportion of broadleaves.

3.5. Soil mean temperature offset

The proportion of broadleaves had a much stronger effect on forest soil temperature in the warmest month than in the coldest month (Fig. 3). A higher proportion of broadleaves made the soil temperature offsets smaller in summer, but had little effect in winter (Fig. 3). When taking into account canopy openness in the coldest month, the percentage of broadleaves had a similar effect as in the warmest month: a higher proportion made the forest soil temperature offsets larger. Of these two models (basal area model and canopy openness model), the basal area model had the lowest AIC value (Table S3). In both the warmest and the coldest month, a higher basal area (or a lower canopy openness) made offsets larger (Fig. 3). Therefore, the temperature buffering capacity was highest when canopy openness was low and the proportion of broadleaves was low (in the coldest month) or when basal area was highest and the proportion of broadleaves was lowest (in the warmest month). The amplitude of the offsets predicted by our models for soil mean temperature was always higher in summer than in winter: in the basal area models it was 2°C, and in the canopy openness models 1.8°C, whilst in winter it was 1.1°C and 0.9°C, respectively.

3.6. Effects of macroclimate drivers on temperature offsets

Meteorological variables (averaged temperature and precipitation in the last five days, wind and snow) generally had consistent effects on our air temperature models regardless of the response variable (Table S4). In these models, increasing PAP and wind decreased the absolute values of the offsets and thereby reduced the temperature buffering effect of the forest in both the warmest and the coldest month (both $p < 0.001$). On the other hand, increasing PAT made the offsets smaller in the warmest month and larger in the coldest month ($p < 0.001$), increasing the general buffering effect of the forest in winter but reducing it in summer. This variable had no significant effect on the maximum air temperature offsets in the warmest month ($p = 0.84$).

Regarding soil temperature (Table S6), increasing snow depth made the offsets larger and thus increased the buffering effect of the forest canopy ($p < 0.001$) while higher PAT made the offsets larger in the warmest month and smaller in the coldest month (both $p < 0.001$), which is the opposite effect as on the air temperatures.

3.7. Distance analyses

These analyses aimed at clarifying the area of influence of the overstory upon mean air and soil temperature offsets. That is, the minimum radial distance from a temperature logger in which all trees should be measured in order to predict temperature offsets. The distance from the data loggers for which basal area and the proportion of broadleaves best predicted mean air temperature offsets in the warmest month was 10 m for basal area and 9 m for the proportion of broadleaves. However, the second best model included both variables at their maximum resolution (i.e. both 10 m) and the third best for basal area was a 9 m radius and the proportion of broadleaves within an 8 m radius. Differences in AIC values in these models were smaller than 0.6, and all models had the same R^2_{adj} (Table S8). For air mean temperature offsets in the coldest month, the best model included basal area calculated in an 8 m radius and proportion of broadleaves within a 9 m, whilst the second best model included broadleaves within 10 m and basal area within 8 m. The third best model included basal area calculated within 7 m and broadleaves in a 9 m radius (Table S8).

Regarding soil temperature offsets in the warmest month, the three best models included broadleaves at the maximum distance at which they were measured (i.e. 10 m) and basal area within these respective radii (from best to worst models): 8 m, 9 m and 7 m (Table S8). During the coldest month, the best models did not include percentage of broadleaves, and the distance at which basal area best predicted temperature offset was at 7, 8 and 6 m radius, respectively (Table S8).

In the case where only site B was considered in air temperature offset models, the lowest AIC value was obtained when including basal area calculated at the maximum radius (i.e. 20 m) and the proportion of broadleaves within 10 m. The two next best models were similar, with basal area calculated at 20 and 19 m, and broadleaves at 10 and 9 m, respectively (Table S9). For the coldest month, the results of the two best models were similar to those of the other sites: the percentage of broadleaves was not relevant, yet the radii at which basal area was calculated were 20 and 19 m, respectively. Contrastingly, the third best model did not include basal area but included the percentage of broadleaves within a 19 m radius (Table S9).

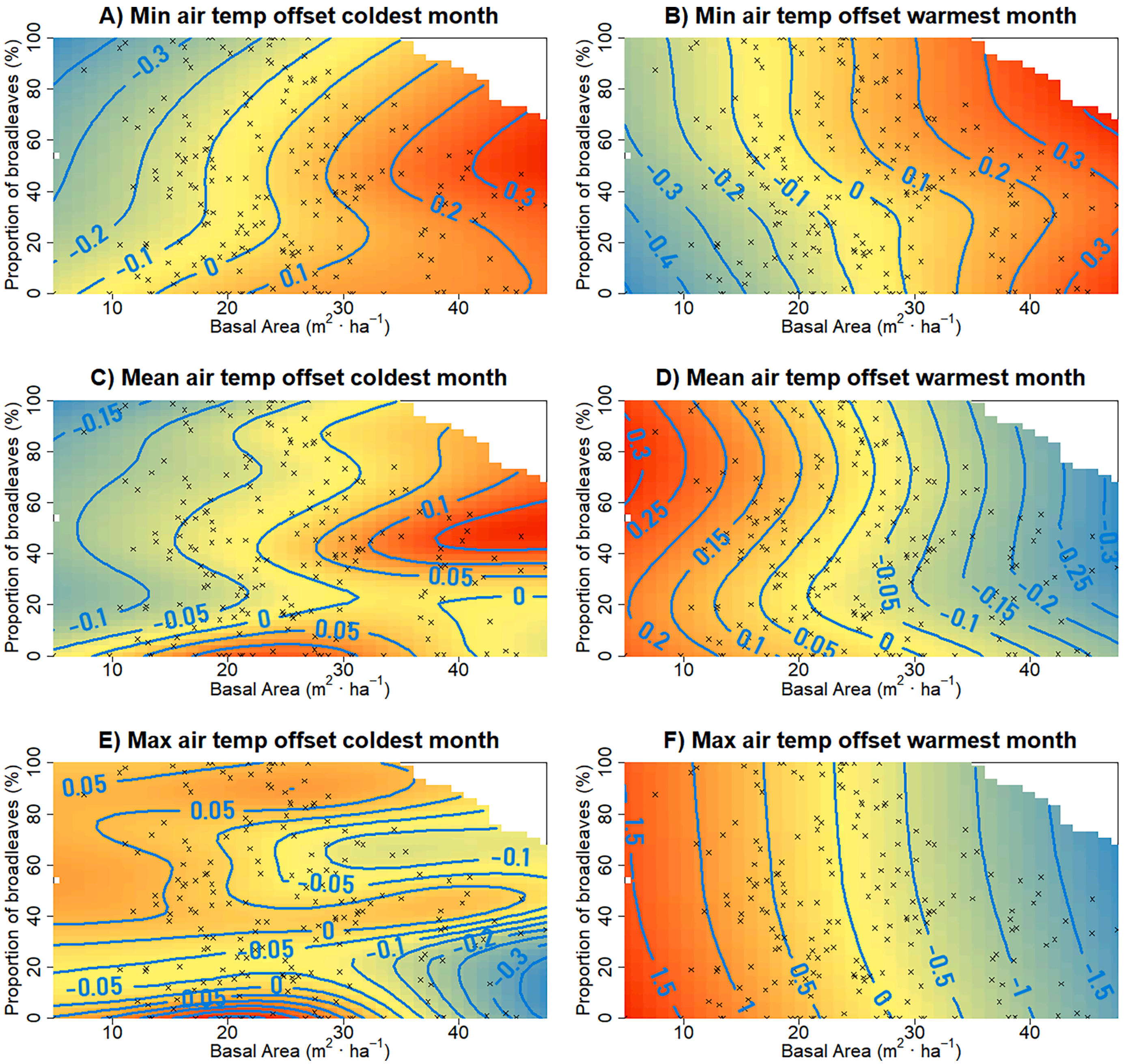

Fig. 2. Model predictions for the minimum, mean and maximum air temperature offsets (forest temperatures minus weather station data) for the warmest and coldest months in our study. In these predictions, basal area was used as a proxy for forest density. The numbers on the isolines indicate the predicted offsets in degrees Celsius. The predictions are centered at the mean and the zero isoline thus depicts the mean of the model predictions. The offsets of these models were calculated from weather station macroclimatic data. The colours represent a gradient from more positive (red) to more negative (blue) offsets. Gaps (i.e. white spaces) represent the model predictions that were too far from our data points. For component smooths with confidence intervals that include the uncertainty on the overall mean, see Fig. S3 in the supplementary material.

4. Discussion

Our results provide five important insights regarding the interaction between macroclimate and the tree canopy on forest understory temperatures. First, we found that both forest density and tree species composition play important roles in determining understory temperature. Second, forest density (i.e. basal area and canopy openness) can act independently or interact with the share of broadleaves to alter microclimate depending on the specific temperature metric assessed. Third, we show that the effect of forest density and percentage of broadleaves on microclimate seems to be consistent over a large latitudinal macroclimate gradient. Fourth, the temperature buffering capacity of forests is affected by meteorological variables such as the ambient temperature, precipitation and wind which thus may affect their local climate change mitigation potential. Finally, we found that the scale at which the tree overstory affects local soil temperature offsets approximated 6-7 m, whilst for air temperature offsets this range was close to 10 m or more.

The temperature buffering effect of forest density was always stronger than that provided by the proportion of broadleaves. According to our models, increasing forest basal area cooled down soil mean temperature and maximum and mean air temperatures in summer. In

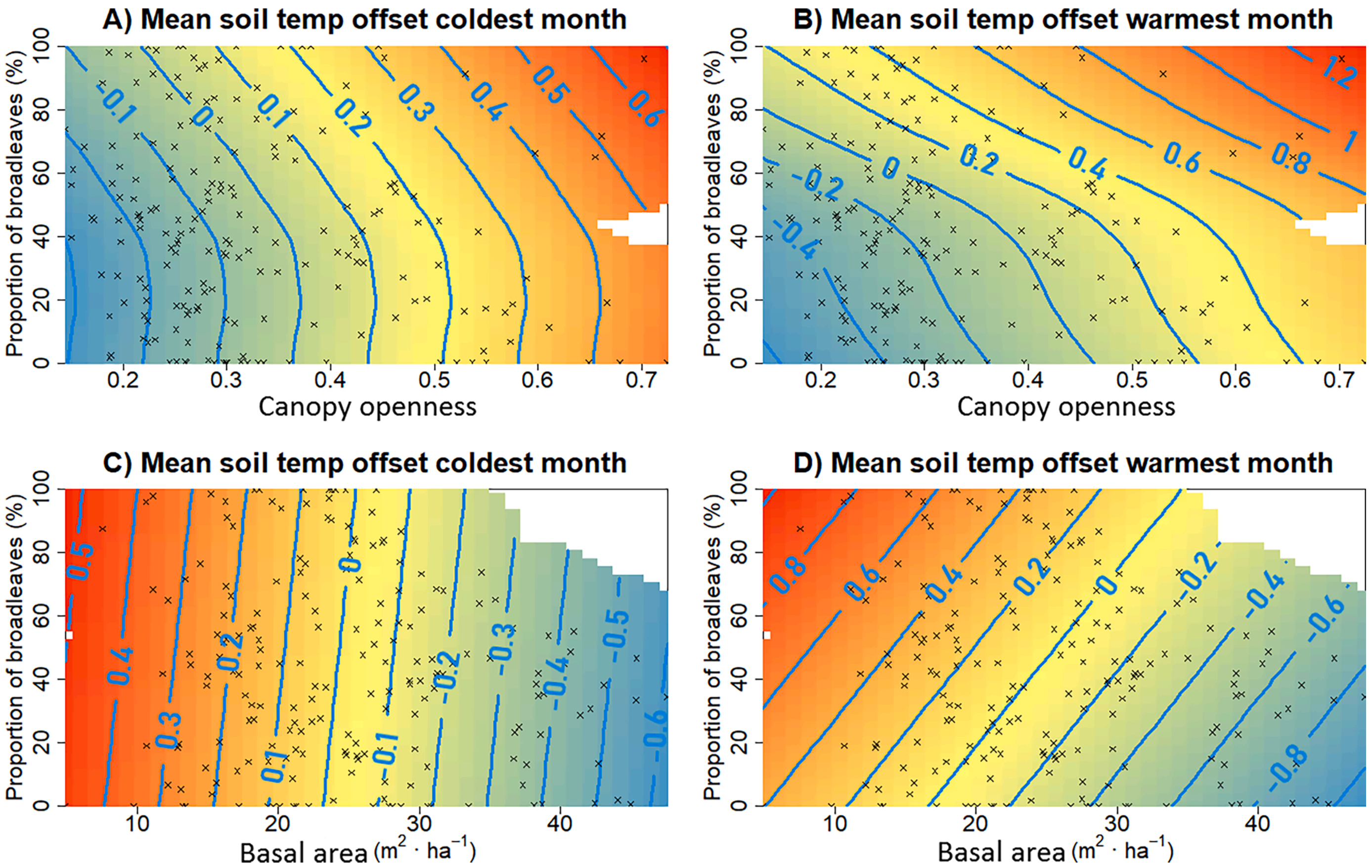

Fig. 3. Model outputs for the mean soil temperature offsets for the warmest and coldest months in our study, using canopy openness (A-B) and basal area (C-D) as a proxies for forest density. The numbers on the isolines indicate the predicted offsets in degrees Celsius where the zero isoline depicts the mean of the predictions of the model. The numbers on the isolines indicate the predicted offsets in degrees Celsius. The predictions are centered at the mean and the zero isoline thus depicts the mean of the model predictions. The offsets of these models were calculated from the ERA5 macroclimatic data. The colours represent a gradient from more positive (red) to more negative (blue) offsets. Gaps (i.e. white spaces) represent the model predictions that were too far from our data points. For component smooths with confidence intervals that include the uncertainty on the overall mean, see Fig. S4 in the supplementary material.

contrast, increasing basal area increased minimum air temperatures in both seasons, as well as mean air temperature in winter (Fig. 2). For instance, our models suggest that an average density forest stand (e.g. basal area of 25 $m^2 \cdot ha^{-1}$) with a share of broadleaves of 50% in northern Sweden would drop the maximum temperature in the warmest month by around 1.3°C, yet drop it by as much as 2.5°C if forest density was increased to a basal area of 40 $m^2 \cdot ha^{-1}$. If all trees were to be replaced by broadleaves, similar buffering effect would be achieved: a cooling of 1.4°C at a basal area of 25 $m^2 \cdot ha^{-1}$ and a cooling of 2.6°C at a basal area of 40 $m^2 \cdot ha^{-1}$. In the case of mean atmospheric temperature for the same site in the warmest month, a drop of around 0.4°C would be achieved at a basal area of 25 $m^2 \cdot ha^{-1}$ and 50% of broadleaves, reaching a cooling of 0.8°C in optimal conditions of forest density and broadleaves share. These projections of our models are similar to other observations in temperate deciduous Central European forests. For instance, Zellweger et al. (2019) found the average cooling effect of the overstory in summer to be of 2.1°C in deciduous forests with an average basal area of 33.2 $m^2 \cdot ha^{-1}$, and the average warming effect in winter of 0.4°C in the same forests. Similarly, in pine forests, Blumröder et al. (2021) showed a cooling effect of *ca.* 2°C between their densest and most open stands.

The range of temperature buffering we observed (which varies within an heterogenous stand), could potentially have an impact on phenology and voltinism of some ectothermic species, causing differences in their development rate compared to their counterparts outside the buffering effect of the forest. For instance, Greiser et al. (2022) found that the probability of diapause and the number of generations of *Pieris napi* (L., 1758) changed within the same forest landscape based on microclimatic variation, with potentially great impacts on survival and fitness. Our results are in accordance with those of De Frenne et al. (2019) and show the potential of forests to provide climate refugia to mitigate the negative effects of warming on species' fitness or phenology.

Often, production forests are kept within narrow ranges of basal area (although this depends on the applied silvicultural system) and therefore their potential to provide variation in microclimatic conditions is reduced. For example, the highest forest densities in our study are only occasionally found in production forests of this region, and by increasing basal area, this buffering potential can be exploited better. Our model predictions show that the buffering effect of the forest is reduced at low forest densities, which may be a result of higher insolation and wind shelter in openings (Baker et al., 2013). In fact, reducing canopy cover is shown to decrease the buffering effect of forest understory temperatures both in coniferous and broadleaves stands (Blumröder et al., 2021). This finding also has implications for choice of forest management system (e.g. single tree, gap, shelterwood, clear-cut; Kermavnar et al., 2020; Menge et al., 2023). For instance, Radler et al. (2010) observed that the maximum air and soil temperature were 2.5°C and 6°C higher (respectively) in a clearcut than in the surrounding spruce forest. However, increasing forest density also decreases light availability, reducing understory plant diversity, reproduction and abundance of many understory species. Consequently, increasing forest density is one of the main drivers behind species turnover and a decreasing understory plant cover in Swedish forests (Hedwall et al., 2019a, 2021). Specifically, Eckerter et al. (2019) showed that increasing canopy cover decreases the number of flowers, ovules, reproductive success and fruit quality of *Vaccinium myrtillus,* L., which is one of the most common and ecologically important understory shrubs in boreal systems, that also occurred in several of our sites. Therefore, even though increasing forest density might show some advantages when temperature buffering is pursued, it can also compromise resource availability for more light demanding understory species, regardless of whether the microclimatic conditions are more suitable.

Our results also indicate that the effect of forest density on the buffering of maximum temperatures in summer is rather independent of the proportion of broadleaves (e.g. Fig. 2F and example in the previous paragraph), which indicates that the same buffering capacity caused by the shade-tolerant Norway spruce is also achieved by shade-intolerant broadleaves (mostly birch and oak). These tree species categories differ largely in their effects on understory light environments, for which Norway spruce has a high leaf area index all year round (Verheyen et al., 2012) and thus has considerably stronger effects on the understory light environment (Hedwall et al., 2019b). Therefore, increasing the forest basal area by increasing the proportion of certain broadleaved tree species could reduce summer air temperatures without inducing the same extent of negative effects on light availability and biodiversity as shade tolerant conifers, while also providing a suite of additional biodiversity, ecosystem services and climate change adaptation benefits (Felton et al., 2010, 2016). Nevertheless, as deciduous trees do not have leaves in winter, their buffering capacity may be lower, potentially leaving frost-sensitive understory species less protected against late frost events than they would be beneath a conifer canopy. In a mixed forest scenario, however, fine-scale heterogeneity in light regimes, as provided by the addition of broadleaves to otherwise conifer dominated stands, benefits biodiversity in the forest understory (Helbach et al., 2022). Given the current trend of replacing conifers with broadleaved tree species (Löf et al., 2012), we recognize this temperature buffering as an added benefit of such changes to silvicultural practice.

The similar buffering effect of broadleaves and Norway spruce on summer maximum temperatures is surprising considering the generally larger radiation transmittance under broadleaves. The reason for this pattern is unknown but is perhaps related to differences in albedo and evaporative cooling (Geiger et al., 1995; Bonn et al., 2020). Species composition has a strong effect on albedo, with broadleaves generally having a higher albedo than most conifer species (Lukeš et al., 2013). Therefore, the higher albedo of broadleaves could dissipate radiation in a way that contributes to macroclimate temperature buffering (Bright et al., 2013). On the other hand, differences in evapotranspiration rates between these overstory species may alter water availability in the surroundings and also affect evaporative cooling in different ways (Moss et al., 2019). These differences in transpiration rate may result from different rooting depth between deep-rooting broadleaves such as oaks and the mostly shallow rooted Norway spruce. Ultimately, it may also be the case that such differences are tree species-specific and dependent on stand characteristics, as light transmittance can also be quite low beneath broadleaf stands.

If the tree species diversity of the overstory is to be increased, this should be done within reasonable limits if accompanied by concomitant increases in forest density. For example, Hedwall et al. (2019b) showed that stand density can override the benefits to understory biodiversity from increasing the broadleaf proportion in the overstory. Moreover, in the studied forests, the effect of the proportion of broadleaves on soil mean temperature offsets was far stronger during summer than winter, with a higher percentage of broadleaves warming up the forest soil significantly. Potential factors driving the contrastingly limited influence of the proportion of broadleaves during winter may stem from an overriding influence of snow and litter that insulated soil temperatures against radiation (Hennon et al., 2010; Fekete et al., 2016). However, as we did not measure differences in litter or snow between plots, this explanation remains speculative. We can however expect that increasing forest density through the increase of broadleaves would have distinctive effects on soil versus air microclimate. As our two primary overstory tree species (spruce and birch) were selected as representatives of late successional evergreen conifers and early successional broadleaves, respectively, our results also provide insights applicable to other forest systems with tree species possessing similar ecological and structural attributes. Furthermore, our results were largely consistent across a latitude gradient of *ca.* 7°C average annual temperature span, which further strengthens the potential for extrapolating our results beyond our specific sites. However, despite our similar results when using either canopy openness or basal area as proxies for forest density, the effect of these variables may differ in other forest systems in which their correlation is less strong.

Allowing for a greater variability of microclimatic conditions can be expected to benefit a greater range of understory biodiversity (Helbach et al., 2022). Microclimatic variation can be enhanced in forest understories by mixing overstory tree species with different structures and traits (Zhang et al., 2022), as well as by taking into account the spatial scale at which the individual trees are mixed (Felton et al., 2022) or allowing spatial coexistence of different forest developmental stages within the landscape (Menge et al., 2023). Our results also show that soil microclimate can be managed through the manipulation of forest density and the share of broadleaves at a scale of 6–9 m in radius (Table S8). These results could be highly relevant for large-scale conversions of conifer-dominated stands to broadleaf or mixed-broadleaf stands, as well as for conservation purposes. Baker et al. (2013) hypothesized that the re-establishment of species in harvested forest areas is in part influenced by microclimate, and distance to the forest edge, which in turn shapes temperature buffering. This was hypothesized to be especially important for vascular plants, bryophytes, lichens, amphibians and reptiles. Therefore, elucidating at what scales microclimate works opens a new door to microclimate management and microclimate restoration, which enables us to target specific microclimatic goals of expected benefit to a given set of species.

Our results were less clear with respect to air temperature, as we were often unable to identify the scale at which understory air microclimate operates. This was because the optimum distance selected by the models was at the limit of what we quantified in the field. This limitation applied to both the analyses that included all sites except B (NS, MS, SS and G; where trees were measured at 10 m; Table S8) and the analyses confined to site B (where trees were measured at 20 m; Table S9). We suggest that the key underlying difference is that soil temperature is more dependent on local radiation, whereas local air temperature is affected by air mixing from a larger surrounding area exposed to greater variation in radiation. Air mixing is also most likely the cause of temperature offsets reducing in size with increasing wind speed. In either regard, more research is needed to clarify the scale at which overstory structure affects understory microclimates. We also emphasize that the forest canopy metrics assessed here capture only a subset of potential influences on understory microclimates. In fact, Hedwall et al. (2019b) showed that the optimal plot size at which forest structure had the strongest influence on understory vegetation was well below 10 m. This contrast between the scale at which forest structure alters temperature (our results), and the scale at which forest structure influences understory vegetation (Hedwall et al., 2019b) would suggest that there are additional microclimatic or ecological factors affecting vegetation community structure at these scales (e.g. light availability; Tinya and Ódor, 2016). For example, in our forest stands an understory shrub layer was generally lacking, but in forests with high shrub cover, their presence can decrease air mixing and therefore reduce the scale at which the microclimate operates. In addition, tree crown dimensions and the height of the canopy itself may play an important role dictating microclimatic scales of influence (Souza et al., 2010; Ehbrecht et al., 2019). The taller the trees, the more evenly the radiation is spread, and thus the larger the scale at which the microclimate can be operating. Our site in B had a very high canopy compared to the other sites, but as we did not quantify this, we cannot draw any conclusions on the effect of this parameter on the scale at which microclimate operates in our sites. Additionally, soil characteristics may also be heterogeneous, and influence soil microclimate correspondingly. For instance, soil moisture is related to temperature differences between open and forested areas (von Arx et al., 2013). In our case, however, we do not expect large differences among our plots, as soil temperature loggers were only buried a few centimeters into the humus layer. In addition, the choice of forest overstory species may affect soil composition differently (e.g. by altering characteristics of the soil organic layer), and thereby change soil microclimate. Such effects were however beyond the scope of our study (Fekete et al., 2016). In conclusion, our results show that it is possible to make predictions of understory temperatures in scenarios where both forest structure and macroclimate are dynamic. This provides an opportunity to include these variables in forest management decision support systems to exploit the potential of forests to act as climatic refugia, and thereby mitigate potentially negative effects of climate change. Importantly however, our results also indicate that macroclimatic drivers like precipitation and wind may affect the buffering capacity of forest overstories, which has implications for the temporal and spatial consistency of these refugia in a changing climate. Moreover, our results can be considered in forest restoration plans and when choosing tree species for afforestation programs.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2023.109684.

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