



## Slow recovery of microclimate temperature buffering capacity after clear-cuts in boreal forests

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### ABSTRACT

The majority of Fennoscandian boreal forests are managed. Forest management inherently changes the physical structure of forests, thus altering ecosystem functions and the conditions for living organisms within these environments. However, the impacts of management on the microclimate buffering of boreal forests have not been comprehensively studied, despite that microclimate is one of the key determinants of biodiversity. Here, we studied the effect of forest structure and management on the temperature buffering capacity of boreal forests using terrestrial laser scanning and microclimate measurements. We measured the temperature variability on forest plots representing two management types: even-aged rotation forestry and uneven-aged forestry. To quantify buffering, we calculated the slope coefficient of the linear regression between microclimate and clear-cut temperatures. We found that the total amount of plant material alone was not an adequate predictor of the buffering. Instead, increasing canopy layers and the density of the understory led to more buffered temperature variability compared to clear-cuts and forests with fewer layers. The buffering was high in both mature even-aged and uneven-aged sites, but the effect in even-aged forests depended on stand age, suggesting that a strong buffering capacity could be reached only after approximately 30 years after clear-cut. In uneven-aged stands, the buffering capacity varied with recurring partial selection cuttings, but never lead to a full coupling with open-air temperatures like in even-aged stands after clear-cuts. We conclude that despite the buffering being on average stronger in mature even-aged stands than in uneven-aged stands, it can take decades for a clear-cut stand to reach the same buffering capacity as an uneven-aged forest with continuous tree cover, and it will eventually disappear after a new clear-cut harvest. From biodiversity perspective, uneven-aged management can create more temporally stable microclimatic conditions and can thus aid in maintaining microrefugia and mitigate climate warming impacts.

### 1. Introduction

Intensive rotation forestry in the boreal regions is responsible for large-scale homogenization of both forest structure and tree species composition at the stand level, causing direct threats to ecosystem functions such as carbon storage and biodiversity (Blumröder et al., 2019; Kuuluvainen, 2009; Kuuluvainen and Gauthier, 2018). In contrast, old-growth forests, defined as forests of high age with no signs of active management (European Commission, 2023), host more

biodiversity than managed forests due to their more complex structures, tree species richness and presence of deadwood (Dittrich et al., 2014; Hyvärinen et al., 2019). Currently, 99.3 % of forests in Europe have undergone some type of management (Sabatini et al., 2018). In Finland, managed forests cover 91 % of the forest area, and the proportion of productive forests that are older than 120 years is only 10 % (Korhonen et al., 2021).

Meanwhile, rising atmospheric temperatures and increasing frequency and severity of climatic extreme events associated with global

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climate change pose an imminent threat to natural habitats, risking species to either go locally extinct, adapt, or move to new, more suitable areas (Antão et al., 2022; Murray et al., 2017; Zellweger et al., 2020). One of the key determinants of species distribution is microclimate, herewith defined as the local climatic conditions experienced by organisms that deviate from large-scale ambient climate conditions, i.e. the macroclimate (Antão et al., 2022; Mönkkönen et al., 2010; Potter et al., 2013). Microclimates are created by variations in local topography, vegetation composition and structure, water bodies and human influence (Davis et al., 2019; Geiger, 1980). Forests, in particular, create distinctive microclimates (De Frenne et al., 2021; Geiger, 1980; Hardwick et al., 2015) because attributes such as tree canopy structure and geometry, stand density, and tree size lead to changes in incoming radiation, mixing of air and evapotranspiration (Chen et al., 1999; Geiger, 1980). Temperature fluctuations in forests and under tree cover are most dampened compared to the macroclimate (Chen et al., 1999; De Frenne et al., 2021; Lee et al., 2011; Wolf et al., 2021). Forests with buffered temperatures can create microrefugia, where more appropriate temperature and humidity conditions are sustained, preserving potentially important habitats for forest species (Ashcroft et al., 2012; Dobrowski, 2011; Greiser et al., 2020; Mazziotta et al., 2016; Wolf et al., 2021), such as bryophytes and lichens (Greiser et al., 2020).

Yet, despite its vital role in shaping species' habitat conditions, microclimates in managed forests remain largely understudied. Given that forest management directly modifies the three-dimensional allocation of plant material in a stand (Aalto et al., 2023), different management strategies can be expected to create and maintain distinct microclimate environments. A recent study conducted in Sweden indicated that topography and management interact to regulate forest microclimatic conditions, but forest features can play a dominant role over topography (Greiser et al., 2018). In turn, Ehbrecht et al. (2019) found that canopy characteristics other than openness had a marginal effect on microclimate in Germany. Frey et al. (2016) showed how old-growth features (e.g. high biomass and complex vegetation structures) created cooler and more buffered temperatures than even-aged monocultures in the Pacific Northwest, and a similar conclusion was drawn by Kovács et al. (2017), who found that mixed forests with complex structures had less temperature and humidity variability compared to oak-dominated, intensively managed forests.

In Finland, continuous cover forestry, or uneven-aged management as one of its applications, has emerged as an alternative for the predominant rotation forestry system, or even-aged management as its primary application, to mitigate the impacts of forestry on biodiversity (Ekholm et al., 2022; Laudon and Maher Hasselquist, 2023; Virkkala et al., 2023). Recent changes in forest legislation (Forest Act 1093/1996, 2014) have made uneven-aged management an alternative option after being banned for a half century (Kuuluvainen et al., 2012). The differences between even-aged and uneven-aged management have been increasingly studied in recent years both in Finland and globally from various aspects (Eyvindson et al., 2021; Peura et al., 2018; Roth et al., 2023; Savilaakso et al., 2021; Schall et al., 2018). In Central Europe, the average diurnal microclimate temperature range in forests under uneven-aged management has not been found to differ significantly from even-aged systems (Ehbrecht et al., 2019; Menge et al., 2023), however these studies did not consider post-harvest stages. In another central European study, Kovács et al. (2020) conclude that thermal changes in continuous cover system after harvest were short-term compared to clear-cuts. Máliš et al. (2023) state that it would take >50 years for a forest to recover its microclimatic conditions after a clear-cut in a temperate forest in Central Europe. However, in boreal systems, such microclimate studies are still lacking. Considering the rapid warming rate at high latitudes (IPCC, 2023), there is an urgent need to understand the effects of different silvicultural practices on the microclimates experienced by organisms.

In this study, we aimed to understand and quantify how managed even-aged and uneven-aged boreal forests differ in terms of

microclimate temperature buffering. More specifically, we addressed the following research questions:

1. What forest structural attributes drive the microclimate temperature buffering?
2. What are the differences in temporal buffering dynamics between even-aged and uneven-aged management?

To investigate the relationship between forest structure and microclimate, we leveraged microclimatic measurements and hundreds of terrestrial laser scanning (TLS) measurements over a controlled forest management experiment in southern Finland. TLS has proven useful in investigating the three-dimensional vegetation structures in high detail and has recently become more popular in assessing forest biodiversity and microclimate (Ehbrecht et al., 2017; Knuff et al., 2020). Provided the vast extent of boreal forests, as well as the high importance of the forestry sector in these regions, clarifying temperature patterns inside boreal forests under different management strategies will play a crucial role in defining future biodiversity conservation practices.

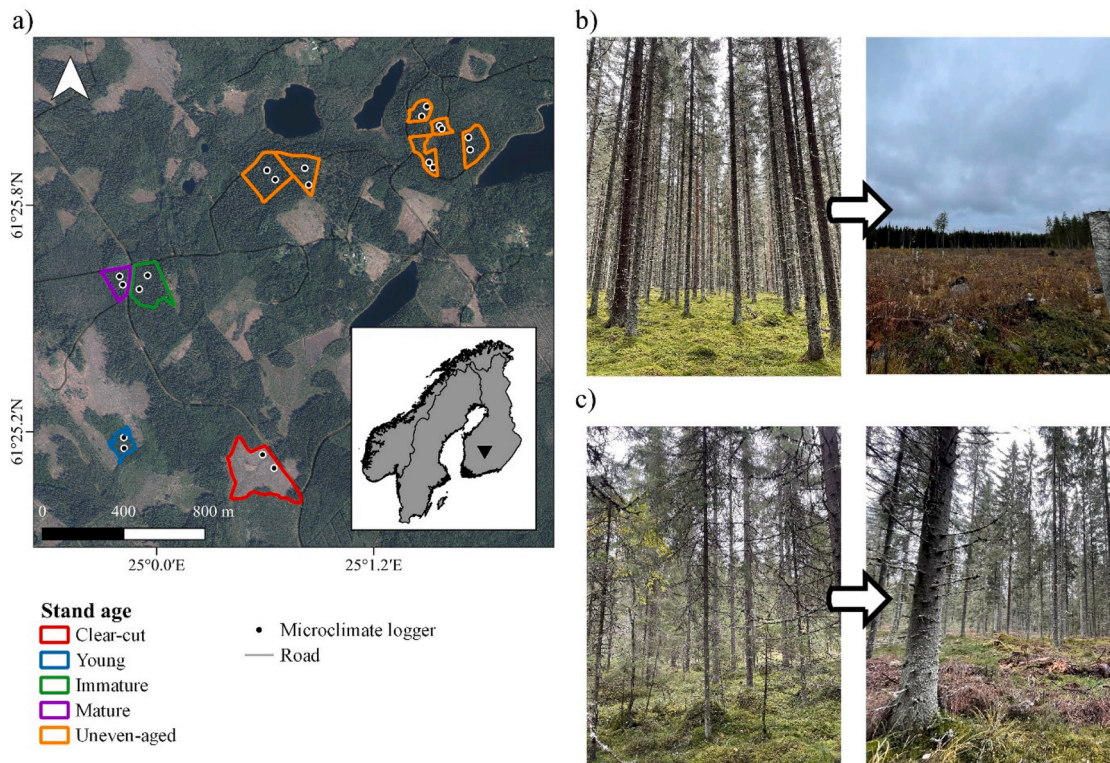
## 2. Material and methods

### 2.1. Study area

The study area is located in Padasjoki, southern Finland (61° 26' 00.4" N, 25° 01' 27.7" E) (Fig. 1). The 17-km<sup>2</sup> Vesijako Research Forest is dominated by boreal forest and lakes. The mean annual temperature is 4.4 °C and mean annual precipitation is 656 mm (1991–2020) (Jokinen et al., 2021). The study area comprises of research forest by the Natural Resources Institute Finland (Luke), including seven stands belonging to the ERIKA experiment that studies the tree and stand development in uneven-aged forests (Saksa and Valkonen, 2011; Valkonen et al., 2020). The ERIKA plots were established in 1991–1992 and selection tree harvesting has since then taken place at 9–15-year intervals, the latest one in 2012. Before establishment, they were treated with selection cuttings of unknown intensity and interval during 1950–1980 and with variable intensity selection cuttings in 1984–1988.

We conducted the study in 20 study plots across 10 stands, of which four represented even-aged management at the subsequent stages of a typical crop rotation (plots named “Ea”) and six uneven-aged management (plots named “Ua”) belonging to ERIKA. Five of the ERIKA stands represented one singular density level throughout the stand, while density did vary somewhat between the stands. Each ERIKA stand had one 40 m × 40 m square plot at the central zone for monitoring tree development and regeneration. One stand represented the subset of stands with intensive plots within ERIKA (“Ueint”). In this stand, density variation was intentionally established within a larger plot (80 m × 80 m). A series of postharvest basal areas of 8, 12, 16 and 20 m<sup>2</sup> ha<sup>-1</sup> was established with two replications on subplots at the first harvest (1992) and reset in the next harvest after a 15-year growth period in 2007. For further details please see Saksa (2004). However, the field plots used in this study were selected independently of the locations of the tree monitoring plots. The even-aged stands, in turn, were classified into four age categories: clear-cut (0 years), young (29–32 years), immature (63–68 years) and mature (75 years) plots. All stands were 1–2 ha in area.

In each stand, we established two 20 m × 20 m study plots selected based on a canopy height model (CHM) and a digital terrain model (DTM) using the open-source airborne laser scanning (ALS) data by National Land Survey (NLS). In the uneven-aged sites, because sample plots from extreme ends of the rotation period were missing, we used the CHMs to select study plots representing both closed and open canopies (gaps) in order to capture the structural heterogeneity within uneven-aged forests. Additionally, we applied the following criteria: the plots had to be located at least 50 m from the road or plot edge; they had to be located at least 100 m from a lake; and they should not be overlapped.



**Fig. 1.** Study area map and example sites. a) The locations of the microclimate loggers and study plots. The basemap is an orthophoto by National Land Survey. b) Photos of a mature even-aged forest and a clear-cut. c) Photos of an uneven-aged forest and a selection harvest.

The locations were adjusted in the field if needed, for instance due to challenging terrain.

The plots represented submesic *Myrtillus* or mesic *Oxalis-Myrtillus* site types (Cajander, 1926), the dominant tree species was Norway spruce (*Picea abies*) with sporadic Scots pine (*Pinus sylvestris* L.) and birch (*Betula pendula* Roth. and *Betula pubescens* Ehrh.) with occasional other broadleaved species.

## 2.2. Microclimate data

In each of our study plots, we had one Onset Hobo Pro V2 logger recording hourly temperatures from June to December in 2021. The accuracy of the loggers is  $\pm 0.25$  °C from  $-40$  °C to  $0$  °C and  $\pm 0.2$  °C from  $0$  °C to  $70$  °C. The loggers were installed in the middle of the plot at 1.5 m height on the northern side of a tree. In the clear-cut plots, the loggers were set on wooden poles at the same height. All loggers were covered with homemade radiation shields.

To account for very high temperatures caused by the excess heating of the radiation shielding due to direct sunlight in low-wind conditions (Maclean et al., 2021), we calculated separately for each logger the 95th percentile of temperature for each day and interpolated over those measurements using a moving average function of the four surrounding measurements (hours) (Figure S1). For the time period needing correction, we considered the dates from June 1 to September 23, which was the autumn equinox. As the reference temperature for the analysis, we used the data from the clear-cut.

All temperature preprocessing and analyses were done in R statistical software version 4.2.2 (R Core Team, 2022).

## 2.3. Terrestrial laser scanning

All 20 plots were measured in April 2021 (broadleaved trees were leaves-off) and August-September 2021 (broadleaved trees were leaves-on) with a Riegl VZ-400i terrestrial laser scanner. Each plot was scanned

from nine different scan positions, both horizontally and vertically to capture the full canopy. The point clouds were co-registered and voxelized as described in Aalto et al. (2023).

Based on the  $1 \text{ m}^3$ -sized voxels, we calculated the Plant Area Density (PAD, units  $\text{m}^2 \text{ m}^{-3}$ ) to measure the amount of plant material in each voxel. For this, we used the software AMAPVox 1.6.1 (Vincent et al., 2017). Based on the PAD, we calculated 16 structural metrics that describe the vertical and horizontal distribution of PAD in the plots in R. The calculated metrics were: total Plant Area Index (PAI, describes the area of plant material per  $\text{m}^2$ ); PAI in six 5-meter thick vertical layers (PAI<sub>0-5</sub>, PAI<sub>5-10</sub>, PAI<sub>10-15</sub>, PAI<sub>15-20</sub>, PAI<sub>20-25</sub>, PAI<sub>25-30</sub>); Relative Heights (RH, describes below which height a certain proportion of the plant material is) of 25 %, 50 %, 75 %, and 98 % (the latter referring to approximate stand height, accounting for possible erroneous points above actual canopy top); Canopy Ratio (CR, describes the vertical evenness of the canopy); Canopy Depth (CD; describes the vertical variability of the canopy); Foliage Height Diversity (FHD; describes canopy layering); Effective Number of Layers of Hill Number <sup>1</sup>D (ENL, describes the number of 1-meter thick canopy layers); and Coefficient of Variation of ENL (CV<sub>ENL</sub>, describes the horizontal variability). For more detailed descriptions of the metrics and how they were calculated, please refer to Aalto et al. (2023). For the calculation of CD, see the Supplementary material.

We only used leaves-off data in further analysis because the differences to leaves-on data were minor and could have resulted from sampling. The plots had only few small broad-leaved trees, therefore we expected there would not be impactful changes in the metrics in the different seasons (Aalto et al., 2023). All the calculated metrics for each plot are listed in Table S1.

## 2.4. Modelling microclimate buffering

The buffering effect can be described with the regression coefficient of forest microclimate and open area temperature in a linear model

(Figure S2), referred to as slope. The temperature at which microclimate temperature equals macroclimate temperature, in turn, is called the equilibrium (Gril et al., 2023a; Lenoir et al., 2017). This approach captures the temperature buffering dynamics in a more indicative and parsimonious way than the usually modelled temperature offsets, i.e. the difference between open area and microclimate temperatures. Perfect coupling between forest microclimate and open area temperature has a slope of 1, while a slope  $<1$  means the temperature extremes are buffered. A slope higher than 1 means that an amplifying effect is present. A slope of 0 means perfect decoupling.

We calculated the slopes separately for summer (June-September) and winter (October-December). This division and naming were made based on the monthly microclimate and macroclimate relationships (Figure S2), even if technically, both periods included also autumn months. Following the approach by Gril et al. (2023a), we first fitted linear mixed-effects models for the two seasons separately for each plot: hourly forest temperatures were the dependent variable, hourly temperature in the clear-cut was the independent variable, and month was considered a random intercept term. We used the *lme4* R-package (Bates et al., 2015). Additionally, using the estimated slopes and equilibria, we predicted average microclimate temperatures for each age category using the following formula:  $\text{offset} (T_{\text{micro}} - T_{\text{clear-cut}}) = \text{equilibrium} \times (1 - \text{slope}) + T_{\text{clear-cut}} \times (\text{slope} - 1)$  (Gril et al., 2023a).

Next, we modeled the slopes with the structural metrics derived from TLS. First, we assessed the bivariate linear relationships separately between each structural trait and slope for winter and summer. We also tested the logarithms and negative exponentials of PAI and RH<sub>98</sub> as predictor variables, as such relationships have been presented in literature (Gril et al., 2023b). However, in our data, the logarithm or the exponential did not increase the model performance or improve the residuals in any of the bivariate models, and we decided to keep to the simpler format of the variables.

To understand the additive effects of different elements of the forest structure, we built a multivariate linear model. First, we fitted a model with all available predictor variables according to the general-to-specific approach, the theoretical advantages of which are discussed in for example Hendry (2024). However, there were exact linear relationships or extremely high correlations between the predictor variables, which led to the need to select a representative and simultaneously as large set of predictor variables as possible. We did the selection based on principal component analysis and a correlation matrix (Figure S3 and Figure S4). The variables should contribute to the axes and have a correlation coefficient within the range  $-1 < r < 1$ . We selected the six different PAI in vertical layers, RH<sub>25</sub> and RH<sub>98</sub>, CR, FHD, ENL and CV<sub>ENL</sub> as predictor variables, and their interaction with season. Total PAI was excluded because it was the sum of the layered PAI, and RH<sub>50</sub> and RH<sub>75</sub> were excluded due to their correlation of 1 with RH<sub>98</sub>. In a second option, we used the same structural variables except we replaced layered PAI with total PAI. We used a stepwise selection with Bayesian Information Criterion (BIC) to select the best model. For this, we used the step () function from *lmerTest* R-package (Kuznetsova et al., 2017). In addition to the automated stepwise selection, we chose the final model based on the residual diagnostics (Figure S5). The final optimized model included season, PAI<sub>0-5</sub>, PAI<sub>5-10</sub>, PAI<sub>15-20</sub>, PAI<sub>20-25</sub>, RH<sub>25</sub>, RH<sub>98</sub>, CR, FHD, ENL and the interaction between season and ENL. Additionally, we ran the model with the same structural variables but with only summer data (referred to as the “summer model”). To assess the relative importance of the multivariate model variables, we used the *relaimpo* R-package (Grömping, 2006).

Finally, because we expected the temperature buffering to change with forest age in even-aged forests (Gril et al., 2023a; Máliš et al., 2023), we fitted another model where we predicted slope with stand age and season. We used generalized additive modelling (GAM) using the *mgcv* R-package (Wood, 2011) and piecewise regression with the *segmented* R-package (Muggeo, 2008). We expected the final harvest (clear-cutting) to take place at 80 years. After the clear-cut, we expected

the relationship between slope and age to return to the original state ( $T_0$ ). We predicted the slope for a time period of 160 years to capture two rotation cycles. We did not apply periodic thinnings in the even-aged model due to lack of data representing these rotation phases. In the uneven-aged sites, we calculated the mean, maximum, minimum, and 98 % confidence intervals of slope estimated from the data to represent expected temporal variability.

To estimate how long it takes for a postharvest even-aged forest starting from  $T_0$  to reach the same buffering capacity as an uneven-aged forest, we determined the intersection of the predicted even-aged and uneven-aged forest curves and their confidence intervals in time.

We acknowledge that criticism has also been raised towards the concept of a stable linear slope between macroclimate and microclimate. For example, there is a strong non-linear effect of soil moisture on forests’ buffering capacity, suggesting linear predictions of microclimate temperatures are not applicable at every forest site (Greiser et al., 2024). Adjusting the time over which the buffering is estimated will also have an influence over the result (De Lombaerde et al., 2022): in our data, the winter slopes were higher compared to summer slopes despite minimal shedding of leaves (Gril et al., 2023a), indicating that there was a shift in the relationship between microclimate temperatures after summer. However, here, the residual diagnostics (not shown) indicated that linear approximation within season adequately described the non-linearity in the data. Additionally, first modelling the slopes and then modelling their explanatory factors is not statistically optimal and not based on the traditional statistical theory. These simplifications are properties of the method proposed by Gril et al. (2023a) and we have accepted them in the modelling.

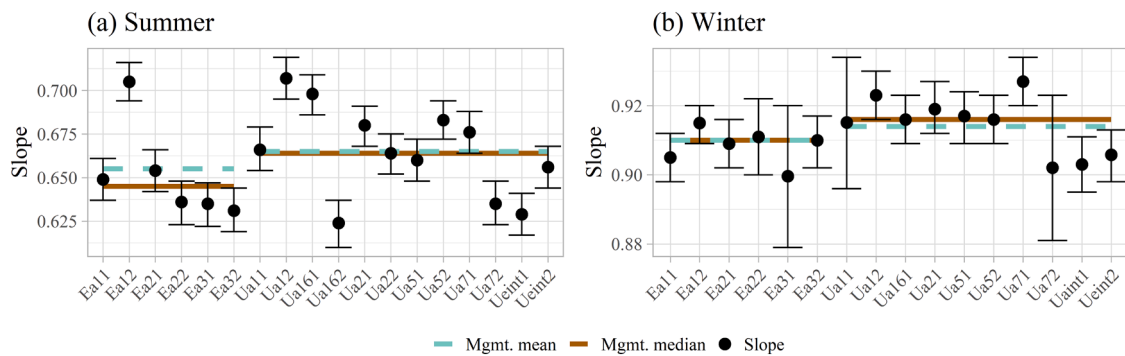
Lastly, we acknowledge that clear-cut temperatures do not directly equate to macroscale temperatures, and that the selected reference data will have an influence on the result. In addition to the clear-cut temperature data, we also estimated slopes using reference data from the nearest weather station and gridded air temperature data (ERA5-Land). The ERA5-Land-based estimations consistently produced forest slopes  $>1.1$ , indicating amplified temperature variability. However, we believe this result is influenced by the high density of lakes in the study area that dampens the large-scale variability, and potential uncertainties associated with the ERA5-Land product. Meanwhile, the nearest weather station was situated on a narrow ridge across a lake, over 30 km from our microclimate sites, making it poorly representative of the climatic conditions in our plots. The slopes derived from this weather station data were very close to 1, suggesting nearly perfect coupling. Given these issues, we ultimately decided to rely on the clear-cut Hobo data as the most appropriate reference for our analysis.

### 3. Results

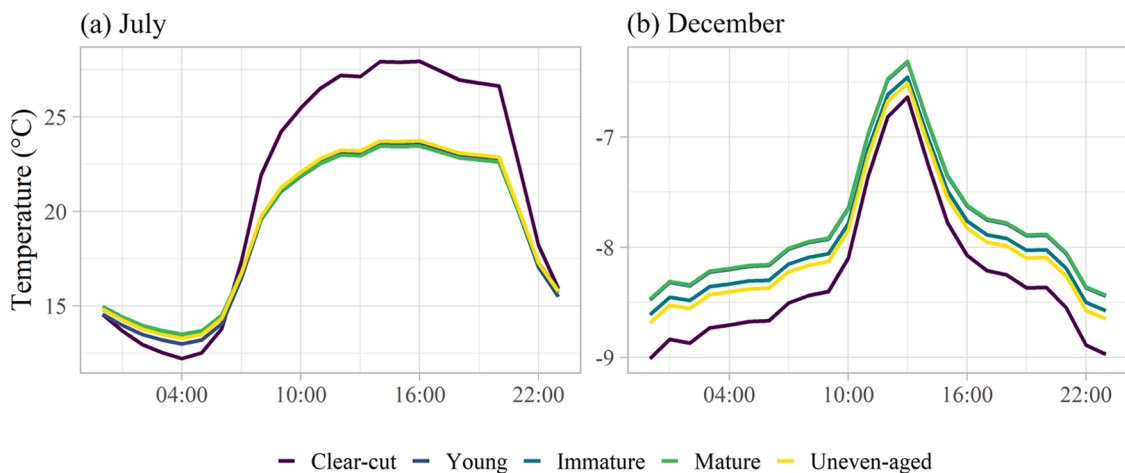
#### 3.1. Seasonal differences in microclimate buffering

The slopes during both winter and summer were consistently below 1, thus demonstrating a continuous buffering effect throughout the study period in all 18 forest sites (Fig. 2). Summer slopes were significantly lower compared to winter slopes when examined with a paired *t*-test ( $t = -46.82, p < 0.01$ ). The mean slope during summer was  $0.66 \pm 0.03$ , ranging from 0.62 to 0.71. In winter, the slopes were  $0.91 \pm 0.01$  on average and ranged from 0.90 to 0.93. When considering the management types separately, the mean slope in even-aged plots was  $0.65 \pm 0.03$  in summer, and  $0.91 \pm 0.01$  in winter, while in the uneven-aged plots, the mean summer slope was  $0.66 \pm 0.03$  and the winter slope was  $0.91 \pm 0.01$ , respectively. A summary of all the calculated slopes can be found in the Supplementary material Table S2.

The microclimate temperature offsets derived from the slopes and equilibria are demonstrated in Fig. 3 as modelled hourly mean temperatures for each age category. In July, which was the warmest month of the study period, the average maximum temperature offset for all forests was negative ( $-4.4$  °C) and moderately positive ( $1.1$  °C) for



**Fig. 2.** Slopes depicting magnitude of the buffering effect, their mean, median, 1st and 99th percentiles for summer and winter over each study plot. The mean and median are given based on the management types (“Mgmt” = management; plot names starting with “Ea” = even-aged and “Ua” = uneven-aged) and season. Note the different scales for the two seasons. a) Summer, b) Winter.



**Fig. 3.** Modelled diurnal average microclimate temperatures for July and December 2021. Color refers to age category. Note the different y-axis scales. a) July, b) December.

minimum, i.e. night temperatures (Table S3). In December, the coldest month of the study period, diurnal temperatures inside forests stayed on average above clear-cut temperatures: maximum positive offset was on average 0.5 °C during the night (Table S3). Differences between age categories were minor (July maximum temperature offset range between managements = 0.3 °C; December minimum temperature offset range = 0.2 °C; see Table S3).

### 3.2. Effects of structural metrics on buffering

In the univariate summer models, the vegetation layering metrics (ENL and FHD) had the strongest relationships of all structural metrics with summer slopes ( $R^2$  being 0.37 and 0.29,  $p < 0.01$  and  $p = 0.01$ , respectively). All four Relative Heights were also statistically significant ( $p < 0.05$ ). Total PAI, instead, was not statistically significant ( $p = 0.06$ ). In winter, FHD was the only metric that was of statistical significance (Table S4). The relationships with PAI, ENL, FHD and  $RH_{98}$  are plotted in the Supplementary material Figure S6.

In the multivariate model, season had the highest relative importance of all variables and explained 98 % of the variation in slopes. The dominance of it caused the adjusted  $R^2$  to be as high as 0.99. The summer model, which only included structural metrics, explained 68 % of the variation (Figure S7). In both models, the directions and magnitudes of the effects of the structural metrics were similar. The coefficients for the multivariate model are shown in the Supplementary material Table S5 and model residuals in Figure S5. The summer model results are found in the Table S6. Due to the similarities in the models,

we will focus here solely on the multivariate model that includes both seasons.

The partial effects of the structural metrics are plotted in Fig. 4. There was a clear pattern: more plant material in the lower canopy layers decreased the slopes (i.e. increased the buffering), whereas more in the upper layers increased it (i.e. decreased the buffering). Among the PAI layers, high PAI in 0–5 m had a negative effect on the slope, while increasing PAI in the other layers had a positive effect. Similarly, the higher  $RH_{98}$ , the higher the slope. CR behaved similarly: lower CR values, indicating that more plant material is found in the upper canopy layers, increased the slope. Contrastingly, higher  $RH_{25}$  implied lower slopes. High understory density was present in the young even-aged plots and it was higher in the uneven-aged plots compared to the other two even-aged categories (Fig. 5a, Fig. 5g).

The metrics describing vertical canopy evenness and layering (CR, FHD and ENL) conveyed similar results: the more evenly the plant material was distributed vertically, the lower the slope and consequently the higher the buffering effect (Fig. 4). From the structural metrics, only ENL had a significant interaction with season, the buffering effect of ENL decreasing considerably in wintertime. The highest ENL and FHD were found in the more mature even-aged plots, but also some uneven-aged sites displayed a high number of filled canopy layers (Fig. 5h and Fig. 5i). Most evenly distributed canopies were found in the young even-aged and uneven-aged plots (Fig. 5g).

There were moderate correlations between the layered and total PAI but replacing the layered PAI with total PAI in the multivariate model produced poor residuals (violation of assumption of linearity) and

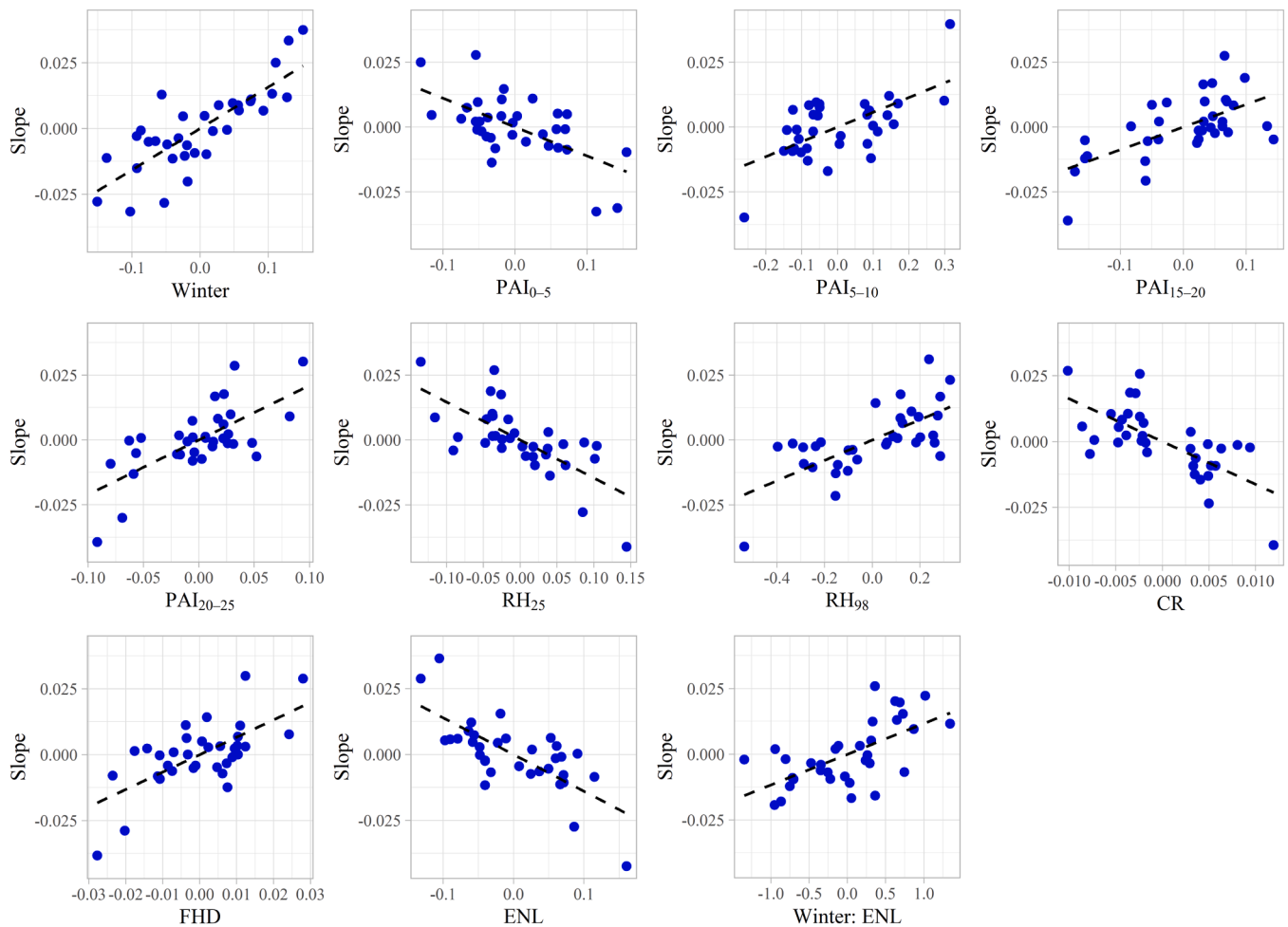


Fig. 4. Partial effects on the slope variation approximated with a smoothing function in each variable when the variables and slope values are centered. All effects are statistically significant ( $p < 0.05$ ).

slightly poorer  $R^2$ .

### 3.3. Differences in buffering dynamics due to management

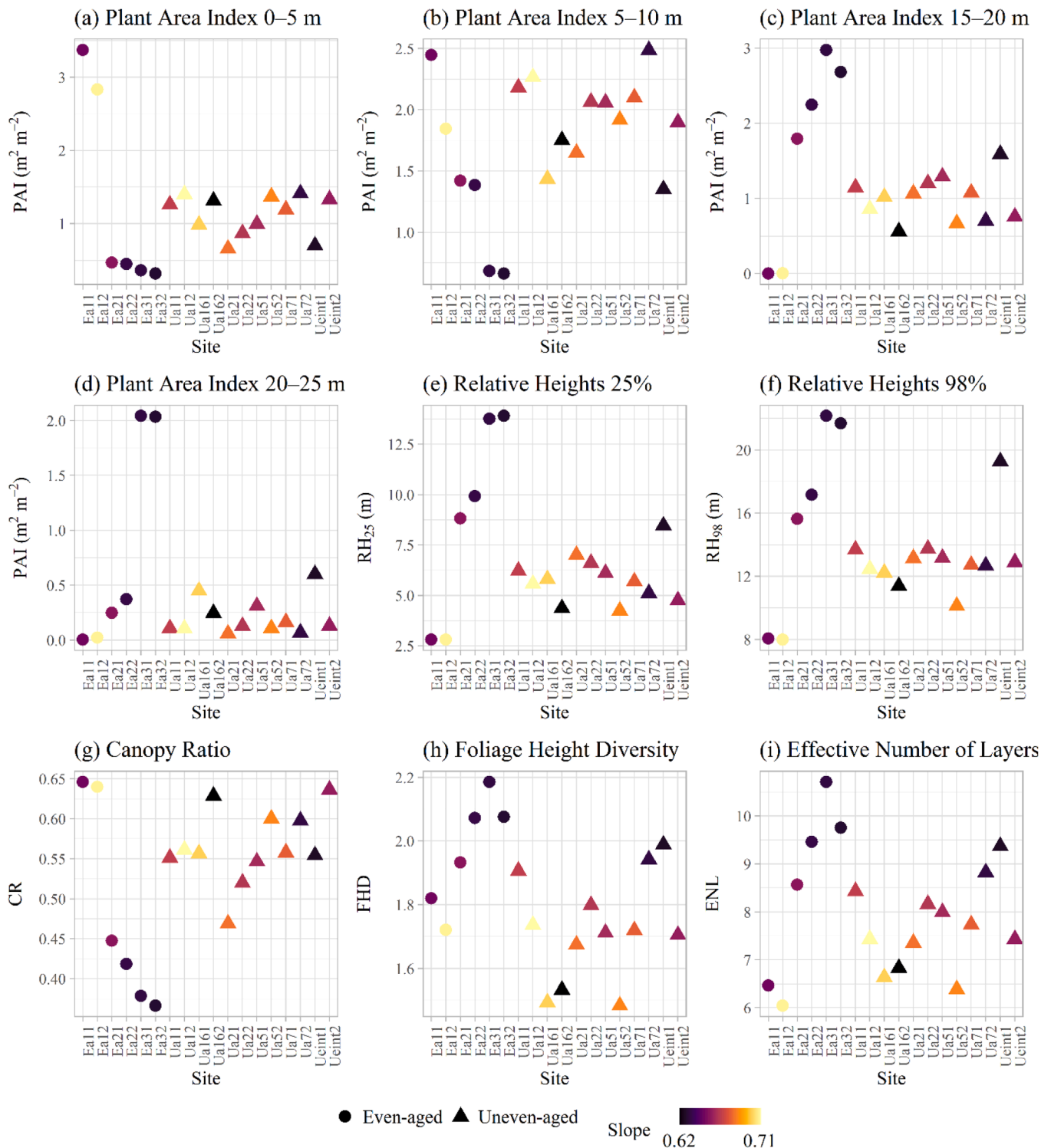
The GAM model suggested that the even-aged stands reached the same summer buffering capacity as uneven-aged stands at approximately 35 years after clearcutting and restocking. They reached the upper confidence interval at 24 years (Fig. 6). After this, the even-aged slopes decreased slowly until time of harvest and remained within the uneven-aged plots' confidence interval. In winter, the pattern was similar yet smaller in magnitude: on average, even-aged slope equaled uneven-aged slope at 28 years but fell inside the uneven-aged confidence interval at 22 years. Then it remained constant and very close to the uneven-aged mean slope. In neither season even-aged slope went below the lower limit of the uneven-aged confidence interval.

## 4. Discussion

This study leveraged terrestrial LiDAR surveys and field measured microclimate temperatures to evaluate the influence of management in regulating the temperatures occurring inside boreal forests. To our knowledge, this is the first study to address the role of even-aged and uneven-aged management strategies on the buffering capacity of boreal forests.

### 4.1. The effects of management on buffering

Both uneven-aged and even-aged stands buffered extreme microclimate temperatures, and the modelled average temperature offsets were very close between the management types. Nevertheless, the buffering capacity of even-aged stands was different at various points into the rotation cycle, whereas uneven-aged stands are expected to exhibit lower temporal variability, making buffered temperature conditions more constant. It is important to note, however, that our data for uneven-aged stands did not include a temporal component, and this interpretation is based on a range of structural conditions analogous to different temporal stages. Such patterns have been found in earlier research in other biomes: in Ehbrecht et al. (2019), mean diurnal temperature range between even-aged and uneven-aged temperate forests were not significantly different, however in the early successional stages, even-aged forests had markedly higher temperature ranges than the old and uneven-aged sites. In a tropical setting, Baker et al. (2014) report that the microclimate differences between a mature and a regeneration forest diminished with forest age. In boreal forests, however, studies on the effect of forest management on microclimate have so far been lacking. Our results shed light on not only the thermal variability over different management regimes but also their ability to buffer macroclimate variability, which has been considered crucial for the survival of forest species with climate change (De Frenne et al., 2021). Here, we did not compare managed forests to old-growth or unmanaged forests, which would be an interesting avenue for future research since unmanaged forests have been found to host more stable microclimates

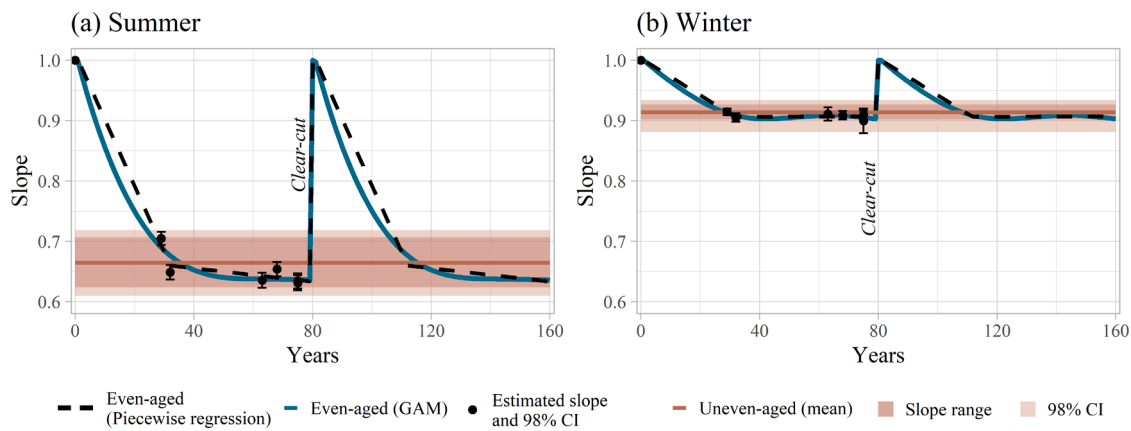


**Fig. 5.** Scatterplots of temperature buffering (slope) against the structural variables included in the multivariate model for each site. Circles represent the even-aged plots and triangles the uneven-aged plots. Point color refers to summer slope value.

compared to managed forests in temperate regions (Menge et al., 2023). For example, in Ehbrecht et al. (2019), unmanaged forests had notably lower temperature variation than even-aged and uneven-aged types. Máliš et al. (2023), instead, found that the microclimatic variability did not differ significantly between mature even-aged and old-growth temperate forests. Nevertheless, considering the full successional gradient, gaps in old-growth forests were more buffered compared to young even-aged stands (Máliš et al., 2023). It would be interesting to

examine uneven-aged and old-growth boreal forests side by side, since gap dynamics are present in both.

Considering the rotational nature of even-aged management, microclimatic conditions depend on the forest’s age (Baker et al., 2014; Ehbrecht et al., 2019; Máliš et al., 2023), with mature forests having the strongest buffering effect. However, when the buffering is at its highest, severe alteration to both structure and composition will take place in the form of final harvest, removing the canopy cover completely in most



**Fig. 6.** Estimated summer and winter slopes in time. The solid blue line represents even-aged management fitted by generalized additive modeling (GAM), and the dashed black line represents even-aged management fitted by piecewise regression. Observed data and 98 % confidence intervals (CI) are plotted as dots and whiskers. CI of modelled slopes are not shown. The solid brown-red line represents mean of uneven-aged data. The narrower shaded area around the uneven-aged line shows the minimum and maximum, and the wider shaded area shows the 98 % CI. a) Summer slopes, b) Winter slopes.

cases. Consequently, along with confronting other ecological changes, the forest entirely loses its ability to buffer temperatures (Aszalós et al., 2023; Blumröder et al., 2019; Kovács et al., 2020). Our results suggest that regaining the buffering capacity will take decades, and the buffering is weakest in young forests. Young forests of the age class 1–20 years make up to one-quarter of Norway spruce forests in Finland (Korhonen et al., 2021), suggesting that a high proportion of spruce forests are still recovering from disturbance and have more fluctuating microclimates.

In contrast, uneven-aged forests experience disturbance in the form of harvests more frequently, but their intensity is lower, especially if single-tree selection is applied. In artificial gaps, microclimates are still more buffered compared to clear-cuts (Kovács et al., 2020; Máliš et al., 2023) and take a shorter time to recover to pre-disturbance levels (Ritter et al., 2005). Considering the temporality of forest management, this result argues that uneven-aged management may be a better alternative to sustain stable forest microclimatic conditions at stand level over long time periods. This bears particular weight in the present era of climate change. It is being hypothesized that warming under forest canopies may be slower than the rate of macroclimatic warming (De Frenne et al., 2013; De Lombaerde et al., 2022), and that forests can create microclimatic refugia for temperature sensitive species (Greiser et al., 2020). Maintaining these refugia can turn out to be paramount for protecting biodiversity (Greiser et al., 2020; Wolf et al., 2021).

It must be noted that we did not consider periodic thinnings in even-aged management in our analyses because they could not be captured in the limited sampling framework. Thinnings decrease the stand density and canopy cover slightly and temporarily, which can be expected to affect the temperature buffering similarly to selection felling in uneven-aged forests (Heithecker and Halpern, 2006; Kovács et al., 2020). However, in uneven-aged management, tree understories are more preserved in harvest operations. Additionally, we acknowledge that the absence of even-aged forests younger than 30 years in our study area influences the robustness of the estimated recovery period, making the result sensitive to individual data points. However, for example Senf et al. (2019) report the recovery period for canopy structure in temperate spruce forests after clear-cut to be 30 years, which supports our estimate of the microclimate recovery time. Notably, structural metric values observed in the uneven-aged plots fall predominantly between the young and immature even-aged plots (Aalto et al., 2023). Adding more even-aged study plots representing additional age categories, rotation phases and thinning treatments would further improve the robustness of the predictions and confidence in recovery length predictions.

Our study sites represent typical Finnish managed forests. Spruce is the second most common tree species in Finland after pine and grows in

almost the entire country except the most northern part (Korhonen et al., 2021). Therefore, a great portion of forested area in Finland is dominated by spruce of various ages, creating stands with high shading, air humidity and soil moisture levels. Spruce is the most suitable tree species for uneven-aged management due to its high shade tolerance, making our experimental sites highly representative of uneven-aged management in Finland.

#### 4.2. Seasonal changes in buffering capacity

Winter and summer slopes were significantly different in our plots despite the plots being dominated by coniferous trees, unlike in Gril et al. (2023a) where coniferous sites had no seasonal differences in buffering. In contrast, below-canopy summer temperatures were clearly more buffered compared to winter, the role of forest structure being amplified during summer. The results are in line with for example Greiser et al. (2018), Ehbrecht et al. (2019), and Gril et al. (2023a) for broadleaved forests. The effect was evident especially on the hottest summer days (Fig. 3a, Figure S8). Previous research has shown that strongest buffering occurs during more extreme temperatures (Baker et al., 2014; Davis et al., 2019; De Frenne et al., 2019; Greiser et al., 2024). When soil water is not a limiting factor, evapotranspiration increases non-linearly with temperature, leading to greater temperature offsets during warm, clear days (De Frenne et al., 2021). In contrast, during overcast conditions when less solar radiation is reaching the ground, plants limit transpiration due to lower vapor deficit pressure and CO<sub>2</sub> uptake, and evaporation decreases, consequently affecting the evapotranspirative cooling (Allen et al., 1998; Bonan, 2016; Davis et al., 2019). The cooling effect at stand level, caused by latent heat release from soil and vegetation surfaces, diminishes during overcast conditions (Dai et al., 1999). Acknowledging the possible errors caused by radiation shielding (Maclean et al., 2021), thorough data masking protocol using for instance cloudiness data would be beneficial in studying the differences in buffering during sunny and cloudy days and assessing the quality of the measurements.

In winter, the processes affecting microclimates in boreal forests are different than in summer leading to smaller spatial variation in buffering: there is less solar radiation and evapotranspiration is low (Bonan, 2016). In our model, we found that the buffering effect of canopy layers decreased in winter. Instead of intercepting insolation, during snow cover, forests have a lower surface albedo compared to open areas, and heat is stored in tree stems and canopy, causing buffered temperatures compared to open areas (Rutter et al., 2023). Notably, forests mostly buffered the minimum temperatures (Figure S8), whereas during the majority of days the temperatures were mild and very similar in forests

and in the clear-cut, which resulted in slopes above 0.9. Most likely, moderate temperatures with little variability in buffering occurred during cloudy days. We did not separate overcast days from clear sky ones, but statistically, months from November to December are the cloudiest months in Finland (Finnish Meteorological Institute, 2024). Complete overcast conditions during winter act as a blanket, clouds reflecting longwave downward radiation that keeps the air warmer compared to clear skies (Dai et al., 1999; Lockwood, 2012), and in high-latitudes the coldest winter days are associated with stable atmospheric conditions and anti-cyclonic circulation.

Unfortunately, due to several loggers failing later during the measurements, we did not analyze midwinter or spring temperatures. These periods would have been intriguing to examine for several reasons: snow cover brings an additional factor to the complex energy exchange between air, canopy and soil surfaces (Baker et al., 1992; Rutter et al., 2023) and its impact on soil and near-ground temperatures has been recognized (Aalto et al., 2018; Baker et al., 1992; Haesen et al., 2021; Mote, 2008). Adding data of snow cover days could have shed light on management's effects on winter buffering, as the distribution of snow inside even-aged and uneven-aged forests due to structural variability may be different (Hojatimalekshah et al., 2021; Varhola et al., 2010), possibly causing microclimate variability. However, capturing such temperature variability would likely benefit from a denser measurement network. Nevertheless, the observed seasonal differences here suggest that the relationship between microclimate and macroclimate temperatures is more complicated than simply linear.

#### 4.3. Canopy structural features controlling buffering

The amount of vertical canopy layers (ENL) was the most important variable determining the buffering effect in our analysis. It is worth noting that in the case of ENL, layers are considered to be 1-meter thick and do not necessarily describe vertical heterogeneity. ENL is correlated with tree height, which was greatest at even-aged mature sites. However, tree height alone was not a good predictor of slope. The result is in accordance with Ehbrecht et al. (2019), who also found ENL to explain more of the microclimate variability than stand height. The effect of filling of canopy layers is likely related to the high insulating effect: the more plant material there is along the vertical axis, the thicker insulating layer there is, which reduces both incoming shortwave radiation that reaches the forest floor as well as outgoing longwave radiation (Aussenac, 2000; Geiger, 1980). More stratified canopies also inhibit the mixing of air, which further enables the below-canopy temperatures to be buffered from macroclimatic conditions (Hardwick et al., 2015).

The evenness of the vertical distribution of tree material, here represented by canopy ratio (CR), had a significant effect on the buffering. In our model, high CR increased the buffering, yet ENL dominated over CR in variable importance. Vertical evenness was also a significant microclimate predictor in Gril et al. (2023b), who suggest that it should be used as a major explanatory variable in microclimate models. The Vertical Complexity Index (VCI) used in Gril et al. (2023b) describes the same thing as CR, however it does not distinguish if the plant material is allocated in the upper or lower canopy. Therefore, theoretically, CR captures vertical variability better than VCI. However, in our study sites there were no forests where more plant material would have been located in the lower canopy than in the upper canopy, thus in this case VCI and CR were presumably very similar to each other.

The lower canopy layers ( $PAI_{0-5}$ ) had a significant effect on buffering: the more plant material in these layers, the lower the amplitude of temperature fluctuations compared to outside forest. Considering that the microclimate loggers were located in this layer, the importance of the variable is instinctive. A denser understory creates more insulation, and the higher leaf area increases evapotranspiration (Aussenac, 2000; Bonan, 2016). A similar result has been reported by for instance Kovács et al. (2017), who found that the understory is more important in determining below-canopy temperatures than the upper canopy in

stands with similar canopy closure. Stickley and Fraterrigo (2021), in turn, report a considerable positive effect of understory vegetation to temperature buffering. However, in short stands such as the young even-aged stand in our study, a dense understory alone was not found to drive the buffering and was weaker compared to a taller stand with more canopy layers and more air mixing.

There are some considerations that must be acknowledged when interpreting the results. All the metrics were derived from PAD profiles, which caused the majority of the TLS-derived structural metrics being highly correlated ( $>|0.7|$ , Figure S3), complicating the interpretation of the coefficients from statistical multivariate models. Many of the metrics are dependent of each other, for example the previously mentioned ENL and  $RH_{98}$ , or CR and  $RH_{25}$ : possible number of layers is higher in tall stands than short, and density of lower canopy layers is related to vertical distribution. For instance, in our model,  $RH_{25}$  showed contradictory direction of effects compared to  $PAI_{0-5}$  and CR, which is likely due to the strong correlation among the three. Nevertheless, this is not an indication of an incorrect model, rather it reflects the complexity of the relationships within the data (Wooldridge, 2009). Therefore, it is difficult to completely tease apart the magnitude and relative importance of effects of different structural characteristics. However, we can conclude that the model results imply an important role of vertical forest structure in temperature buffering.

Secondly, the strong cooling effect of daytime shading raises the question of how much of the buffering can be explained by canopy cover alone, which has been found a strong predictor of understory microclimate (I. Aalto et al., 2022a; Aalto et al., 2022b; Greiser et al., 2018; Jucker et al., 2018; Lenoir et al., 2017). However, PAI is closely related to canopy cover (Chen et al., 1997; Gonsamo et al., 2013) as it describes the total vegetation area capable of intercepting insolation (Lenoir et al., 2022), and we found it to have a weaker explanatory power than the vertical structure. Importantly, our results are in line with earlier research (De Frenne et al., 2021; Ehbrecht et al., 2017, 2019; Gril et al., 2023a, 2023b; Kovács et al., 2017), confirming that vertical structure is a major driver of temperature buffering also in boreal forests.

Finally, tree species determines forest structure to a high degree, and consequently affects the forest's temperature buffering capacity. The structure of, for example, pine is very different from spruce with a higher proportion of tree material located in the upper canopy, and in a mixed or pure broadleaved stand, seasonal changes in structure, such as changes in PAI and its allocation, will inevitably affect the buffering capacity (von Arx et al., 2013; Ehbrecht et al., 2019; Gril et al., 2023a). This study covered stands dominated by Norway spruce, which is economically a highly important tree species in Fennoscandia, yet microclimate studies have been lacking. Earlier research has been focused on deciduous tree species (e.g. Ehbrecht et al., 2019; Mális et al., 2023; Menge et al., 2023; but see also Greiser et al., 2018), making this study an important contribution to boreal forest management and microclimate literature.

#### 4.4. Climate change and management considerations

Considering the increasing likelihood of extreme temperatures and drought in the boreal region with climate change (IPCC, 2023), the role of forests in temperature and humidity buffering is growing (De Frenne et al., 2021). The summer of 2021 was the hottest in Finnish measurement history since 1937 (Finnish Meteorological Institute, 2021), thus the results of this study are indicative of future behavior of forest microclimates. Since the buffering increases non-linearly with macroclimate temperature, theoretically, the summer temperature offsets may increase accordingly (De Lombaerde et al., 2022). Nevertheless, also forest temperatures are expected to increase due to the macroclimate warming (De Frenne et al., 2021; Wolf et al., 2021). Additionally, since evapotranspiration is dependent on water availability (Davis et al., 2019; Greiser et al., 2024), more severe and frequent droughts may disturb the capability of forests to buffer high temperatures (Haesen

et al., 2021; Liao et al., 2023). Similarly, if winters become milder with climate change, winter buffering may decrease (De Frenne et al., 2021; De Lombaerde et al., 2022), reducing total annual buffering.

There are several biodiversity implications induced by climate warming. The warming forces cold-adapted species to move northwards and upwards in elevation, causing community turnover and loss of cold-adapted species (Antão et al., 2022; De Frenne et al., 2013; Zellweger et al., 2020). This thermophilization effect is buffered when forests become denser, but increases with the opposite development, for instance with clear-cuts (Christiansen et al., 2021; De Frenne et al., 2013). Considering the cyclic nature of even-aged forestry, a dramatic shift in species composition is expected after every clear-cut (Aszalós et al., 2023; Majasalmi and Rautiainen, 2020; Virkkala et al., 2023) and with a warming climate, there will likely be species turnover towards more warm-adapted species (Mazziotta et al., 2016). Cold-adapted species at the range margins, in turn, are threatened by increasing temperatures and could benefit from management that supports the buffering capacity of the forests (Greiser et al., 2020) and protects microclimate refugia (Ashcroft et al., 2012). Uneven-aged forest management could potentially provide habitats for such temperature-sensitive species.

Ultimately, it must be noted that different species require different microclimatic environments, and one management type or developmental stage does not host all forest-dwelling species. In addition to stand-level microclimate, forest management shapes the microclimatic gradients across the landscape (Greiser et al., 2018; Schall et al., 2018). Schall et al. (2018) found that a landscape with even-aged stands representing different fertility classes hosted more biodiversity than only uneven-aged forests, microclimate being one factor. Savilaakso et al. (2021) recommend that to protect biodiversity, the landscape should consist of forests of different ages and management types. This study showed that both even-aged and uneven-aged managed forests created buffered microclimate conditions, but that they varied at different points of the rotation cycle. Nevertheless, maintaining microrefugia is pivotal for the survival of temperature-sensitive species under warming climate, and uneven-aged management is a promising option to conserve such environments, especially in wood production landscapes where natural forest is lacking.

## 5. Conclusion

Forest canopies play a crucial role in regulating the microclimate temperatures in terrestrial boreal ecosystems. Here, we demonstrate that changes in the structural characteristics of vegetation arising from forest management can substantially alter the spatial and temporal dynamics of microclimate inside boreal forests. Filling of canopy layers was the most important metric for increasing buffering, and most present in even-aged mature stands, causing these forests to have on average the strongest buffering capacity in our data. Nevertheless, we did not observe large differences in the different forests' temperature offsets. However, even-aged stands may take up to 30 years to achieve the same buffering capacity of uneven-aged stands after clear-cut. Therefore, uneven-aged management is likely to offer a better alternative to sustain stable microclimate conditions over longer time periods. Uneven-aged management could be an alternative to maintain microrefugia for species that require continuous forest cover, especially in areas where there are no natural forests.

## CRedit authorship contribution statement

**Iris Starck:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Juha Aalto:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Steven Hancock:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Sauli Valkonen:** Writing – review & editing, Resources. **Leena**

**Kalliovirta:** Writing – review & editing, Methodology. **Eduardo Maeda:** Writing – review & editing, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

## 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.

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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.2025.110434.

## Data availability

Data will be made available on request.

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