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Retention forestry amplifies microclimate buffering in boreal forests

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ABSTRACT

Retention forestry is increasingly adopted as an alternative to clearcutting practices and involves retaining structural and compositional complexity (e.g., living and dead trees) from preharvest to postharvest. Past studies have examined the role of retention forestry in supporting various ecosystem functions and biodiversity, whilst its microclimate buffering capacity has been largely neglected. We investigated the microclimates and the underlying mechanisms of retention forests relative to clearcuts and old forests in a boreal forest landscape in central Sweden. We found that both air temperature and vapour pressure deficit (VPD) differed significantly between the forest types. Old forests consistently exhibited the most buffered forest microclimates, followed by retention forests, while clearcuts displayed the lowest. Basal area and canopy cover were identified as the key determinants influencing air temperature and VPD across the forest types. Retention practices can also impact a stand's microclimates. Specifically, maintaining diverse tree species had the potential to lower the stand's maximum temperature, given its positive association with canopy cover. Large volumes of lying deadwood were found to be negatively correlated with both basal area and canopy cover, likely contributing to increased maximum temperatures. Furthermore, standing deadwood directly lowered the maximum temperature within forest stands. Finally, edge effects were observed in the retention forests, with south-facing edges experiencing significantly higher maximum temperature and VPD compared to north-facing edges and forest interiors. These south-facing edge effects were positively associated with the difference in lying deadwood volumes between forest edges and interiors. Our findings support the positive influence of retention practices on a stand's microclimate buffering, achieved through preserving diverse tree species, standing deadwood, and implementing measures to prevent severe wind-induced tree mortality, particularly in south-facing edges (e.g. creating south-facing buffer zones). Forest managers and policy makers can utilize these results to minimize the climate-change impacts on below-canopy biodiversity and functioning.

1. Introduction

Our planet is warming significantly. The current surface temperature has been risen 1.1 ± 0.13 °C above the pre-industrial average (1850–1900), and this value was expected to reach/exceed 1.5 °C in the next two decades (IPCC, 2021; WMO, 2022). Forests, however, can mitigate macroclimate temperature and humidity changes below the canopy (De Frenne and Verheyen, 2016; Zellweger et al., 2020). Both radiation and evapotranspiration modified by the forest canopy give rise to lower maximum temperatures and elevated air humidity near the forest floor in such a way that the microclimatic variation is lower inside than outside the forest (macroclimatic buffering sensu; De Frenne et al., 2019; De Frenne and Verheyen, 2016). As such, forests can serve as a protective blanket that potentially reduces the effects of climate change on understorey communities (Bertrand et al., 2011; Castaño et al., 2018; De Frenne et al., 2013). Hence, determining the optimal forest management to amplify a forest's thermal buffering capacity is of rising importance, especially in the face of climate change.

Globally, approximate 30 percent of global forest area is used for the production of wood and non-wood forest products (FAO, 2020). Wood removals from these production forests, primarily through clearcutting, aim to supply an adequate amount of forest goods, including forest foods and fuelwood, to meet the demands for human well-being (FAO, 2014). More recently, global biodiversity conservation and the impacts of climate change have proposed new requirements for forests managed for timber. For example, Closer-to-Nature Forest Management has been proposed in the EU Forest Strategy for 2030 to improve the conservation values and climate resilience of multifunctional, managed forests in

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Europe (Larsen et al., 2022). The Closer-to-Nature Forest Management include principles of retention of habitat trees, special habitats, and dead wood, promoting natural tree regeneration, partial harvests and promotion of stand structural heterogeneity, promoting tree species mixtures and genetic diversity, and avoidance of intensive management operations (Larsen et al., 2022). A wider adoption of Closer-to-Nature Forest Management will require a substantial effort in knowledge transfer from existing management efforts, to provide evidence for practices that improve the conservation value and climate resilience of managed forests. Retention forestry which involves retaining structures and organisms such as live and dead trees, as well as small areas of intact forests during harvest, is increasingly practiced as an alternative to clearcutting in temperate and boreal forests in North America, Australia and northern Europe (Gustafsson et al., 2012). By maintaining the continuity of structural and compositional complexity from preharvest to postharvest, retention forests can support higher richness and abundance of forest understorey species than traditional clearcuts, but certain 'cold-favoured' or 'forest-interior' species adapted to stable environments may not survive long-term in retention forests (Fedrowitz et al., 2014; Jönsson et al., 2022). The ability of retention forests to preserve biodiversity is most likely influenced by forest microclimates (Hylander et al., 2022). However, these microclimates within retention forests have not been quantified so far. We thus do not know to what extent retention forests differ from clearcuts and old forests in microclimates. Understanding this aspect is crucial for comprehending the ecological resilience of retention forestry to climate change and for determining its relevance to emerging guiding principles (e.g., Closer-to-Nature Forest Management) and expanding its uses to forest restoration and the management of uneven-aged forests (Ekholm et al., 2023; Gustafsson et al., 2012).

Stand characteristics such as tree species composition, and structural attributes such as canopy cover and basal area have been proven as the key determinants of forest microclimate (De Frenne et al., 2021; Zellweger et al., 2019) and shown to shape the composition and diversity of many organism groups (e.g. Barbier et al., 2008; Boudreault et al., 2002; Klein et al., 2021, 2022). Retention forestry, by preserving the structural and compositional diversity of forests, is therefore expected to have a greater effect on macroclimate buffering compared to clearcuts. This is due to the fact that clearcutting often results in simplified and homogeneous forest structures after harvesting (Franklin et al., 2000). In retention forestry, it is common to preserve certain elements typically found in old or intact forests, such as standing and lying deadwood, large living trees, and species from different taxonomic groups, while these features are rarely observed in clearcuts (Kyaschenko et al., 2022). These retained elements, often considered as biological legacies following natural disturbances in intact forests, have been shown to positively affect forest dependent species (e.g. Fedrowitz et al., 2014), and potentially affect the thermal buffering of retention forests, while via different pathways. First of all, by leaving dead trees instead of removing or destroying organic materials through clearcutting and scarification, the growth of retained trees as well as regenerating trees likely to benefit from this practice (Mayer et al., 2022). Second, by leaving mature trees during harvest, retention forests can provide shelters for understorey species, such as herbivorous plants, ectomycorrhizal fungi and soil fauna, which contribute to nutrient cycling and in turn, facilitate the growth of the trees (Sterkenburg et al., 2019). Finally, tree species diversity was found to have a positive impact on forest production in numerous previous studies (e.g. Gamfeldt et al., 2013; Van de Peer et al., 2018). Given the highly correlated relationship between biomass production and canopy closure (Zhang et al., 2022), and considering their crucial role in thermal buffering (Zellweger et al., 2019), it is expected that leaving live and dead trees, as well as retaining diverse tree species could impact the macroclimate buffering capacity of a forest stand. The retained elements in forests should influence microclimates not only between forest stands, but also between forest edges and interiors within a stand. This distinction is crucial due to the pronounced exposure of forest edges to heightened solar radiation and wind intensity in comparison to the more sheltered conditions within the forest interiors. Consequently, these contrasting environments generate variations in the growth of trees, as well as the abundance of both living and dead trees, a more pronounced difference of forest microclimates between forest edges and forest interiors is indeed expected (e.g. Hylander, 2005; Rudolphi and Gustafsson, 2011).

Here we investigate the thermal buffering capabilities of retention forests relative to clearcuts and old/mature forests and identify the underlying drivers using data collected in a boreal landscape in central Sweden, where the retention approach has been implemented for over 20 years, while the old/mature forests have likely been selectively cut historically and regenerated naturally over a period reaching an average forest stand age ranging from 93 to 150 years (hereafter referred to as 'old forests'). Hence, the term 'old forests' in this study denotes areas that have undergone long-term (93–150 years) natural regeneration processes without clearcutting and recent human management interventions. The selected forest stands, characterized by distinct forest types (clearcut, retention, and old forests), exhibit significant variations in species diversity, and the abundance of living and dead trees (Kyaschenko et al., 2022). This selection enables us to investigate whether these elements can indeed influence microclimatic conditions between the different forest stands. Within all research sites, we installed 130 microclimate loggers continuously monitoring air temperature and humidity during the growing seasons (June, July and August) in both 2019 and 2020. Based on these data, we test (a) whether thermal buffering of retention forests differ from clearcuts and old forests; (b) whether preserving biological legacies, i.e. live and dead trees, and taxonomic tree diversity can influence the thermal buffering of a forest stand directly or indirectly through a more complex forest structure including canopy cover and basal area; and (c) whether microclimates differ between the forest edges and forest interiors and the underlying mechanisms.

2. Materials and methods

2.1. Study area

Measurement and data collection was conducted in 130 plots in a boreal forest landscape in central Sweden (Fig. 1), with forest stands predominately composed of *Picea abies* (Norway spruce), *Pinus sylvestris* (Scots pine), and to a lesser extent *Betula spp* (birch), *Populus spp* (aspen), *Alnus spp* (alder) and *Salix spp* (willow). The forest ground vegetation is mostly dominated by ericaceous dwarf shrubs (*Vaccinium myrtillus* and *V. vitis-idaea*) and the forest floor is typically covered by pleurocarpous mosses (*Hylocomium splendens* and *Pleurozium schreberi*). Elevations range from approximately 256–425 m a.s.l., mean annual temperature is around 3.48 °C, and the region receives mean annual precipitation of around 552 mm. The forests of central Sweden has gone through a more than 70 year long history of intensive management, giving rise to a mosaic of forests with different ages and clearcuts characterizing the research landscape (e.g., Jönsson et al., 2009). In this study, the 130 plots spread across the three main forest types, i.e. larger old forests (3.97–10.97 ha), clearcuts and smaller retention forests (patches 0.015–0.563 ha retained after final harvest), totalling to 30 research sites. Remaining old forest stands are few in the landscape, generally representing less than 5–10 % of the forestland in the region, and occur isolated in the matrix of young, intensively managed forest stands (e.g., Jönsson et al., 2011). The old forests in our study are separated but located nearby (within 11.1 km) from the continuous retention and clearcut patches, we thus have ten sites for old forests, and twenty sites for each of spatially continuous retention forests and clearcuts (Fig. 1).

2.2. Microclimate

Within each retention forest, the sampling design consist of a transect starting at the southern edge of the forest (0 m = the backside of the

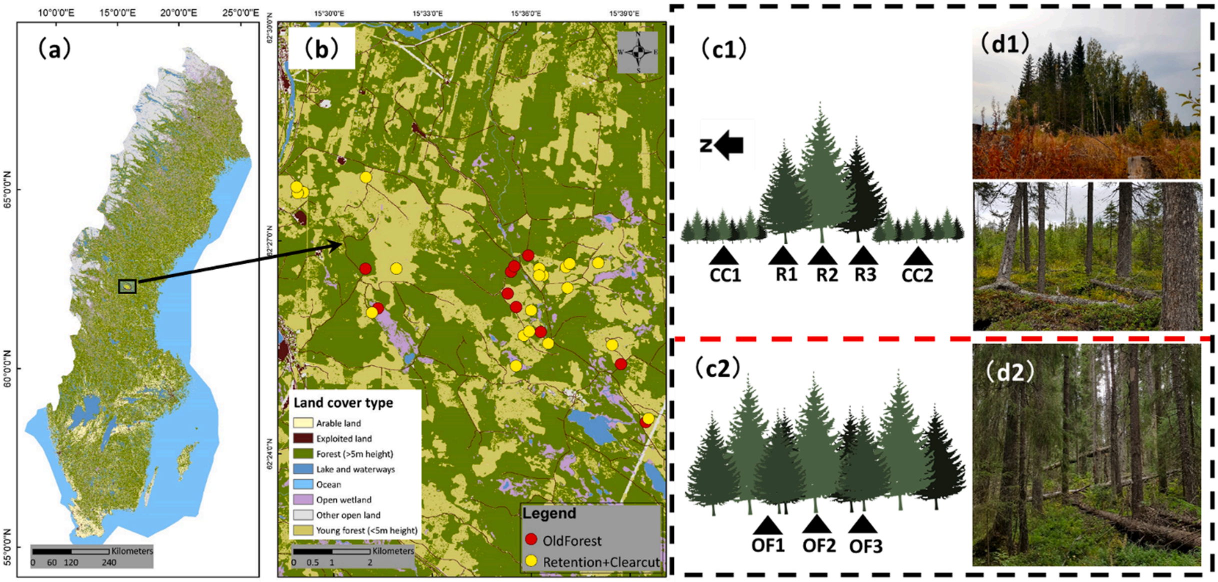

Fig. 1. Locations and layout of the 30 research sites (Site ID) in central Sweden ((a) and (b)). Specifically, there are ten sites for old forests (circles in red), and twenty sites (circles in yellow) for each of the spatially continuous retention forests and clearcuts in (b). The detailed sampling design for spatially continuous clearcuts and retention forests is presented in (c1) and old forests in (c2). In the (c1) panel, black triangles CC1 and CC2 represent the relative locations of plots (referred to as `Plot location') in the northern and southern clearcuts, respectively. In the same panel, R1, R2, and R3 indicate the plot setups in the retention forests. In the (c2) panel, OF1, OF2, and OF3 denote the plot setups in the old forests. The black triangles in panels (c1) and (c2) indicate the locations where we installed data loggers and collected forest structural data. Furthermore, some field photos from the sites are depicted in panels (d1) and (d2). The upper image in the (d1) panel showcases a dense retention patch, featuring mixed tree species when viewed from the outside clearcut. The lower photo in (d1) displays another retention patch with lower canopy cover and a reduced variety of tree species when observed from within the patch. Moving to the (d2) panel, a photo captures the essence of one of the mature, old forests. Maps are based on the Swedish National Land Cover Database (2018) supplied by NMD, Naturvårdsverket.

line of trees at the south-facing forest edge (see Fig. 1)) and ending in the northern edge of the forest patch (-0 m = the backside of the line of trees at the north-facing forest edge). Along this transect, three data loggers (Lascar Easylog EL-USB-2, accuracy at −35 to +80 °C: ±0.5 °C) were installed to monitor in-situ microclimates, i.e. air temperature and humidity, with a temporal resolution of 6 h in 2019 (June, July and August) and of 1 h in 2020 (June, July and August), at the following distances of the edge:

- Plot 1: data loggers at 1.5 m,
- Plot 2: data loggers at the centre of the retention patch,
- Plot 3: data loggers at −1.5 m.

Plot 1, 2 and 3 are respectively referring to the location of R1, R2 and R3 in Fig. 1(c1).

It is important to note that as the temporal resolution differed between 2019 and 2020, we applied hierarchy models with a consistent random structure for variables such as 'Year' to account for compositional differences (see 2.4 Data analyses). Besides retention forests, we additionally installed data loggers in clearcut patches (c. 30 m away from both of the south- and north-facing edges of retention forests) and in interior old forests (three plots spread across *c.* 30 m transects in the centre of the old forests). The microclimate data collected in the clearcuts and old forests respectively represented scenarios of intensive forest management (i.e. clearcutting) and without recent human disturbances (i.e. intact forest, never clearcut and interior condition >50 m away from a forest edge). We mounted the loggers hanging on a wooden stick at *c.* 75 cm above ground under a white radiation shield (i.e., a small plastic cup to protect the logger from rain and direct sunlight, while still allowing some ventilation). It is widely acknowledged that a temperature sensor exposed to sunlight has the potential to absorb radiation. This might not be fully overcome by our custom-built radiation shields as the shields themselves can also absorb solar radiation, potentially resulting in an overestimation of maximum temperatures outside forests (e.g., Maclean et al., 2021). While this measurement bias is less pronounced in shaded environments (Maclean et al., 2021), such as retention and old forests in this study, maximum temperature offsets between retention/old forests and clear-cuts might be overestimated, especially under sunny and low-wind conditions. However, this concern may not be significant in our study, given the extended duration of our experiment spanning two complete summer seasons in 2019 and 2020. This timeframe incorporates a diverse range of weather conditions, effectively minimizing potential biases. The coherence of this argument can be further reinforced by the comparable coefficient of variation (CV) observed in daily maximum temperatures across different forest types: clear-cuts (32.8 %), retention forests (32.3 %), and old forests (28.0 %).

We applied vapour pressure deficit (VPD) as the measure of below-canopy microclimatic moisture, calculated as the difference between the saturated (*Psat*) and the effective air pressure (*Pair*), based on temperature *T* (°C) and relative humidity RH (%) (Barrass, 1974; Davis et al., 2019; Von Arx et al., 2013).

$$Psat = 0.6112 \times \exp\left(\frac{17.62 \times T}{T + 243.12}\right),$$

$$Pair = Psat \times RH / 100,$$

$$VPD = Psat - Pair.$$

We summarized our observations into daily statistics, exclusively focusing on maximum and minimum daily values in this study.

2.3. Forest structure

To characterize species composition and forest structure, measurements were conducted for all living trees with a minimum diameter at breast height (DBH) of 2 cm within a 5-m radius around the installed sensors (see Fig. 1c). DBH was measured with a calliper at 1.30 m above the ground during May 2023. Subsequently, basal area (BA, m^2 ha^{-1}) of individual species was calculated based on these DBH measurements. Canopy cover (percentage layer formed by the branches and crowns of trees) was measured at the same location of the sensors using hemispherical photography with a standard angle camera lens and digital analysis in the program ImageJ. The measurements of canopy cover were performed during cloudy conditions in August 2020, to represent canopy conditions in the growing season. All standing and lying dead trees (with a DBH > 2 cm or maximum diameter >2 cm, respectively) that originated within the plot were inventoried. A tree was considered dead when missing living needles, leaves or buds. Dead standing tree snags and stumps were defined as standing deadwood, while logs, pieces of deadwood lying on the ground, and downed dead trees were categorized as lying deadwood. For standing deadwood with a height greater than 1.30 m, the DBH was measured, while for stumps, measurements were taken at the point where the tree was cut or the stem was broken. Based on these measurements, the basal area of standing deadwood were calculated (m^2 ha^{-1}). For lying deadwood, the length as well as the top and bottom diameter were measured to obtain their volume (m^3 ha^{-1}) using the formula for a truncated cone. The forest structural characteristics of different forest types are reported in Table 1.

2.4. Data analyses

We applied linear mixed models (LMMs) with ‘forest type’ as a fixed effect and ‘1 | Plot ID (depicted in Fig. 1)’ as a random effect to test whether forest microclimates (T and VPD) differed between the forest types (i.e. clearcut vs. retention vs. old forests). To account for temporal autocorrelation of microclimate data (Koenig and Liebhold, 2016; Ruel and Ayres, 1999), the corGaus (form = ~Date (referring to the date of data collection by the data loggers)| Plot ID) variance structure was incorporated in this model (Zuur et al., 2007). We applied the *lme* function from the *nlme* package to fit these models (Zuur et al., 2007). To examine the potential forest edge effects, similar analyses were conducted by setting ‘plot location’ as a fixed effect and ‘1 | Site ID (see distribution in Fig. 1)’ as a random effect, to compare forest microclimates among south-facing and north-facing edges and forest interiors within each forest type.

To examine the effects of stand structural attributes, i.e. basal area and canopy cover, on type-specific forest microclimates and microclimates across all the forest types pooled, we applied multivariate linear mixed models (multi-LMMs). For these LMMs, normalized ‘basal area’ and ‘canopy cover’ were set as fixed effects and crossed terms ‘(~1| Year, ~1| Plot ID)’ were set as random effects. We applied the ‘scale’ function from the ‘scale’ package to conduct normalizations.

Finally, piecewise structural equation models (pSEM) were applied to test for direct and indirect effects of the biological legacies, i.e., taxonomic diversity of tree species, standing and lying deadwood, on forest microclimates across the forest types and in each specific forest type. We applied Shannon diversity index as a measure of taxonomic diversity, which can also account for community species evenness. Shannon index was calculated as:

$$H\ index = -\sum_{i}^{s} Pi * \ln(Pi)$$

where s is the number of tree species in the community (tree species richness) and Pi is the relative proportion of species i (based on basal area). In this study, we calculated Shannon index via the *diversity* function from the *vegan* package. We modelled forest microclimates as a function of the biological legacies, or indirectly via their effects on basal area and canopy cover. Considering that stand age is a pivotal factor influencing the growth conditions of trees and the development of trees’ crowns, we have incorporated regeneration age (defined as the time since clearcut recording) into the random structure as a control variable to address potential compositional variations. To be precise, for each path in the structural equation model, we employed mixed-effect models with `1| Regeneration age / Forest Type/ Site ID’ as the random effects. We also added correlation structures when the global p value of this SEM structure was found to be lower than 0.05. SEM models were fitted using the piecewiseSEM-package (Lefcheck, 2016).

Similar pSEMs were applied to explain the detected edge effect based on the results conducted from the LMMs. We introduced delta (Δ; referring to differences between forest edges and forest interiors at each site) as both independent and dependent variables in the model. Specifically, we modelled Δ forest microclimates as a function of Δ biological legacies, indirectly via their effects on Δ basal area and Δ canopy cover. For each path in the structural equation model, we fitted mixed-effect models with ‘(~1| Year, ~1| Site ID)’ as random terms. All analyses were performed in R version 4.2.3.

3. Results

3.1. Microclimates in the clearcut, retention and old forests

Forest microclimates differed significantly between the forest types (Fig. 2). Both the below-canopy maximum temperature and VPD (T_{max} and VPD_{max}) were highest in the clearcuts (28.1 ± 0.46 °C, 2.7 ± 0.11 kPa (Mean ± SE)), followed by the retention forests (22.3 ± 0.38 °C, 1.6 ± 0.09 kPa), and lowest in the old forests (17.1 ± 0.56 °C, 0.7 ± 0.13 kPa; all $p < 0.05$). Additionally, the below-canopy minimum temperature (T_{min}) was lowest in the clearcuts (6.1 ± 0.17 °C), followed by the retention forests (7.9 ± 0.14 °C), and highest in the old forests (9.0 ± 0.21 °C). Surprisingly, the minimum VPD (VPD_{min}) was the highest in the retention forests, which was 0.08 ± 0.003 kPa, followed by the old forests (0.06 ± 0.005 kPa), and the lowest found in the clearcut forests (0.02 ± 0.004 kPa). In sum, retention forests provided more buffered microclimate conditions than clearcuts, with an average T_{max} and VPD_{max} in these forests being 5.78 ± 0.59 °C and 1.12 ± 0.14 kPa (Mean ± SE) lower than that in clearcut forests during the growing seasons. Notably, old forests offered the most buffered forest microclimates, with an average T_{max} 11.04 ± 0.72 °C lower than that of clearcut forests and 5.26 ± 0.68 °C lower than retention forests. The impact of forest type on below-canopy microclimates remained largely consistent between 2019 and 2020 when analyzed individually, except for VPD_{min}. Nevertheless, the differences in VPD_{min} between the forest types were minute and continued to exhibit the same trend in 2019 and 2020 when considering only the absolute values. This information is reported in Supplementary Information Fig. S3.

Table 1

Characteristics of each forest type (Clearcuts vs. Retention forests vs. Old forests). Summary data (Mean ± Standard Deviation) of basal area (m^2 ha^{-1}), canopy cpver (%), Standing deadwood (m^2 ha^{-1}), lying deadwood (m^3 ha^{-1}), the proportion of deciduous tree species ($P_{deciduous}$), and tree species diversity (H index) for each forest type.

Forest type	Basal area (m^2 ha^{-1})	Canopy cover (%)	Standing deadwood (m^2 ha^{-1})	Lying deadwood (m^3 ha^{-1})	$P_{deciduous}$	H index
Clearcuts	4.64 ± 6.13	19.4 ± 23.4	3.12 ± 6.74	0.57 ± 2.00	0.38 ± 0.38	0.39 ± 0.34
Retention	30.5 ± 22.6	57.8 ± 18.7	4.64 ± 13.6	6.54 ± 15.2	0.29 ± 0.26	0.57 ± 0.34
Old forests	51.4 ± 16.4	71.9 ± 9.8	0.48 ± 1.06	1.42 ± 3.60	0.10 ± 0.10	0.44 ± 0.27

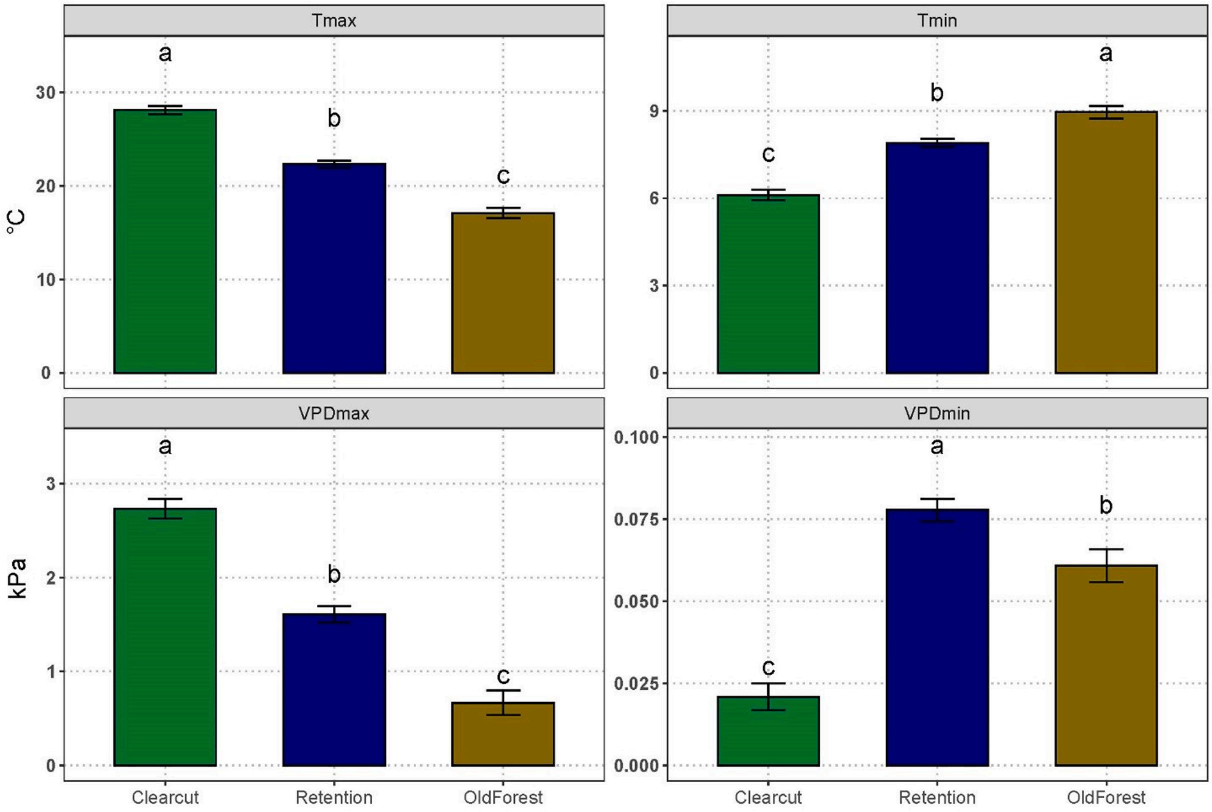

Fig. 2. Air temperature and VPD in the different forest types (i.e. clearcut vs. retention vs. old forest), based on the summer microclimate data averaged between 2019 and 2020. Bars display mean air temperature (T_{max} and T_{min}) and VPD (VPD_{max} and VPD_{min}) across each forest type. Full statistical results are reported in Table S1. Different letters denote significant differences among different forest types. Error bars display the standard error [SE] within each forest type.

3.2. The effects of canopy cover and basal area on macroclimate buffering

Canopy cover and basal area were identified as key determinants influencing air temperature and VPD (Fig. 3). We found canopy cover and basal area were both significantly and negatively correlated with T_{max} and VPD_{max} while positively associated with T_{min} across the pooled forest types (all $p < 0.05$). Moreover, VPD_{min} exhibited a positive association with canopy cover across the pooled forest types. Specific to the clearcut forests, we detected that both canopy cover and basal area were negatively associated with T_{max} across the clearcut stands. In addition, canopy cover was found being negatively associated with VPD_{max} while being positively correlated with T_{min} in these stands. In the retention forests, we found that T_{max} were negatively correlated with basal area and canopy cover (both $p < 0.05$). Similar results were found for VPD_{max}, which exhibited negative associations with canopy cover ($p < 0.05$) and basal area ($p = 0.051$). Lastly, we found that basal area was the key factor affecting the microclimates in the old forests. Specifically, we observed a significant negative correlation between basal area and both T_{max} and VPD_{max} in the old forests. However, no significant effect of canopy cover on microclimates was found across these old-forest stands.

3.3. Direct and indirect effects of biological legacies on microclimates

We found that biological legacies potentially impacted forest microclimates (Fig. 4). The effects of biological legacies on forest microclimates were first detected when analyzing data for all forest types pooled. Specifically, the Shannon diversity index had the potential to indirectly lower the stand's T_{max} and VPD_{max} while increasing T_{min} and VPD_{min}, as it showed a positive association with both canopy cover ($p < 0.05$) and basal area ($p = 0.071$) across the pooled forest types. Increasing volumes of lying deadwood had the potential to indirectly increase T_{max} and VPD_{max} while decreasing T_{min} and VPD_{min}, given their negative relationship with both canopy cover and basal area (both $p < 0.05$). However, increasing volumes of lying deadwood also directly increased T_{min} and VPD_{min}, potentially increasing air temperature and dryness during cooler time periods such as nights. Similarly, increasing standing dead trees directly lowered T_{max} and increased T_{min} and VPD_{min} within these forest stands.

In the retention forests, maintaining diverse tree species had the potential to indirectly lower the stand's T_{max} and VPD_{max}, while increasing T_{min} and VPD_{min} through its positive impact on basal area ($p < 0.05$). Conversely, large volumes of lying deadwood, negatively associated with both canopy cover and basal area (both $p < 0.05$), may potentially contribute to increased T_{max} and VPD_{max} as well as lowered T_{min} and VPD_{min}. Furthermore, increasing standing dead trees directly lowered T_{max} and VPD_{max} and increased T_{min} and VPD_{min} in the retention forests. Finally, positive correlations between basal area and canopy cover were consistent in both retention forests and across the forest types pooled. The effects of the listed biological legacies on microclimates in individual clearcut forests and old forests are shown in Supplementary Information Figs. S1 and S2.

3.4. Edge effects

We detected that T_{max} in the south-facing edges (24.1 ± 0.58 °C; Mean ± SE) were significantly higher than T_{max} in the north-facing edges (21.9 ± 0.59 °C) and the forest interiors (21.0 ± 0.58 °C) in retention forests (Fig. 5a). Similar results were found for VPD_{max}, where the VPD_{max} in the south-facing edges (1.96 ± 0.11 kPa) were significantly higher than that in the north-facing edges (1.50 ± 0.11 kPa) and the forest interiors (1.36 ± 0.11 kPa) of retentions. No differences were detected for T_{min} and VPD_{min} between retention forest edges and forest

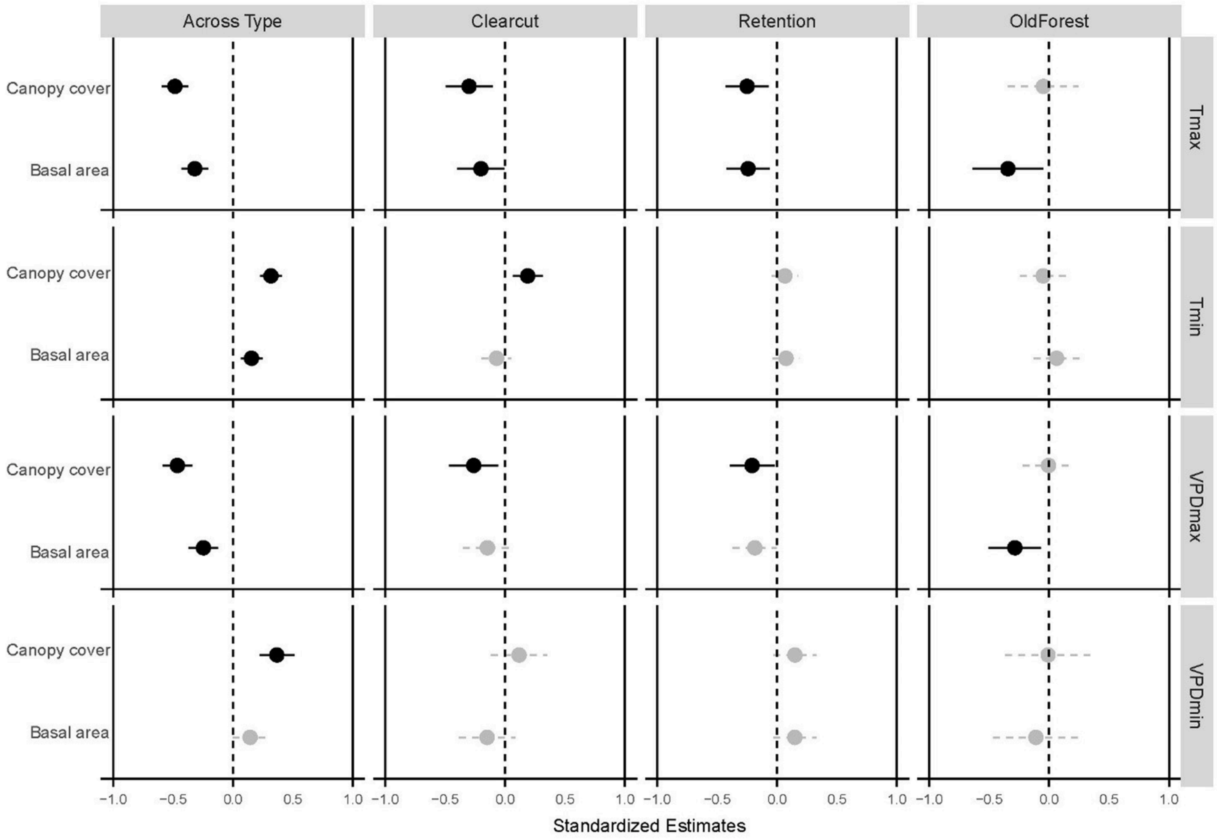

Fig. 3. Standardized estimates and 95 % confidence intervals of the effect sizes of forest structural attributes (i.e. basal area and canopy cover) for the estimation of microclimates (i.e. T_{max}, T_{min}, VPD_{max}, and VPD_{min}). For these LMMs, normalized ‘basal area’ and ‘canopy cover’ were set as fixed effects and crossed terms ‘(∼1| Year, ∼1| Plot ID)’ were set as random effects. Full statistical results are reported in Table S2. The symbols in black indicate the effect sizes of the key drivers ($p < 0.05$) and the symbols in grey represent the effect sizes of non-significant variables ($p > 0.05$).

interiors (Fig. 5a). Additionally, no significant differences were detected for forest microclimates between different locations in clearcut forests as well as in old forests (Fig. S4).

Lastly, we detected that the difference in lying deadwood volumes was positively associated with both T_{max} and VPD_{max} differences (both $p < 0.05$) between south-facing edges and interiors in the retention forests (Fig. 5b). The difference in standing deadwood tended to be positively correlated with the difference in T_{max} between south-facing edges and forest interiors ($p < 0.1$).

4. Discussion

The continuing/escalating global increase in temperature and the induced rising VPD (Hatfield and Prueger, 2015) emphasize the pressing need to comprehend the thermal buffering provided by various land-use management practices. These factors have significant ramifications for water resources, as well as the intricate interplay between plants and water in ecological systems (Grossiord et al., 2020). Here, we try to bridge this knowledge gap for forest management practices by studying the microclimate of clearcut, retention and old forests in a boreal landscape in Sweden, where retention forestry have been practiced for 20–30 years. Not only did we find that retention forests make significant contributions to macroclimate buffering, we also uncovered the underlying mechanisms behind this phenomenon. When retention practices preserve biological legacies of both live and dead standing trees, as well as higher tree species diversity, this may directly or indirectly via higher canopy cover and basal area, influence forest microclimates. Our results also indicate that the south-facing edges in the retention forests experienced more severe hot and dry weather conditions than forest interiors, despite the relatively small size of the retained patches (0.015–0.563 ha). Implementing measures to prevent wind-induced tree mortality, especially in the south-facing edges of retention forests where lying deadwood is likely to accumulate, can mitigate such negative edge effects. Our results have important implications for integrating retention practices into actions aimed at mitigating macroclimate warming.

4.1. Forest macroclimate buffering and the underlying mechanisms

First of all, we showed that the T_{max} in the retention forests was on average 5.78 ± 0.59 °C (Mean ± SE) lower than in the clearcut forests during the growing seasons. This value is of greater magnitude than the global warming over the pre-industrial (1850–1900) averages (1.1 ± 0.13 °C (IPCC, 2021)), and greater than the cooling effect of the global forests on maximum temperatures (4.1 ± 0.5 °C (De Frenne et al., 2019)), suggesting the importance of retention forests in mitigating warming temperatures and increasing water availability below the canopy. In addition, we showed that the old forests had the lowest T_{max}, with an average of 11.04 ± 0.72 °C lower than the clearcut forests and 5.26 ± 0.68 °C lower than the retention forests. The maximum VPDs, as well, were detected at their lowest in the old forests (0.7 ± 0.13 kPa), with an average of 2.06 ± 0.17 kPa lower than the clearcuts and 0.94 ± 0.16 kPa lower than the retention forests, indicating that the old forests exhibited the best buffering capacity against summer droughts. The differences in maximum temperatures and VPDs between the forest types can be attributed to variations in basal area and canopy cover (Table 1), which have been identified as key drivers of thermal buffering in other studies as well (Von Arx et al., 2013; Zellweger et al., 2019; Zhang et al., 2022). The fact that the old forests provide the superior thermal buffering for maximum temperatures and VPDs suggests that the thermal buffering capacity of a forest is greatly influenced by its age.

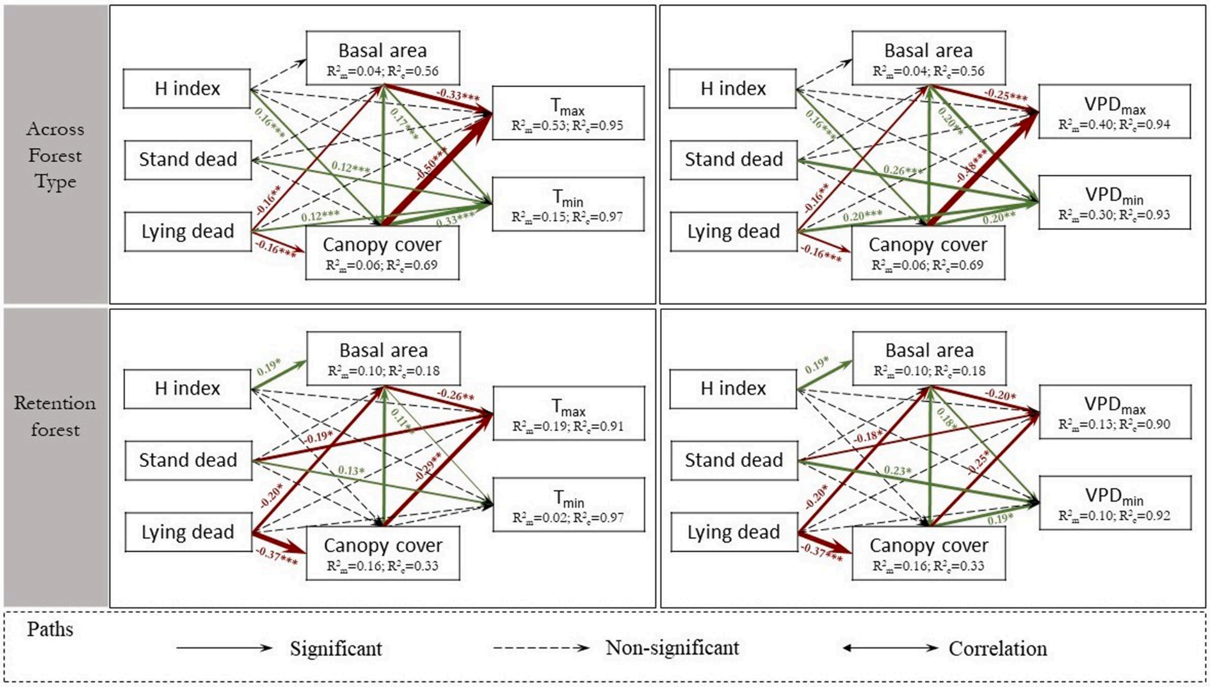

Fig. 4. Direct and indirect effects of retention practices including preserving tree species from different taxonomic groups (Shannon diversity index, denoted as H index in the panel), standing and lying deadwood, as well as forest structural attributes (i.e. basal area and canopy cover) on microclimates (T and VPD) in the retention forests and across the three forest types pooled. Marginal (R^2m) and conditional (R^2c) R^2 of fitted linear regression models showed below each estimator. Positive effects are illustrated with green arrows, while negative relationships are indicated by red arrows. The dashed and solid arrows respectively represent the non-significant and significant effects, and the varying widths of the solid arrows denote the strength of the detected significant effects. The numbers associated to each arrow indicate the standardized estimates of the fitted models. Labels *, **, *** indicate significance at the $p < 0.05$, $p < 0.01$ and $p < 0.001$ levels, respectively.

Interestingly, past studies have suggested that relatively high temperature offsets (the difference between below-canopy and free-air temperatures) can be realised shortly after planting, once a canopy cover of *c.* 75 % is attained (Zellweger et al., 2019), implying that forest age has minimal effect on thermal buffering (Zhang et al., 2022). We showed that thermal buffering increased with the canopy cover of planted forests on clearcuts, but was still substantially lower after two decades compared to retention forests and old forests. Hence, our own research highlights the significance of old forests (both as retained patches of older forests and especially as larger intact old forests) in macroclimate buffering, with great implications for heat-sensitive species conservation and biodiversity in the face of global climate change (Hylander et al., 2022; Máliš et al., 2023).

We identified stand structural attributes as key determinants of forest microclimates, with increased thermal cooling observed in stands characterized by greater basal area and canopy cover. This finding supported the hypothesis that leaving large living trees can efficiently impact forest microclimates. However, the relative importance of these drivers varied depending on the forest type. We noticed that the impact of canopy cover was more pronounced in the clearcut microclimates, whereas it became negligible in the old-forest microclimates. This absence of the canopy cover effect in the old forests can be attributed to their consistently dense canopy, averaging 71.9 ± 9.8 %. This finding aligns with the research by Zellweger et al. (2019), which reported a threshold of *c.* 75 % canopy cover, below which a forest's buffering capacity rapidly decreases. Instead, increasing basal area was associated with lower maximum temperatures and VPDs in the old forests. This basal area effect is indeed expected since a stand's basal area is a measure of a stand's density and the trees' growth conditions, and that is highly correlated with crown volume, leaf area index, and other factors known to influence light interception and macroclimate buffering in the canopy (De Frenne et al., 2021). Nevertheless, the basal area effect in the clearcut forests was limited, showing significance only for maximum temperatures. This limitation is most likely due to the fact that the regenerating trees in the clearcuts remained quite small at the time of investigation (4.6 ± 6.1 m^2 ha^{-1}). The differences in basal area between the stands were thus insufficient to explain variations in forest microclimates. In the retention forests, both increased basal area and canopy cover substantially lowered T_{max} and VPD_{max}. This can be attributed to the significant variation in stand attributes among the retention forests, characterized by a relatively higher range of basal area (30.5 ± 22.6 m^2 ha^{-1}) and canopy cover (57.8 ± 18.7 %).

4.2. *Impact of biological legacies on forest microclimates*

The next question addressed whether biological legacies can have an impact on forest microclimates directly and/or indirectly. It is important to reiterate that the primary objective of this study is to provide specific guidelines for practices in retention forests, while also offering general suggestions for forest management to mitigate warming temperatures and induced summer droughts. Therefore, we comprehensively examined these effects within the context of retention forests as well as considering all forest types collectively. As the clearcut and/or old forests exhibited minimal variations in certain biological legacies, such as the negligible influence of lying deadwood on thermal buffering (Fig. S1), attributed to the low volumes of lying deadwood (0.57 ± 2 m^3 ha^{-1}) found in the clearcut forests, we opted to only report and discuss the notably inconsistent findings observed within stands of these two forest types.

We found that tree species diversity is likely to contribute indirectly to thermal cooling, as a positive correlation was found between the H index and canopy cover for all forest types pooled and between the H index and basal area in the retention forests. This outcome is indeed expected, as tree species diversity often results in high forest production (e.g. Van de Peer et al., 2018). Within a mixed stand, diverse tree species that differ in phenology and morphology likely also result in crown

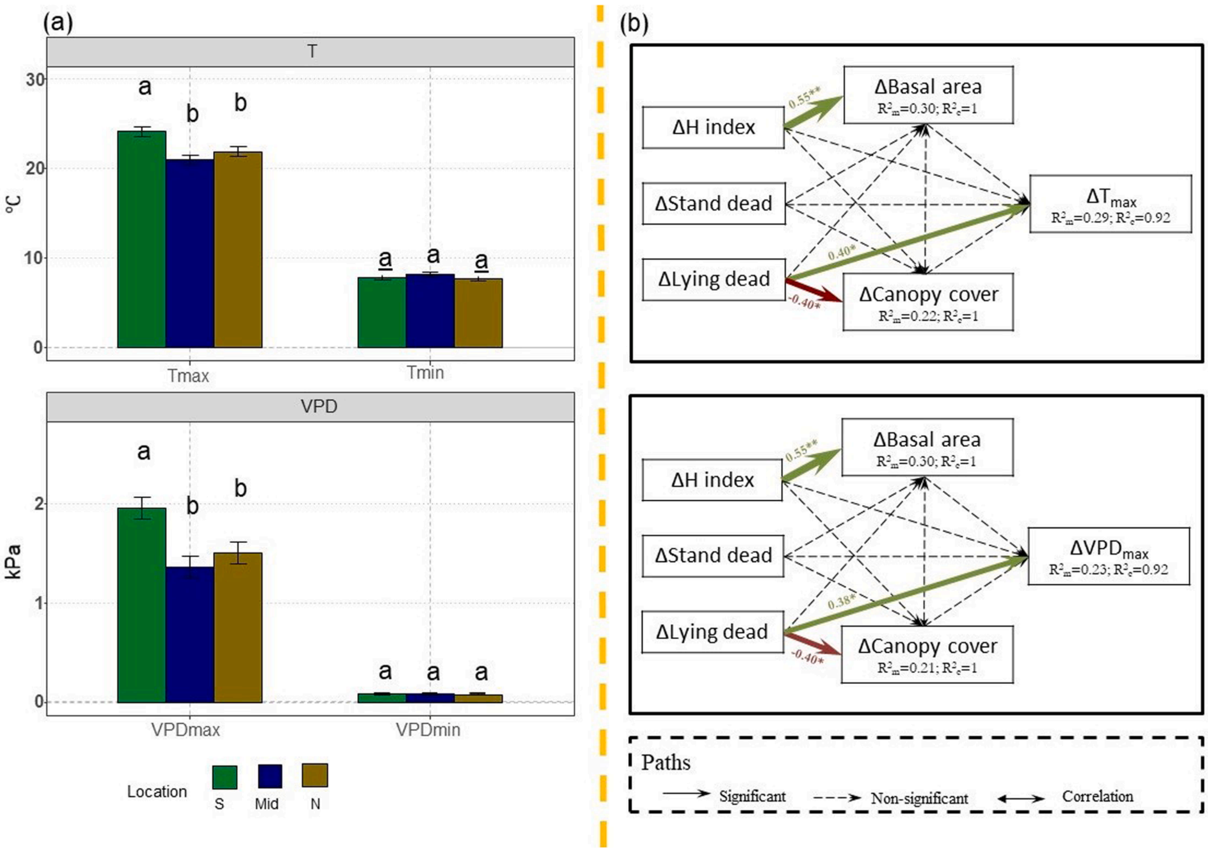

Fig. 5. Edge effects on microclimates and the underlying mechanism in retention forests. (a) air temperature and VPD in the two forest edges (south- and north-facing) and the interiors of the retention forests, and (b) direct and indirect effects of the biological legacies including preserving tree species from different taxonomic groups (Shannon diversity index, denoted as H index in the panel), standing and lying dead trees, as well as forest structural attributes (i.e. basal area and canopy cover) on the detected south-facing edge effects on $\Delta T_{\max}$ and $\Delta \text{VPD}_{\max}$ (based on the results in panel (a)). In panel (a), bars display air temperature ($T_{\max}$ and $T_{\min}$) and VPD ($\text{VPD}_{\max}$ and $\text{VPD}_{\min}$) across each location. Different letters denote significant differences among different forest locations. Error bars display the standard error [SE] within each forest location. In panel (b), delta (Δ) denotes the difference between south-facing forest edges and forest interiors. Marginal (R^2m) and conditional (R^2c) R^2 of fitted linear regression models showed below each estimator. Positive effects are illustrated with green arrows, while negative relationships are indicated by red arrows. The dashed and solid arrows respectively represent the non-significant and significant effects, and the varying widths of the solid arrows denote the strength of the detected significant effects. The numbers associated to each arrow indicate the standardized estimates of the fitted models. Labels *, ** indicate significance at the $p < 0.05$, and $p < 0.01$ levels, respectively.

complementarity (Pretzsch, 2014). This complementarity caused by neighbouring species can lead to higher efficiency in light interception and use, subsequently enhancing forest productivity (Pretzsch, 2014; Van de Peer et al., 2018). The mechanism behind this increased productivity, as well as the increased productivity *per se,* can explain the enhanced thermal buffering observed in retention forests with higher tree species diversity. Notably, the diversity effect on thermal cooling based on data collected across different types with a wide range of regeneration ages (*c.* 3–150 years) were found via the same effect on both basal area and canopy cover. These findings align with and reinforce the research conducted by Zhang et al. (2022) in young forest plantations, indicating the potential generality of the detected tree species diversity effect. However, it is essential to note that the observed diversity effect showed inconsistencies in old forests, as depicted in Fig. S2. Surprisingly, an increase in tree species diversity in these older forests led to an unexpected decrease in both basal area and thermal buffering capacity. This phenomenon can be attributed to the positive correlation between the proportion of deciduous tree species (based on basal area) and tree species diversity (measured using the Shannon diversity index). Our study focused on boreal forests in central Sweden, where evergreen coniferous species, predominantly Norway spruce, followed by Scots pine, dominated the research area. In general, the proportion of deciduous species was positively associated with tree species diversity (the statistical results related to these relationships are reported in Table S3), except in clearcuts, where birch and spruce were almost equally regenerated. The pronounced composition effect, specifically a high proportion of deciduous species, only resulted in decreased basal area in the old forests (see Fig. S5). This finding is most likely due to the significant size disparity between deciduous tree species (e.g., birch) and evergreen tree species (e.g., Norway spruce and Scots pine), which reaches its maximum in old stands. Moreover, pioneer deciduous tree species typically regenerate in forest gaps with reduced basal area after small-scale disturbances (e.g. König et al., 2022). Consequently, the increased presence of deciduous tree species and the induced increase in tree species diversity led to decreased stand basal area, as well as a reduced thermal buffering capacity in the old forests.

Additionally, our results support the hypothesis that deadwood legacies can affect macroclimate buffering, although the standing and lying deadwood contributed in different ways. The presence of standing deadwood consistently lowered maximum temperatures and increased water availability in retention patches. Our findings are in line with the research by Castro et al. (2011), Kovács et al. (2017), Marcolin et al. (2019), and Thom et al. (2020), which suggest that standing deadwood with bare crowns can still shield the ground from insolation, and thus reduce energy input and amplify thermal cooling. On the other hand, the presence of lying deadwood may negatively impact macroclimate buffering for solar radiation, as a negative correlation was observed between lying deadwood and both canopy cover and basal area. This corroborates the findings of Thom et al. (2020), which reported a significant increase in light reaching the forest floor due to specific deadwood disturbances, with a relative radiation increase of 306.7 % compared to undisturbed plots (i.e., intact forests). The increased tree death and associated canopy openness in our study could have allowed more heat energy to enter the forest floor, leading to a reduction in thermal buffering and an intensification of summer drought conditions (Schmidt et al., 2017; Thom et al., 2020). Notably, we also observed direct positive correlations between the volume of standing and lying deadwood and both minimum temperature and VPD in forests, indicating that both standing and lying deadwood contributes to warmer and drier conditions during nights. This finding aligns with the research of Spears et al. (2003) and Zalamea et al. (2016), which detected that minimum soil temperatures under decaying lying deadwood were higher than those away from the logs. Indeed, while deadwood with bare crowns may not cast much shade, it acts as a ground barrier, slowing the loss of heat from the soil (cf. Geiger et al., 2003), which, in turn, leads to increased warmth and dryness of the understory during summer nights. Hence, both standing and lying deadwood can absorb heat during the day and trap some of this heat in the understory at night, thereby being related to increasing night-time $T_{\min}$ and $\mathrm{VPD}_{\min}$. This phenomenon can potentially contribute to stabilizing daily climate variability within forest soil (Spears et al., 2003; Zalamea et al., 2016) and the understory (as demonstrated in this study). Increasing basal area of standing deadwood in retention patches was related to both reduced daytime $T_{\max}$ and $\mathrm{VPD}_{\max}$ and increased night-time $T_{\min}$ and $\mathrm{VPD}_{\min}$, both leading to narrower climate ranges and thus stabilized daily climate cycles. We acknowledge that the role of deadwood in climate buffering can be difficult to disentangle from the effects of other related factors such as canopy cover and sapling regeneration. Lying deadwood might create favourable microhabitats, such as nurse logs and beneficial light conditions, increased water and nutrient availability for saplings (Marangon et al., 2022; Seibold et al., 2015), and shelters of saplings against ungulate browsing (Hagge et al., 2019), which may in turn influence shade conditions and microclimate. Hence, forest disturbance can yield both positive outcomes, such as increased canopy openness and light availability fostering tree regeneration, and negative consequences, including diminished microclimatic buffering and heightened drought reducing tree regeneration (Thom et al., 2023). These effects are likely contingent upon factors such as tree mortality severity, gap size, and time since disturbance. Importantly, our results do not endorse the removal of standing and lying deadwood, such as salvage logging. Instead, they underscore the critical need to implement preventive measures against severe wind-induced tree mortality in small and exposed retention forests. This emphasis is rooted not only in the essential role that lying deadwood plays as a substrate for below-canopy organisms, including bryophytes, lichens, and fungi, but also in our findings indicating that basal area and canopy openness are the main drivers of microclimates in retention forests.

4.3. Edge effects on macroclimate buffering

The last question addressed whether edge effects on macroclimate buffering are present. We found that edge effects were pronounced in the retention forests, with south-facing edges experiencing warmer temperatures and more dry conditions than forest interiors and north-facing edges. This finding corroborates Buras et al. (2018), Chen et al. (1993), Matlack (1993) and Young & Mitchell (1994), suggesting edge effects to be most pronounced at southern expositions. Indeed, the south-facing edges receive more direct sunlight throughout the day in the northern hemisphere, resulting in higher temperatures and greater temperature fluctuations compared to edges in other orientations. We also explored the efficacy of retention practices in alleviating edge effects, and our results highlight that the difference in lying deadwood volumes between south-facing edges and forest interiors significantly contributes to the observed warmer and drier south-facing edges. This observation aligns with numerous previous studies, e.g., Buras et al. (2018) and Young and Mitchell (1994), indicating pronounced differences in lying deadwood volumes between forest edges and interiors. Given the prevailing south-westerly winds in Sweden and the small sizes of the retained forests, differences in lying deadwood emerges as a plausible explanation for the observed edge effects on forest microclimates. Differences in tree diversity (H index) between south-facing edges and forest interiors was associated with greater differences in basal area between these locations, presumably the result of a greater number of small and young early successional deciduous trees establishing in south-facing edges compared to the interiors. These differences in H index and basal area between locations may also have contributed to microclimatic differences, although no significant relationships could be statistically established.

5. Management implications and conclusion

In summary, our findings demonstrate that retention forests have a greater capacity to buffer macroclimate compared to clearcut forests, and the retention practices effectively influence microclimates within stands. Particularly, old forests exhibit the superior macroclimate buffering capacities. Stand structural attributes, i.e. basal area and canopy cover, can be treated as key determinants of forest microclimates. This further suggests the preservation of large living trees can indeed increase thermal buffering of forests. Besides, preserving tree species diversity has the potential to increase thermal cooling and mitigate dry conditions, given its positive association with both basal area and canopy cover. Conversely, large volumes of lying deadwood are found to be negatively correlated with canopy cover and basal area, potentially leading to a decreased stand’s capacity to buffer solar radiation and provide thermal cooling. However, standing deadwood can directly lower maximum temperatures and increase water availability. Notably, edge effects are pronounced in the south-facing edges, implementing measures (e.g., leaving buffer zones with partial harvests, retaining a mixture of tree species) to prevent wind-induced mortality should be considered especially in the south-facing edges. Our findings are valid not only for short-term retention forests but also for forests intended to persist for centuries, given that our results encompassed forests spanning a wide range of regeneration ages (3–150 years). Foresters and policy makers should exploit our findings in the practices aimed at mitigating macroclimate warming in production forests, with great implications for heat-sensitive species conservation and below-canopy biodiversity and functioning.

CRediT authorship contribution statement

Shengmin Zhang: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jörgen Sjögren:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **Mari Jönsson:** Writing – review & editing, 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.

Data availability

Data are made available on Figshare https://doi.org/10.6084/m9.figshare.24072282.v1 (Zhang, 2024).

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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.2024.109973.

References

Barbier, S., Gosselin, F., Balandier, P., 2008. Influence of tree species on understory vegetation diversity and mechanisms involved—A critical review for temperate and boreal forests. For. Ecol. Manag. 254 (1), 1–15. https://doi.org/10.1016/j.foreco.2007.09.038.

Barrass, T.R., 1974. Principles of Environmental Physics. Phys. Bull. https://doi.org/10.1088/0031-9112/25/2/025.

Bertrand, R., Lenoir, J., Piedallu, C., Dillon, G.R., De Ruffray, P., Vidal, C., Pierrat, J.C., Gégout, J.C., 2011. Changes in plant community composition lag behind climate warming in lowland forests. Nature. https://doi.org/10.1038/nature10548.

Boudreault, C., Bergeron, Y., Gauthier, S., Drapeau, P., 2002. Bryophyte and lichen communities in mature to old-growth stands in eastern boreal forests of Canada. Can. J. For. Res. 32 (6), 1080–1093. https://doi.org/10.1139/x02-027.

Buras, A., Schunk, C., Zeiträg, C., Herrmann, C., Kaiser, L., Lemme, H., Straub, C., Taeger, S., Gößwein, S., Klemmt, H.-J., 2018. Are Scots pine forest edges particularly prone to drought-induced mortality? Environ. Res. Lett. 13 (2), 25001.

Castaño, C., Lindahl, B.D., Alday, J.G., Hagenbo, A., Martínez de Aragón, J., Parladé, J., Pera, J., Bonet, J.A., 2018. Soil microclimate changes affect soil fungal communities in a Mediterranean pine forest. New Phytol. https://doi.org/10.1111/nph.15205.

Castro, J., Allen, C.D., Molina-Morales, M., Marañón-Jiménez, S., Sánchez-Miranda, Á., Zamora, R., 2011. Salvage logging versus the use of burnt wood as a nurse object to promote post-fire tree seedling establishment. Restor. Ecol. 19 (4), 537–544. https://doi.org/10.1111/j.1526-100X.2009.00619.x.

Chen, J., Franklin, J.F., Spies, T.A., 1993. Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. Agric. For. Meteorol. 63 (3), 219–237. https://doi.org/10.1016/0168-1923(93)90061-L.

Davis, K.T., Dobrowski, S.Z., Holden, Z.A., Higuera, P.E., Abatzoglou, J.T., 2019. Microclimatic buffering in forests of the future: the role of local water balance. Ecography. https://doi.org/10.1111/ecog.03836.

De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B.R., Zellweger, F., Aalto, J., Ashcroft, M. B., Christiansen, D.M., Decocq, G., De Pauw, K., Govaert, S., Greiser, C., Gril, E., Hampe, A., Jucker, T., Klinges, D.H., Koelemeijer, I.A., Lembrechts, J.J., Marrec, R., Hylander, K., 2021. Forest microclimates and climate change: importance, drivers and future research agenda. Glob. Change Biol. https://doi.org/10.1111/gcb.15569.

De Frenne, P., Rodríguez-Sánchez, F., Coomes, D.A., Baeten, L., Verstraeten, G., Vellen, M., Bernhardt-Römermann, M., Brown, C.D., Brunet, J., Cornelis, J., Decocq, G.M., Dierschke, H., Eriksson, O., Gilliam, F.S., Hédl, R., Heinken, T., Hermy, M., Hommel, P., Jenkins, M.A., Verheyen, K., 2013. Microclimate moderates plant responses to macroclimate warming. Proc. Natl. Acad. Sci. USA. https://doi.org/10.1073/pnas.1311190110.

De Frenne, P., Verheyen, K., 2016. Weather stations lack forest data. Science. https://doi.org/10.1126/science.351.6270.234-a.

De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B.R., Hylander, K., Luoto, M., Vellend, M., Verheyen, K., Lenoir, J., 2019. Global buffering of temperatures under forest canopies. Nat. Ecol. Evol. https://doi.org/10.1038/s41559-019-0842-1.

Ekholm, A., Lundqvist, L., Petter Axelsson, E., Egnell, G., Hjältén, J., Lundmark, T., Sjögren, J., 2023. Long-term yield and biodiversity in stands managed with the selection system and the rotation forestry system: a qualitative review. For. Ecol. Manag. 537, 120920 https://doi.org/10.1016/j.foreco.2023.120920.

FAO, 2014. State of the World's Forests 2014: Enhancing the Socioeconomic Benefits from Forests. Food and Agriculture Organization of the United Nations. https://books.google.be/books?id=PAX5oAEACAAJ.

FAO. (2020). *Global Forest Resources Assessment 2020: Main Report*. https://books.google.be/books?id=L4JVzgEACAAJ.

Fedrowitz, K., Koricheva, J., Baker, S.C., Lindenmayer, D.B., Palik, B., Rosenvald, R., Beese, W., Franklin, J.F., Kouki, J., Macdonald, E., Messier, C., Sverdrup-Thygeson, A., Gustafsson, L., 2014. REVIEW: can retention forestry help conserve biodiversity? A meta-analysis. J. Appl. Ecol. 51 (6), 1669–1679. https://doi.org/10.1111/1365-2664.12289.

Franklin, J.F., Lindenmayer, D., MacMahon, J.A., McKee, A., Magnuson, J., Perry, D.A., Waide, R., Foster, D., 2000. Threads of continuity. Conserv. Pract. 1 (1), 8–17. https://doi.org/10.1111/j.1526-4629.2000.tb00155.x.

Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M.C., Fröberg, M., Stendahl, J., Philipson, C.D., Mikusiński, G., Andersson, E., Westerlund, B., Andrén, H., Moberg, F., Moen, J., Bengtsson, J., 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. Nat. Commun. 4 (1), 1340. https://doi.org/10.1038/ncomms2328.

Geiger, R., Aron, R.H., Todhunter, P., 2003. The Climate Near the Ground. Rowman & Littlefield. https://books.google.se/books?id=KaJHBv9FbYIC.

Grossiord, C., Buckley, T.N., Cernusak, L.A., Novick, K.A., Poulter, B., Siegwolf, R.T.W., Sperry, J.S., McDowell, N.G., 2020. Plant responses to rising vapor pressure deficit. New Phytol. 226 (6), 1550–1566. https://doi.org/10.1111/nph.16485.

Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., Lindenmayer, D. B., Lõhmus, A., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, W.J.A., Wayne, A., Franklin, J.F., 2012. Retention forestry to maintain multifunctional forests: a world perspective. Bioscience 62 (7), 633–645. https://doi.org/10.1525/bio.2012.62.7.6.

Hagge, J., Müller, J., Bässler, C., Biebl, S.S., Brandl, R., Drexler, M., Gruppe, A., Hotes, S., Hothorn, T., Langhammer, P., Stark, H., Wirtz, R., Zimmerer, V., Mysterud, A., 2019. Deadwood retention in forests lowers short-term browsing pressure on silver fir saplings by overabundant deer. For. Ecol. Manag. 451, 117531 https://doi.org/10.1016/j.foreco.2019.117531.

Hatfield, J.L., Prueger, J.H., 2015. Temperature extremes: effect on plant growth and development. Weather Clim. Extrem. 10, 4–10. https://doi.org/10.1016/j.wace.2015.08.001.

Hylander, K., 2005. Aspect modifies the magnitude of edge effects on bryophyte growth in boreal forests. J. Appl. Ecol. 42 (3), 518–525. https://doi.org/10.1111/j.1365-2664.2005.01033.x.

Hylander, K., Greiser, C., Christiansen, D.M., Koelemeijer, I.A., 2022. Climate adaptation of biodiversity conservation in managed forest landscapes. Conserv. Biol. 36 (3), e13847. https://doi.org/10.1111/cobi.13847.

IPCC, 2021. Climate Change Widespread, Rapid, and Intensifying. IPCC.

Jönsson, M., Fraver, S., Jonsson, B.G., 2009. Forest history and the development of old-growth characteristics in fragmented boreal forests. J. Veg. Sci. 20 (1), 91–106. https://doi.org/10.1111/j.1654-1103.2009.05394.x.

Jönsson, M., Fraver, S., Jonsson, B.G., 2011. Spatio-temporal variation of coarse woody debris input in woodland key habitats in central Sweden. Silva Fenn. 45 (5), 957–967.

Jönsson, M., Perhans, K., Appelgren, L., Gustafsson, L., 2022. Bryophytes of conservation concern decline and traits change in retention patches during two decades following forest harvest. Biol. Conserv. 273, 109647 https://doi.org/10.1016/j.biocon.2022.109647.

Klein, J., Low, M., Sjögren, J., Eggers, S., 2022. Short-term experimental support for bird diversity retention measures during thinning in European boreal forests. For. Ecol. Manag. 509, 120084 https://doi.org/10.1016/j.foreco.2022.120084.

Klein, J., Low, M., Thor, G., Sjögren, J., Lindberg, E., Eggers, S., 2021. Tree species identity and composition shape the epiphytic lichen community of structurally simple boreal forests over vast areas. PLoS One 16 (9), e0257564. https://doi.org/10.1371/journal.pone.0257564.

Koenig, W.D., Liebhold, A.M., 2016. Temporally increasing spatial synchrony of North American temperature and bird populations. Nat. Clim. Change. https://doi.org/10.1038/nclimate2933.

König, L.A., Mohren, F., Schelhaas, M.-J., Bugmann, H., Nabuurs, G.-J., 2022. Tree regeneration in models of forest dynamics—Suitability to assess climate change impacts on European forests. For. Ecol. Manag. 520, 120390 https://doi.org/10.1016/j.foreco.2022.120390.

Kovács, B., Tinya, F., Ódor, P., 2017. Stand structural drivers of microclimate in mature temperate mixed forests. Agric. For. Meteorol. 234–235, 11–21. https://doi.org/10.1016/j.agrformet.2016.11.268.

Kyaschenko, J., Strengbom, J., Felton, A., Aakala, T., Staland, H., Ranius, T., 2022. Increase in dead wood, large living trees and tree diversity, yet decrease in understory vegetation cover: the effect of three decades of biodiversity-oriented forest policy in Swedish forests. J. Environ. Manag. 313, 114993 https://doi.org/10.1016/j.jenvman.2022.114993.

Larsen, J.B., Angelstam, P., Bauhus, J., Carvalho, J.F., Diaci, J., Dobrowolska, D., Gazda, A., Gustafsson, L., Krumm, F., Knoke, T., 2022. Closer-to-Nature Forest Management. From Science to Policy, 12. EFI European Forest Institute.

Lefcheck, J.S., 2016. piecewiseSEM: piecewise structural equation modelling in *r* for ecology, evolution, and systematics. Methods Ecol. Evol. 7 (5), 573–579. https://doi.org/10.1111/2041-210X.12512.

Maclean, I.M.D., Duffy, J.P., Haesen, S., Govaert, S., De Frenne, P., Vanneste, T., Lenoir, J., Lembrechts, J.J., Rhodes, M.W., Van Meerbeek, K., 2021. On the measurement of microclimate. Methods Ecol. Evol. 12 (8), 1397–1410. https://doi.org/10.1111/2041-210X.13627.

Máliš, F., Ujházy, K., Hederová, L., Ujházyová, M., Csölleová, L., Coomes, D.A., Zellweger, F., 2023. Microclimate variation and recovery time in managed and old-growth temperate forests. Agric. For. Meteorol. 342, 109722 https://doi.org/10.1016/j.agrformet.2023.109722.

Marangon, D., Marchi, N., Lingua, E., 2022. Windthrown elements: a key point improving microsite amelioration and browsing protection to transplanted seedlings. For. Ecol. Manage 508, 120050. https://doi.org/10.1016/j.foreco.2022.120050.

Marcolin, E., Marzano, R., Vitali, A., Garbarino, M., Lingua, E., 2019. Post-fire management impact on natural forest regeneration through altered microsite conditions. Forests 10 (11). https://doi.org/10.3390/f10111014.

Matlack, G.R., 1993. Microenvironment variation within and among forest edge sites in the eastern United States. Biol. Conserv. 66 (3), 185–194. https://doi.org/10.1016/0006-3207(93)90004-K.

Mayer, M., Rosinger, C., Gorfer, M., Berger, H., Deltedesco, E., Bässler, C., Müller, J., Seifert, L., Rewald, B., Godbold, D.L., 2022. Surviving trees and deadwood moderate changes in soil fungal communities and associated functioning after natural forest disturbance and salvage logging. Soil Biol. Biochem. 166, 108558 https://doi.org/10.1016/j.soilbio.2022.108558.

Pretzsch, H., 2014. Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. For. Ecol. Manag. 327, 251–264. https://doi.org/10.1016/j.foreco.2014.04.027.

Rudolphi, J., Gustafsson, L., 2011. Forests regenerating after clear-cutting function as habitat for bryophyte and lichen species of conservation concern. PLoS One 6 (4), e18639. https://doi.org/10.1371/journal.pone.0018639.

Ruel, J.J., Ayres, M.P., 1999. Jensen's inequality predicts effects of environmental variation. In: . https://doi.org/10.1016/S0169-5347(99)01664-X.

Schmidt, M., Jochheim, H., Kersebaum, K.-C., Lischeid, G., Nendel, C., 2017. Gradients of microclimate, carbon and nitrogen in transition zones of fragmented landscapes—A review. Agric. For. Meteorol. 232, 659–671. https://doi.org/10.1016/j.agrformet.2016.10.022.

Seibold, S., Bässler, C., Brandl, R., Gossner, M.M., Thorn, S., Ulyshen, M.D., Müller, J., 2015. Experimental studies of dead-wood biodiversity—A review identifying global gaps in knowledge. Biol. Conserv. 191, 139–149. https://doi.org/10.1016/j.biocon.2015.06.006.

Spears, J.D.H., Holub, S.M., Harmon, M.E., Lajtha, K., 2003. The influence of decomposing logs on soil biology and nutrient cycling in an old-growth mixed coniferous forest in Oregon, U.S.A. Can. J. For. Res. 33 (11), 2193–2201. https://doi.org/10.1139/x03-148.

Sterkenburg, E., Clemmensen, K.E., Lindahl, B.D., Dahlberg, A., 2019. The significance of retention trees for survival of ectomycorrhizal fungi in clear-cut Scots pine forests. J. Appl. Ecol. 56 (6), 1367–1378. https://doi.org/10.1111/1365-2664.13363.

Thom, D., Ammer, C., Annighöfer, P., Aszalós, R., Dittrich, S., Hagge, J., Keeton, W.S., Kovacs, B., Krautkrämer, O., Müller, J., von Oheimb, G., Seidl, R., 2023. Regeneration in European beech forests after drought: the effects of microclimate, deadwood and browsing. Eur. J. For. Res. 142 (2), 259–273. https://doi.org/10.1007/s10342-022-01520-1.

Thom, D., Sommerfeld, A., Sebald, J., Hagge, J., Müller, J., Seidl, R., 2020. Effects of disturbance patterns and deadwood on the microclimate in European beech forests. Agric. For. Meteorol. 291, 108066 https://doi.org/10.1016/j.agrformet.2020.108066.

Van de Peer, T., Verheyen, K., Ponette, Q., Setiawan, N.N., Muys, B., 2018. Overyielding in young tree plantations is driven by local complementarity and selection effects related to shade tolerance. J. Ecol. https://doi.org/10.1111/1365-2745.12839.

Von Arx, G., Graf Pannatier, E., Thimonier, A., Rebetez, M., 2013. Microclimate in forests with varying leaf area index and soil moisture: potential implications for seedling establishment in a changing climate. J. Ecol. 101 (5), 1201–1213. https://doi.org/10.1111/1365-2745.12121.

WMO. (2022). *State of the Global Climate 2021*.

Young, A., Mitchell, N., 1994. Microclimate and vegetation edge effects in a fragmented podocarp-broadleaf forest in New Zealand. Biol. Conserv. 67 (1), 63–72. https://doi.org/10.1016/0006-3207(94)90010-8.

Zalamea, M., González, G., Lodge, D.J., 2016. Physical, chemical, and biological properties of soil under decaying wood in a tropical wet forest in Puerto Rico. Forests 7 (8). https://doi.org/10.3390/f7080168.

Zellweger, F., Coomes, D., Lenoir, J., Depauw, L., Maes, S.L., Wulf, M., Kirby, K.J., Brunet, J., Kopecký, M., Máliš, F., Schmidt, W., Heinrichs, S., den Ouden, J., Jaroszewicz, B., Buyse, G., Spicher, F., Verheyen, K., De Frenne, P., 2019. Seasonal drivers of understorey temperature buffering in temperate deciduous forests across Europe. Glob. Ecol. Biogeogr. https://doi.org/10.1111/geb.12991.

Zellweger, F., de Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-Römermann, M., Baeten, L., Hédl, R., Berki, I., Brunet, J., van Calster, H., Chudomelová, M., Decocq, G., Dirnböck, T., Durak, T., Heinken, T., Jaroszewicz, B., Kopecký, M., Máliš, F., Coomes, D., 2020. Forest microclimate dynamics drive plant responses to warming. Science. https://doi.org/10.1126/science.aba6880.

Zhang, S., Landuyt, D., Verheyen, K., De Frenne, P., 2022. Tree species mixing can amplify microclimate offsets in young forest plantations. J. Appl. Ecol. https://doi.org/10.1111/1365-2664.14158. *n/a*(n/a).

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., Walker, Z.I., Smith, S., 2007. Mixed Effects Models and Extensions in Ecology With R, first ed. Springer. https://doi.org/10.1007/978-0-387-87458-6.

Further reading

Zhang, S.. *Retention forestry amplifies microclimate buffering in boreal forests*. https://doi.org/10.6084/m9.figshare.24072282.v1.