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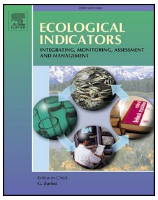

Spatial microclimatic heterogeneity is associated with forest structure and biodiversity

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ABSTRACT

Forest microclimates, their buffering through forest structure, and their impact on biodiversity are crucial for future forest management under climate change. However, standard approaches for measuring forest microclimates do not capture small-scale heterogeneity, which, according to the habitat heterogeneity hypothesis, is a driver of biodiversity.

We quantified horizontal and vertical microclimatic heterogeneity within 30 broad-leaved forest plots (0.25 ha) in Central Europe using a three-dimensional design with high spatial resolution. Moreover, we examined whether microclimatic heterogeneity differs among silvicultural treatments and whether it can be predicted using forest structure indices derived from laser scanning. Additionally, we explored the relationship between microclimatic heterogeneity and biodiversity.

In canopy gaps, warm and cold habitats co-existed in close proximity, leading to a high horizontal microclimatic heterogeneity. In closed stands with high structural complexity, we found steep gradients of decreasing temperature and vapor pressure deficit from the canopy to deep shade conditions at the forest floor during midday. Canopy cover and forest structural complexity were strong indicators of microclimatic heterogeneity. We found positive relationships between herb layer temperature heterogeneity and the diversity of plants, Hymenoptera, and Diptera.

Our results demonstrate that single-point measurements fail to capture the substantial microclimatic heterogeneity within plots, potentially misrepresenting the conditions experienced by forest species. However, laser scanning provides reliable indicators for within-plot microclimatic heterogeneity. With canopy gaps featuring high horizontal microclimatic heterogeneity and promoting the biodiversity of several taxonomic groups, we argue that managing forests for maximized temperature buffering should not be the only strategy to conserve forest biodiversity.

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1. Introduction

Forest microclimate has recently received a surge of interest, with a rapidly growing body of studies emphasizing its ecological importance, especially with regard to temperature buffering and the provision of cool microrefugia in the context of climate change (De Frenne et al., 2021). Compared to macroclimate, microclimate better represents the conditions that organisms are experiencing (Haesen et al., 2023; Maclean and Early, 2023). Therefore, microclimate is central for understanding ecological patterns and processes from species niches and distributions (Gril et al., 2025; Lembrechts et al., 2019), over community composition and diversity (Govaert et al., 2024; Zellweger et al., 2020), to ecosystem functioning and forest dynamics (Beugnon et al., 2024; Braziunas et al., 2025). However, the spatial resolutions at which forest microclimate is usually measured are still relatively coarse compared to the scales relevant to many forest-dwelling species, especially sessile organisms and species of small body size (Pincebourde and Woods, 2020; Sears et al., 2011). In most studies, microclimate has been measured with one sensor per permanent plot (typically 0.25 ha to 1.00 ha) at standardized heights, which was then assumed to be representative of the plot. Yet, typical forest plots of these dimensions likely provide a broader suite of microclimatic habitats than the one captured by a point measurement (De Frenne et al., 2025). To address this knowledge gap, here we investigate spatial microclimatic heterogeneity within forest plots.

Small-scale microclimatic heterogeneity can be separated into horizontal and vertical heterogeneity. Both have been mapped before the advent of modern sensor and data logger technology (Geiger, 1927), but have barely ever been represented in the recent wave of microclimatic research. In fact, several recent studies have explicitly named vertical microclimate profiles as a major research gap (Bramer et al., 2018; De Frenne et al., 2021; Lenoir et al., 2017). In the few published examples, steep vertical gradients in temperature and vapor pressure deficit were observed in temperate (Zahnd et al., 2023; Zweifel et al., 2002), but also tropical forests (Schuldt et al., 2011). Consequently, vertical microclimatic gradients provide a turnover in thermal habitats for canopy-dwelling arthropods (De Smedt et al., 2019; Saudreau et al., 2013). Furthermore, with their influence on the leaf gas exchange in different strata of tree crowns, vertical microclimatic gradients directly affect tree performance, and hence ecosystem-climate feedbacks (Vinod et al., 2023).

Not only vertical, but also horizontal microclimatic heterogeneity remains poorly understood. Small-scale heterogeneity of light availability, temperature, and soil moisture creates a mosaic of microhabitats on the forest floor, which increases understory plant diversity (Helbach et al., 2022), and the performance of ectotherms (Woods et al., 2015). Previous work focused on descriptive analyses of small-scale horizontal or vertical microclimatic patterns (Ashcroft and Gollan, 2012; Horváth et al., 2023; Zellweger et al., 2024). However, in order to compare microclimatic heterogeneity between forests and relate it to other variables, it is necessary to quantify the microclimatic heterogeneity within observational units such as permanent plots.

The knowledge gap concerning spatial microclimatic heterogeneity is surprising, given how crucial heterogeneity is for biodiversity according to the habitat heterogeneity hypothesis. It states that heterogeneous habitats support the coexistence of more species with different niches (Eisenhauer et al., 2023). There is plenty of evidence for positive heterogeneity-diversity relationships (Heidrich et al., 2020; Stein et al., 2014). However, in most cases, heterogeneity of vegetation, land cover, or topography was investigated, while (micro)climatic heterogeneity remains understudied (Heidrich et al., 2020; Stein and Kreft, 2015). The abundance of research on structural heterogeneity, compared to microclimatic heterogeneity, may stem from the fact that remote sensing methods like LiDAR enables efficient high-resolution measurement of forest structure. Spatially highly resolved, three-dimensional measurements of microclimate, on the other hand, are still methodically challenging and resource-consuming.

Forest structure is one of the key factors determining sub-canopy microclimate (Borderieux et al., 2025; Zellweger et al., 2019a). Canopy cover, structural complexity, and vertical layering are key structural properties that directly impact ecologically relevant microclimatic variables such as air temperature, vapor pressure deficit (VPD), and soil moisture (Kovács et al., 2017; Von Arx et al., 2013). If the relationships of these structural indices with microclimatic heterogeneity are as strong as with microclimate per se, inferring microclimatic heterogeneity from structural data would become straightforward (Zellweger et al., 2019b).

Ultimately, the relationships between forest structure, microclimate, and biodiversity are central to the question of how biodiversity conservation should be integrated into forest management under climate change. Forest management influences microclimate via its impact on forest structures (Ehbrecht et al., 2019; Kovács et al., 2020). Silvicultural interventions leading to large canopy gaps, as well as natural disturbances, decrease microclimatic buffering locally (Thom et al., 2020). Structurally complex forests, on the other hand, have an especially pronounced buffering effect on sub-canopy microclimates (Máliš et al., 2023; Wolf et al., 2021). While many recent studies on forest microclimate conclude that temperature buffering should be optimized by aiming at maximally dense canopies to maintain cool microhabitats (e.g. De Lombaerde et al., 2022; Sanczuk et al., 2023), others argue that the microclimate found in canopy gaps is important for biodiversity (Müller et al., 2023; Schall and Heinrichs, 2020). With this study, we aim to contribute to this debate with insights into small-scale vertical and horizontal microclimatic heterogeneity and its relationship with biodiversity.

We measured horizontal and vertical heterogeneity of temperature, VPD, and soil moisture in an intensive three-dimensional design within forest plots, and test the hypotheses that (1) forest structure and microclimatic heterogeneity indices differ between experimental silvicultural treatments; (2) forest structure indices describing structural complexity, canopy cover, and vertical layering are good indicators for microclimatic heterogeneity; and (3) microclimatic heterogeneity is positively associated with the biodiversity of different taxonomic groups.

2. Material and methods

2.1. Study areas

The study was conducted at two sites in Germany resembling typical broadleaf production forests of Central Europe with a comparable stand age of approximately 80–90 years, but differing in site conditions (Fig. 1a). The northern site, University Forest Sailershausen, is located at lowland elevations (300–360 m a.s.l.) in north-western Bavaria and features a comparatively warm and dry climate for Central European standards (mean annual temperature (MAT): 8.8 °C; mean annual precipitation (MAP): 732 mm (1981-2010; DWD Climate Data Center (CDC), 2025a, 2025b). The southern site, Bavarian Forest, is located in the homonymous low mountain range (490–850 m.a.s.l.) in south eastern Bavaria and features a colder and wetter climate (MAT: 5.9–7.8 °C; MAP: 1080–1416 mm). During the measurement periods in 2023 and 2024, monthly average air temperatures at the respective sites were consistently 1 °C to 2 °C warmer than the 30-year average from 1981-2010 (Fig. S1). The stands in Sailershausen were species-rich mixed broad-leaved forests dominated by ash (*Fraxinus excelsior*), European beech (*Fagus sylvatica*), hornbeam (*Carpinus betulus*), maple (*Acer* spec.), and oak (*Quercus* spec.) with a maximum stand height of 25.9 ± 2.3 m (mean ± SD), whereas the Bavarian Forest stands were beech forests with small shares of admixed Norway spruce (*Picea abies*) and a maximum stand height of 29.0 ± 2.3 m.

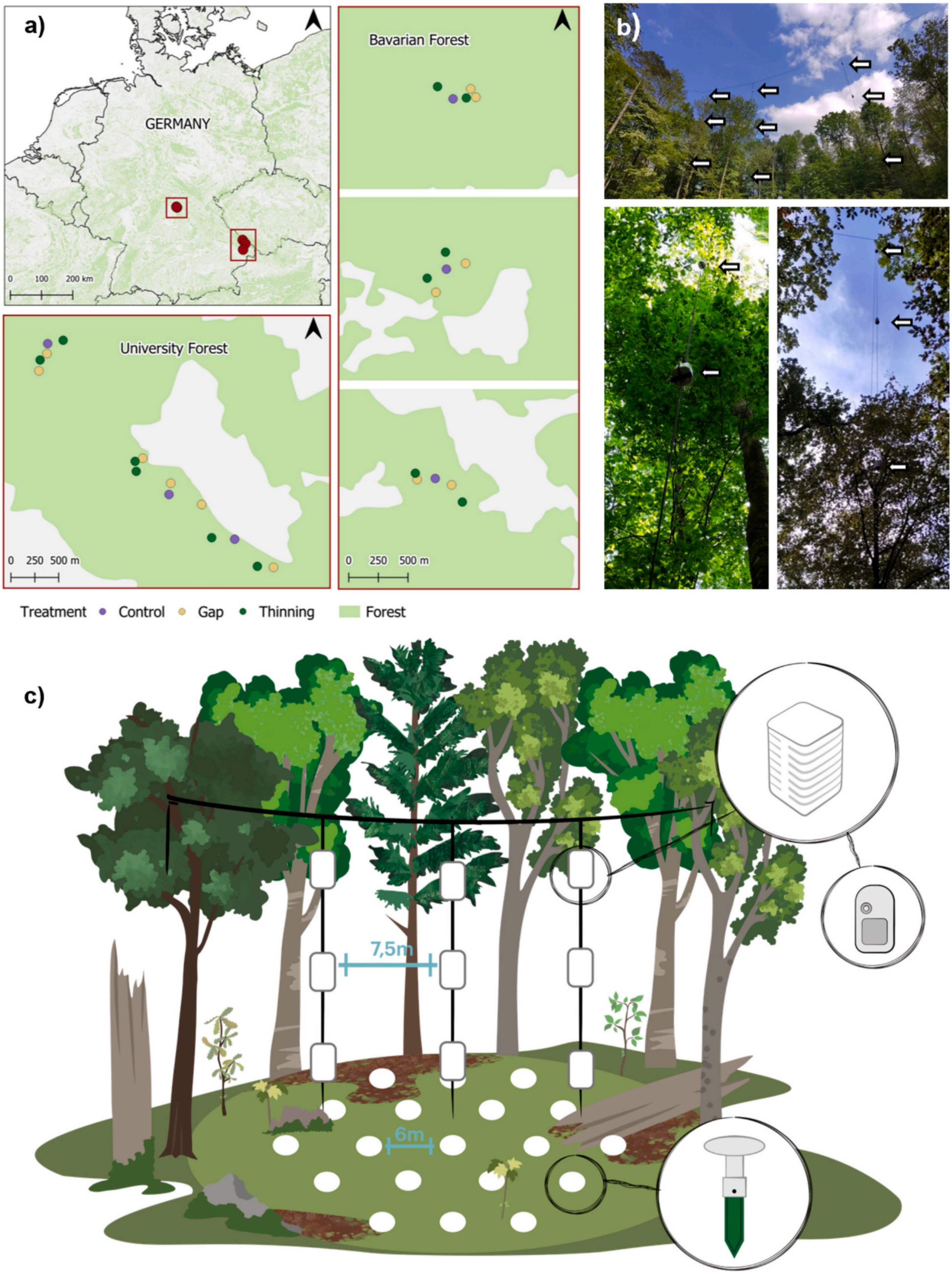

Fig. 1. Experimental setup. a) Locations of the study sites, and spatial arrangement of the plots within the sites. b) Examples of loggers installed in sun shields on vertical ropes. Arrows highlight the positions of loggers. c) Logger installation scheme within the plots. The circles at the forest floor represent Tomst TMS-4 loggers, the rectangles along the ropes represent Onset Hobo MX2301A loggers installed within sun shields.

2.2. Experimental design

The study was conducted in 30 plots (50 m × 50 m; 0.25 ha) from the BETA-FOR experiment (Müller et al., 2023), each 15 plots at both sites. In the winters of 2015/2016 (Bavarian Forest) and 2018/2019 (University Forest), ~30% of the stand basal area was removed from treated plots, either aggregated in the center of the plot (“Gap”) with a diameter of the canopy opening of 30 m, or evenly distributed throughout the plot (“Thinning”). Both Gap and Thinning treatments were applied in two versions, either harvesting the trees normally or retaining snags of 5 m height. However, since our key variables of interest were not significantly impacted by the presence of snags (Fig. S2), we pooled the versions with and without snags. Additionally, Control plots without any interventions during the experiment were established. In total, there were six Control plots, and each twelve Gap and Thinning replicates (Fig. 1a).

2.3. Microclimatic measurements

Microclimatic measurements were conducted respectively from June 8 to September 30, in 2023 in the University Forest, and in 2024 in the Bavarian Forest.

2.3.1. Temperature and vapor pressure deficit in the tree layer

For measuring air temperature and relative humidity in higher stand layers with “Hobo loggers” (Hobo MX2301A, Onset, Bourne, USA) protected from direct solar radiation with TX Cover sun shields (Technoline, Bernburg, Germany), we installed three vertical ropes in the canopy of each plot (Fig. 1 b, c). One vertical rope was positioned directly at the plot center, the other two 7.5 m north and south of the central rope, respectively. The ropes were installed as high as possible, depending on the local forest structure, and carried three loggers each, yielding nine loggers per plot and 270 devices in total. Due to technical malfunctions or storm damage, six loggers from the University Forest site and eight from the Bavarian Forest site had to be excluded. The lowest logger was installed at 5 m, the uppermost as high as the local conditions allowed (ranging from 12.5 m to 24.2 m with a distance between mean stand height and upper sensor height from 1.4 m to 7.5 m), and the middle logger with approximately equal distances between these two. Logger heights were recorded with a tree height meter (Vertex 5, Haglöf, Långelse, Sweden). The data were logged in 30-min intervals, and subsequently vapor pressure deficit (VPD) was calculated according to Goff and Gratch (1946). These measurements are referred to as “tree layer” measurements from here on.

2.3.2. Temperature near the ground surface and soil moisture

Near the ground surface, temperature and volumetric soil water content (VWC) were measured with 19 devices (TMS-4, Tomst, Czech Republic; “Tomst loggers”) arranged in a hexagonal grid covering the center of each plot with a distance of 6 m between loggers (Fig. 1 c). This design was chosen in order to measure the entire cut-open area of the Gap treatments. In total, 570 devices were installed. Of these, four loggers from the University Forest and six from the Bavarian Forest had to be excluded. Tomst loggers feature temperature sensors at three positions, 6 cm beneath, 2 cm and 15 cm above the soil surface, the latter defined as “herb layer” measurements. A proxy for VWC in the uppermost horizon (Wild et al., 2019) was transformed into VWC based on plot-specific soil texture data (Method S1). The data were logged at 15-min intervals.

2.4. Measuring forest structure

We used a mobile laser scanner (ZEB Horizon laser scanner, GeoSLAM, Nottingham, UK) to measure forest structure during the microclimatic measurements. The device was carried from the center in outward spirals until reaching a radius of 30 m, then returning to the center (Neudam et al., 2022). The point clouds were processed in the Faro Connect software (Faro Technologies, Lake Marry, USA). See Method S2 for more details. We calculated three forest structural indices: box dimension (D_b), canopy cover, and effective number of layers (ENL).

D_b is a measure for forest structural complexity based on the three-dimensional fractal dimension of the stand. Forests with high vegetation density and homogenous distribution of plant material in the three-dimensional space receive highest values (Seidel, 2018; Seidel et al., 2020). Canopy cover (%) expresses the fraction of the area vertically covered by vegetation elements and was calculated based on a 20 cm × 20 cm ground resolution and considering all points higher than 5 m above ground as “canopy” (Höwler et al., 2024). ENL describes the vertical layering of the forest via the occupation of 1 m layers with points, analogously to describing diversity with Hill numbers (Ehbrecht et al., 2016; Hill, 1973). We calculated ENL1D, i.e., weighting the layers by their occupancy as in Hill numbers of $q = 1$.

2.5. Biodiversity

Using data from the BETA-FOR experiment (Müller et al., 2023), we selected four exemplary clades spanning different levels of mobility: vascular understory plants, spiders, Diptera (flies), and Hymenoptera (sawflies, bees, wasps, and ants). Organism groups with such different levels of mobility represent different adaptive strategies to microclimatic extremes, i.e. avoidance in mobile organisms vs. tolerance in immobile organisms (Geres et al., 2025). Vascular plant species were recorded with vegetation surveys (Bradler et al., 2025), spiders sampled using pitfall traps and identified to the species level by experts (Stör et al., 2025), while Diptera and Hymenoptera were sampled with Malaise traps and OTUs identified through metabarcoding (Rothacher et al., 2025). Further details regarding the sampling protocols are given in Methods S3 and in the original publications cited above.

2.6. Data analysis

2.6.1. Continuous predictions over sensor heights

In order to describe temperature and VPD at different heights during the day, we fitted generalized additive models (GAM) of the microclimatic time series in dependency of treatment, sensor height, time of the day, and day of the measurement period. We then generated predictions for an average day at each combination of treatment, sensor height, and time of the day. For details, see Method S4. These models were only used for graphically summarizing the data, not for statistical hypothesis testing.

2.6.2. Quantifying microclimatic heterogeneity

To quantify horizontal heterogeneity of the microclimatic variables measured with Tomst loggers, we calculated the standard deviation of the 19 measured values per plot and variable at each point in time. Then, we calculated the plot averages of these standard deviations over the whole study period.

For the Hobo loggers, we separated between horizontal and vertical heterogeneity. We first aggregated the measured time series to the logger level by calculating the average daily maximum temperature and VPD of each logger. We focused on daily maximum values because they drive heat and drought stress of organisms (Bristow and Abrecht, 1991; Macek et al., 2019). Next, we fitted one linear model per plot, where the nine average daily maximum values were modeled in dependency of height and horizontal position, performed variance decompositions of each of the models using the Lindeman, Merenda, and Gold (LMG) approach (Lindeman et al., 1980) for obtaining the variance explained by the linear vertical gradient, the variance explained by the horizontal position, and the unexplained variance. We interpret the explained variance components as horizontal and vertical heterogeneity of average daily maximum temperature and VPD in the tree layer.

2.6.3. *Relationships between treatment, forest structure, and microclimatic heterogeneity*

We tested whether the forest structure indices and the microclimatic heterogeneity variables differed between treatments using Kruskal-Wallis tests and post-hoc Dunn tests. For the Dunn tests, we used the R package dunn.test version 1.3.6 (Dinno, 2024). Furthermore, we tested whether the microclimatic heterogeneity variables depended on forest structure indices using linear models. We fitted one separate model for each pairwise combination of response and predictor.

2.6.4. *Relationships between microclimatic heterogeneity and biodiversity*

In order to account for differences in coverage (sample completeness), we used a rarefaction approach to estimate the sample coverage of the measured data and to standardize the taxonomic species richness data to identical sample coverages by inter- or extrapolation (Chao and Jost, 2012) by applying the estimate3D function from the iNEXT.3D R package version 1.0.6 (Chao et al., 2021), run in R version 4.3.0 (R Core Team, 2025). The taxonomic species richness data were standardized to sample coverage values of 0.900 for vascular plants, 0.950 for spiders, 0.996 for Diptera, and 0.997 for Hymenoptera for acquiring a majority of the data from interpolation, not extrapolation (for details, see Rothacher et al., 2025).

As the biodiversity data were strongly dominated by site differences (Fig. S4), we first fit a linear model with site as predictor for each taxonomic group, extracted the residuals and used the scaled residuals as site-corrected biodiversity data for fitting linear models for each pairwise combination of microclimatic heterogeneity variable and taxonomic group. If not stated otherwise, the data analysis was conducted in R version 4.5.0 (R Core Team, 2025).

3. Results

3.1. *Within-plot microclimatic patterns*

Air temperatures showed diurnal oscillations at all heights, with maximum temperatures around 15:00 CET. During this time of the day, differentiation of temperatures along vertical profiles and between treatments was most pronounced (Fig. 2 a, b, c). During the evening, night, and morning, air temperatures in the tree layer (>5 m) on average showed no clear vertical gradients, but during the afternoon, they increased from lower to higher air layers in thinned and control plots (Fig. 2 a, Fig. S5). At the University Forest site, average temperatures in the Control treatment at 15:00 increased from 22.5 °C at 5 m to 24.1 °C at 20 m (Fig. 2 a). In the canopy gaps, no such pronounced vertical gradient existed: there, the average predicted temperatures at 5 m height were 23.7 °C, and at 20 m height 24.3 °C. As a result, air temperatures in the Gap treatment were warmer than in the Control, especially during the noon and afternoon hours, and only in the lower air layers, with differences between 1 °C and 2 °C (Fig. 2 b). At the Bavarian Forest site, apart from overall lower air temperatures, the patterns were similar. Vapor pressure deficit (VPD) displayed similar patterns as temperature, with the exception that a vertical gradient was also present in the gaps (but less pronounced than in the thinned and control plots, Fig. S5). Individual vertical profiles partly differed from the predicted average patterns (Fig. 2c, S6).

Temperatures close to the ground surface also showed the clearest vertical stratification and differentiation between treatments in the afternoon (Fig. 3 a). During these hours, average temperatures increased from Control over Thinning to the Gap treatment at all measuring heights and at both sites, even though the differences were always smaller than 1 °C (Fig. 3 a, Fig. S7 a). The temperatures measured simultaneously within the same plot and at the same height could vary by several degrees in some plots, but were relatively homogeneous in others. For example, in one gap plot (#2), average temperatures at 15:00 ranged from 21.8 °C to 27.5 °C, whereas in a thinned plot (#60), they only ranged from 21.5 °C to 22.2 °C (Fig. 3 b). Volumetric water content of the topsoil (VWC) did not oscillate diurnally like temperatures and VPD, but rapidly increased during precipitation events and slowly decreased between them. In the Bavarian Forest, Control displayed lower VWC than the other two treatments in the early measurement period. In the University Forest, the gaps were drier than the closed stands in the early phase, but wetter towards the end of summer (Fig. S7 b).

3.2. *Treatment effects on forest structure and microclimatic heterogeneity*

Box dimension (D_b) and canopy cover, but not effective number of layers (ENL), differed significantly between treatments. In gaps, D_b and canopy cover were significantly lower than in the other treatments, while they were not significantly different between thinned and control plots (Fig. 4 a, Fig. S8, Table S1). Canopy cover and D_b were highly correlated with each other ($r = 0.88$), while ENL was independent from them (Fig. S8).

Horizontal temperature heterogeneity close to the soil surface (−6 cm, 2 cm and 15 cm) was higher in the Gap treatment than in Thinning and Control, but treatment had no effect on VWC heterogeneity (Fig. 4 b, Fig. S9, Table S1). Vertical heterogeneity of temperatures and VPD in the tree layer were significantly lower in the gaps than in thinned and control plots, whereas horizontal temperature heterogeneity in the tree layer was significantly higher in gaps than in thinned plots. For none of these variables, the difference between Thinning and Control was significant (Fig. 4 c, d, Table S1). Treatment had no effect on horizontal VPD heterogeneity (Fig. S9, Table S1).

3.3. *Effects of forest structure on microclimatic heterogeneity*

D_b and canopy cover were significantly associated with all microclimatic heterogeneity variables except VWC heterogeneity, which had no significant relationship with any predictor (Fig. 5, Fig. S10, Table S2). ENL did not have significant effects on any of the response variables. The relationships of D_b and canopy cover with all variables describing horizontal heterogeneity were negative, i.e., the higher the structural complexity and denser the canopy, the more horizontally homogeneous were the temperatures and VPD. In contrast, the relationships of the vertical heterogeneity variables with D_b and canopy cover were positive, i.e., in structurally more complex plots with denser canopies, vertical gradients were steeper (Fig. 5, Fig. S10, Table S2). Of the significant relationships, the least amount of variance was explained by the predictors for soil temperature heterogeneity (16% for D_b, 17% for canopy cover). The highest fraction of variance levels was explained for horizontal herb layer temperature heterogeneity (70% for D_b, 79% for canopy cover). All other models with significant relationships explained between 28% and 49% of the variance in the data, with canopy cover usually explaining slightly more variance than D_b (Table S2).

3.4. *Relationships between biodiversity and microclimatic heterogeneity*

While heterogeneity of microclimatic conditions in higher strata and VWC heterogeneity were not significantly associated with ground-level biodiversity (i.e., coverage-standardized species richness), heterogeneity of temperatures near the soil surface was significantly associated with increased diversity of vascular plants, Diptera, and Hymenoptera (Fig. 6, Fig. S11, Table S3). The relationships were significant for temperatures at 15 cm in all three groups, at 2 cm for Hymenoptera and vascular plants, and at −6 cm just for vascular plants. The models explained between 14% and 39% of the variance in the data. Spider diversity was not significantly associated with any of the variables (Table S3).

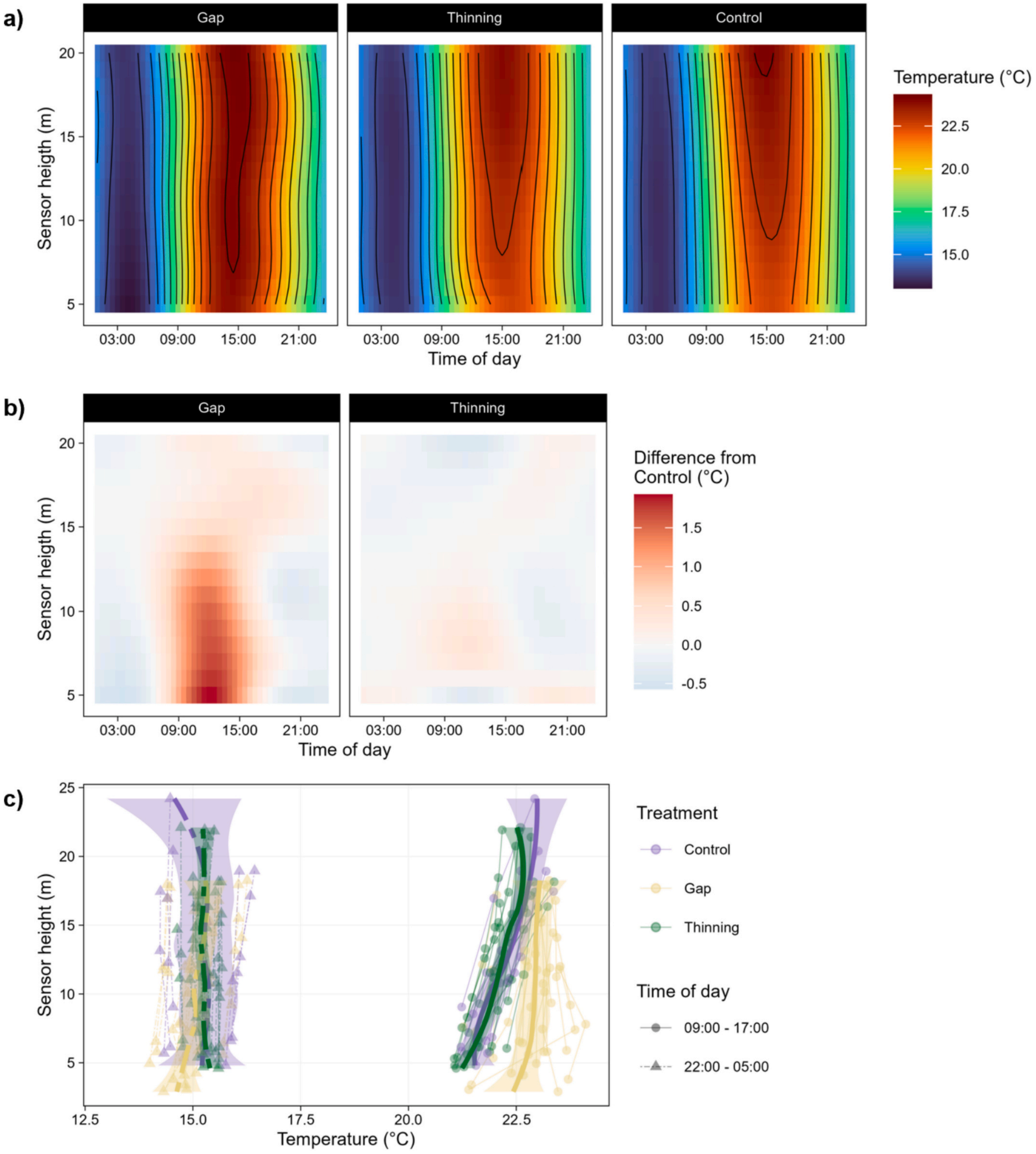

Fig. 2. Temperature patterns in the tree layer (shown are only data for the University Forest). All data are summarized over the study period from June 8 to September 30, 2023. a) Estimated average air temperatures in the tree layer. Shown are predictions from a generalized additive model (GAM). b) Temperature differences between Control and the other treatments for different heights throughout the day. We subtracted the GAM predictions shown in Fig. 2a) for the control plots from the predictions of each of the two treatments to illustrate the magnitude of the differences. c) Average day and night vertical profiles. Each point is one logger, with the thin lines connecting loggers installed on the same rope. The bold lines are loess smoothers for each group along the y axis. For equivalent results from the Bavarian Forest site and VPD, please see Fig. S5 and S6.

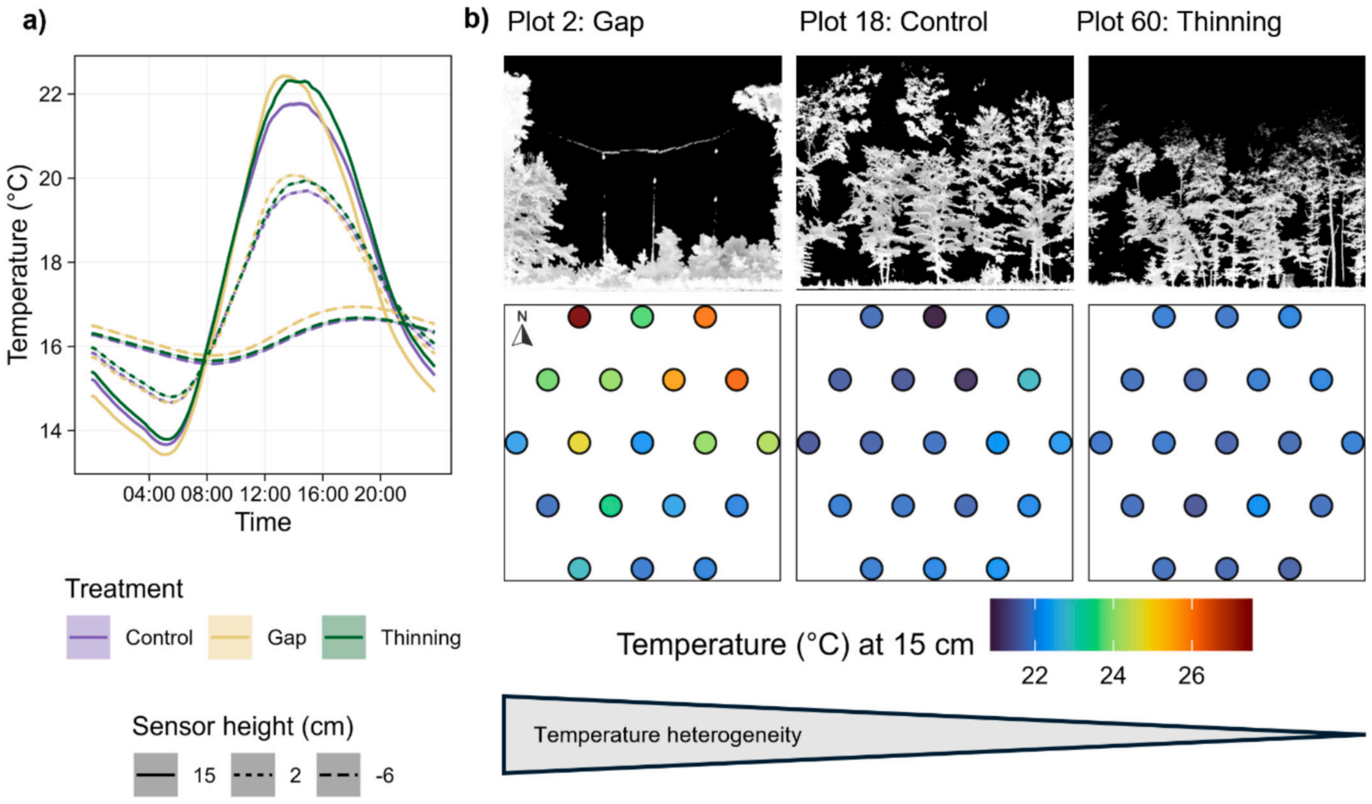

Fig. 3. Temperature patterns in the herb layer. All data are summarized over the study period from June 8 to September 30, 2023. a) Mean temperatures close to the soil surface, measured with 19 Tomst loggers per plot, averaged over all loggers per treatment and all days of the observation period. b) Average temperatures in the herb layer (15 cm height) at 15:00in three exemplary plots. Each point represents one Tomst logger from a bird's perspective. In the top row, projections of cross sections through the 3D point clouds illustrate the forest structure. The three exemplary plots were selected to represent high, intermediate, and low horizontal temperature heterogeneity. For results from both sites, please see Fig. S7.

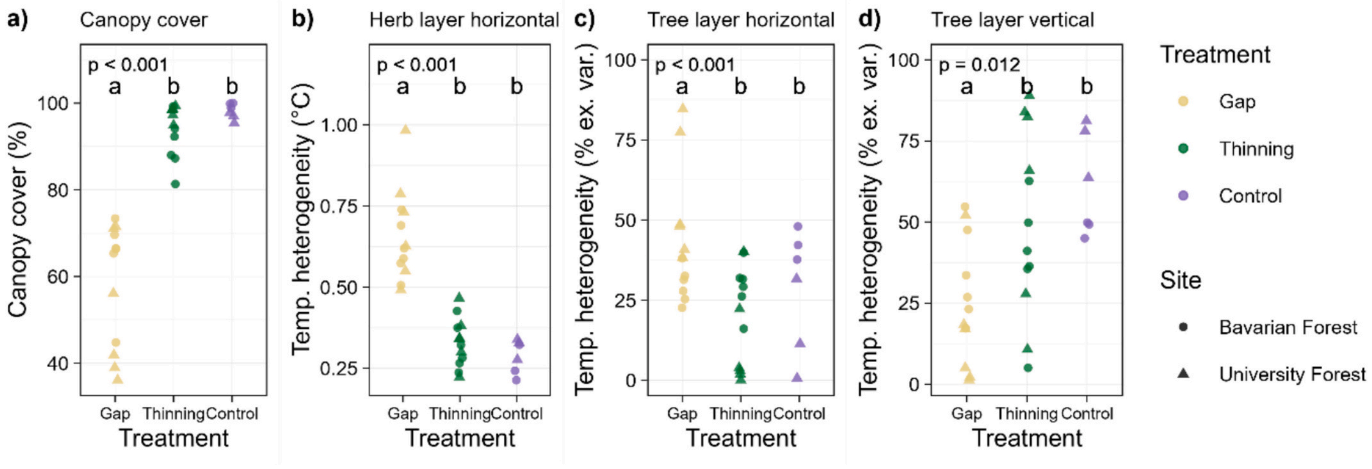

Fig. 4. Effect of treatments on forest structural complexity and within-plot temperature heterogeneity. Each point represents one forest plot. Significant differences were tested with Kruskal-Wallis tests and post-hoc Dunn's tests, see Table S1 for the full test output. The abbreviated y axis labels stand for temperature heterogeneity, either quantified as average within-plot standard deviation (°C) or as % explained variance (% ex. var.). See Fig. S8 and S9 for results for all forest structure and microclimatic heterogeneity variables.

4. Discussion

4.1. Microclimatic heterogeneity in gaps and closed stands

Our first hypothesis, stating that microclimatic heterogeneity varies between canopy gaps, thinned stands, and control plots, was partly supported by our results: gaps differed both in horizontal and vertical microclimatic variability from the two other treatments. However, there was no significant difference between thinned and control plots. Forest structural complexity and canopy cover showed the same pattern. A high degree of structural similarity between thinned and control plots in this experiment was also found using other forest structure indices, and is presumably caused by rapid crown expansion of the remaining trees after the thinning operations (Kacic et al., 2025; Pierick et al., 2025).

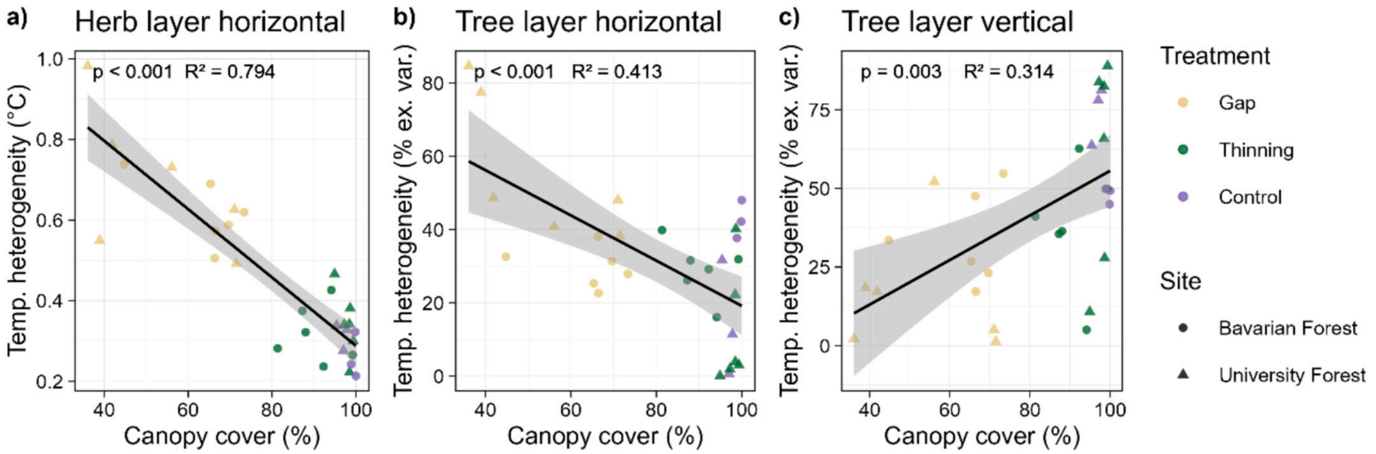

Fig. 5. Temperature heterogeneity indices in dependency of canopy cover. Each point represents one forest plot. The lines represent predictions from linear models with 95% confidence intervals. The slope parameters were significantly different from 0 for all three pairwise relationships. See Table S2 for model results. The abbreviated y-axis labels stand for temperature heterogeneity, either quantified as average within-plot standard deviation (°C) or as % explained variance (% ex. var.). See Fig. S10 for results for all variables.

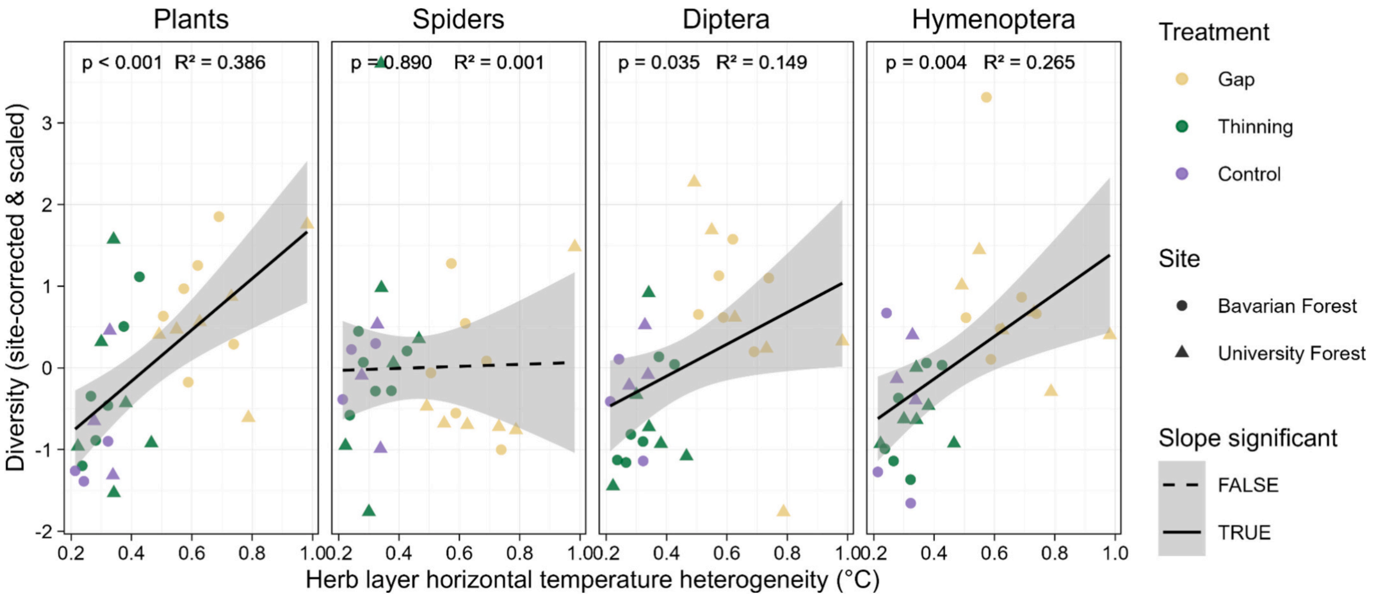

Fig. 6. Relationships between within-plot temperature heterogeneity at 15 cm height and diversity of selected taxa. Each point represents one forest plot. Shown are the data together with predictions and 95% confidence intervals from linear models. See Table S3 for model results and Fig. S11 for relationships between other microclimatic heterogeneity variables and biodiversity.

Therefore, differences in microclimatic heterogeneity that might have been present directly after the interventions did not prevail.

We found steep vertical gradients of air temperature and vapor pressure deficit (VPD) during midday in closed-canopy stands, with a gradual decrease from warmer and drier air in the upper strata of the forest to cool, moist conditions towards the forest floor. This is a result of large proportions of the incoming short-wave radiation being absorbed or reflected by the upper strata (Geiger, 1927). In gaps, the solar radiation penetrates to the understory vegetation or forest floor, where the energy transfer from short- to longwave radiation takes place. The emitted long-wave radiation in combination with air mixing leads to comparatively warm, vertically homogeneous air temperatures in the tree layer (Geiger, 1927).

As expected, the horizontal heterogeneity of temperature and VPD was higher in gaps than in closed stands as these are homogeneously cold during the diurnal maximum temperatures, while gaps featured cooler and warmer temperatures in close proximity. It is well established that, during the vegetation period, midday air temperatures and VPD are on average higher in canopy gaps (Abd Latif and Blackburn, 2010). However, the coexistence of colder and warmer microhabitats within gaps has typically been overlooked (but see Gálhidy et al. (2006), Gray et al. (2002), and Horváth et al. (2023) for maps of microclimatic mosaics within canopy gaps). Two likely contributing factors are north-south gradients of shading by the gap edges (Ritter et al., 2005), and understory vegetation emerging after the opening of the canopy. Our measurements took place five and nine years after the interventions, leaving enough time for plants to form a dense understory as a reaction to the increased light availability (Pierick et al., 2025). This provides patches of deep shade under otherwise hot gap conditions (Brůna et al., 2024; Stickley and Fraterrigo, 2021).

We found no impact of the treatments on VWC heterogeneity. Previous studies reported effects of canopy openings on soil moisture (Belmonte et al., 2022; Horváth et al., 2023), driven by opposing mechanisms of increased evaporation from the soil, but decreased interception and transpiration (Abd Latif and Blackburn, 2010). It is possible that during the cycles of rapidly increasing VWC during rain events and slowly decreasing VWC in between rain events, spatial heterogeneity of VWC differed between gaps and closed stands (possibly due to different spatial heterogeneity in interception, transpiration and evaporation), but these short-time differences disappeared when summarizing the whole study period).

4.2. *Forest structure indices as proxies for microclimatic heterogeneity*

Our second hypothesis was that forest structure indices quantifying forest structural complexity, canopy cover, and vertical layering can be used as indicators for within-plot microclimatic heterogeneity. Our results show that especially temperature heterogeneity in the herb layer is strongly associated with forest structural complexity (as quantified by the box dimension index) and canopy cover. Even though we pooled data from two dissimilar forests and different years, bivariate linear models of herb layer temperature heterogeneity in dependency of box dimension or canopy cover explained over 70% of the variance. Metrics describing canopy cover and structural complexity can not only be obtained from ground-based, but also airborne LiDAR, and have been successfully linked to forest microclimate (Gril et al., 2023; Vandewiele et al., 2023). While LiDAR data from different sensors and platforms vary largely in perspective, resolution, and scale, our results suggest that vertical profiles and small-scale horizontal microclimatic heterogeneity could potentially be inferred from LiDAR data for whole landscapes.

4.3. *Associations of microclimatic heterogeneity with biodiversity*

In line with our third hypothesis, we found positive associations between horizontal temperature heterogeneity in the herb layer and the ground-level biodiversity of plants, Diptera, and Hymenoptera. One possible explanation is that, as predicted by the habitat heterogeneity hypothesis, plots with more heterogeneous thermal conditions could harbor more species with contrasting niches (Stein et al., 2014). Plant diversity benefits from stand-scale microclimatic heterogeneity (Helbach et al., 2022), and the majority of plant species in Central European forests are not adapted to deep shade, but semi-open conditions (Czyżewski and Svenning, 2025).

Ectotherm animals rely on keeping their operational temperature within a range between delayed physiological processes and heat stress (Colinet et al., 2015; Huey et al., 2012). Heterogeneous thermal environments can facilitate thermoregulatory behavior, i.e., moving to optimal thermal microenvironments, of arthropods (Pincebourde and Suppo, 2016). Biodiversity and performance of arthropod taxa can both be negatively impacted by heat stress (Asch et al., 2025; Junggebauer et al., 2024), or higher in warmer than in colder environments (Lettenmaier et al., 2022; Woods et al., 2015), depending on the taxonomic group. For several arthropod groups, there is evidence for thermal heterogeneity on different spatial scales positively affecting their biodiversity and performance (Seibold et al., 2016; Terlau et al., 2023). Thus, it is plausible that the heterogeneous microclimatic conditions are one factor driving forest structure-biodiversity relationships of both plants and arthropods.

However, other mechanisms might also come into play. In our design, average microclimate per se and its heterogeneity are correlated, making their effects impossible to distinguish (Dormann et al., 2020). In large canopy gaps, not only temperature and its small-scale heterogeneity, but also other factors differ from those in closed-canopy forests. The most obvious example is light availability instead of temperature as a driver of plant diversity (Degen et al., 2005; Helbach et al., 2022). Experimental evidence implies that light, not temperature, drives plant community responses to canopy openings (De Pauw et al., 2022; Xu et al., 2023). This makes it more likely that, also in our experiment, vascular plant diversity was responding to the within-plot heterogeneity of light. Furthermore, altered mineralization rates and nutrient availability in the soil after the interventions (Kovács et al., 2018; Schwarz et al., 2025) could be another contributing factor to the higher vascular plant diversity in gaps. Since many species-rich groups within Diptera and Hymenoptera rely directly on plants, and Dipteran and Hymenopteran diversity often increase with plant diversity (Scherber et al., 2014; Sobek et al., 2009), it is plausible that higher trophic levels (arthropods) followed the change at the lower trophic level (plants) as a bottom-up diversity effect in gaps (Scherber et al., 2010). Significant positive relationships between plant and insect diversity in our dataset support this theory (Fig. S12). These complex interacting mechanisms are impossible to disentangle within this framework. Nevertheless, our results suggest that small-scale microclimatic heterogeneity could be an important contributing factor to the increased biodiversity often observed in canopy openings (Perlík et al., 2023; Rothacher et al., 2025).

Microclimatic heterogeneity in the tree layer was not associated with biodiversity, likely because we only sampled arthropods close to the ground. However, communities of these groups are often highly vertically stratified in forests (Aikens and Buddle, 2012; Sobek et al., 2009). Therefore, future studies should better match spatial proximity of microclimatic and biodiversity data (Klinges et al., 2024).

4.4. *Implications for forest management*

With canopy gaps providing a highly heterogeneous mosaic of warmer and cooler microhabitats in close proximity at the forest floor, and featuring increased biodiversity of plants, Diptera, and Hymenoptera, our results challenge the paradigm of maximized temperature buffering through management towards dense canopies as the only approach to conserve forest biodiversity during climate change. Our results strongly imply that, under current climatic conditions, several species groups profit from small- to intermediate scale (i.e., not stand-replacing) disturbances of the canopy. However, one has to be careful with extrapolating these findings into future climatic conditions. As droughts and heat spells become more frequent and extreme in Central Europe (Vautard et al., 2023), previously buffered forest microclimates will increasingly be impacted by these extremes (De Frenne et al., 2021), and thermophilization of forest communities could threaten cold-adapted species (Zellweger et al., 2020).

Our results show that with higher structural complexity and canopy cover, vertical microclimatic heterogeneity increased, potentially positively affecting the vertical stratification of arthropod communities (Decker et al., 2025) and providing deep shade and cool microhabitats at the forest floor. This trades off with horizontal microclimatic heterogeneity, which is optimized through the opposite forest structural characteristics. Forest management approaches that provide both dense stands and canopy gaps are most likely to harbor a high diversity of microclimatic habitats in the horizontal and vertical dimension. Such approaches could combine irregular shelterwood systems, group selection and strip cuttings (i.e. harvesting systems that cause small to intermediate canopy gaps) with areas where single-tree selection harvesting disturbs the canopy as little as possible (Aszalós et al., 2022).

4.5. *Conclusions*

In conclusion, our results demonstrate that standardized point measurements only poorly represent the microclimatic variability within forest plots, but forest structure can be used to predict vertical and horizontal microclimatic heterogeneity. Canopy gaps promote high small-scale horizontal heterogeneity of microclimatic conditions, which was associated with increased biodiversity of plants, Diptera, and Hymenoptera. However, under climate change, highly buffered microclimatic habitats might be increasingly threatened, with negative consequences for species adapted to such conditions. We therefore recommend forest management approaches that reconcile horizontal with vertical microclimatic heterogeneity and provide a mosaic of different habitats that enables the co-existence of forest organisms with different microclimatic requirements.

Data and code availability

All data and R scripts are availble at https://doi.org/10.5281/zenodo.19883322.

CRediT authorship contribution statement

Kerstin Pierick: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Dominik Seidel:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization. **Pia Bradler:** Writing – review & editing, Investigation. **Simone Cesarz:** Writing – review & editing, Supervision, Funding acquisition. **Orsi Decker:** Writing – review & editing, Methodology, Investigation. **Benjamin M. Delory:** Writing – review & editing. **Sebastian Dittrich:** Writing – review & editing, Investigation. **Martin Ehbrecht:** Writing – review & editing, Methodology. **Nico Eisenhauer:** Writing – review & editing, Funding acquisition. **Andreas Fichtner:** Writing – review & editing, Supervision, Funding acquisition. **Michael Junginger:** Writing – review & editing, Investigation. **Michael Köhler:** Writing – review & editing, Methodology. **Ludwig Lettenmaier:** Writing – review & editing, Investigation. **Roman M. Link:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Soumen Mallick:** Writing – review & editing, Investigation. **Jörg Müller:** Writing – review & editing, Supervision, Funding acquisition. **Julia Rothacher:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Lena Rugen:** Writing – review & editing, Investigation. **Guido F. Scholz:** Writing – review & editing, Investigation. **Jean-Léonard Stör:** Writing – review & editing, Investigation. **Kim K. Weißing:** Writing – review & editing, Visualization. **Clara Wild:** Writing – review & editing, Investigation. **Goddert von Oheimb:** Writing – review & editing, Supervision, Funding acquisition. **Christian Ammer:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Bernhard Schuldt:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

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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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Appendix A. Supplementary data

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