Effects of canopy gaps on microclimate, soil biological activity and their relationship in a European mixed floodplain forest

Annalena Lenk [a,*], Ronny Richter [a,b], Lena Kretz [a], Christian Wirth [a,b,c]

[a] Systematic Botany and Functional Biodiversity, Leipzig University, Johannisallee 21, 04103 Leipzig, Germany
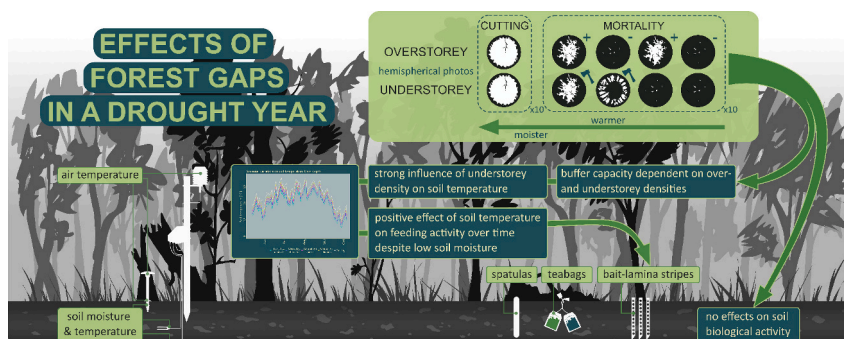[b] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstraße 4, 04103 Leipzig, Germany
[c] Max-Planck Institute for Biogeochemistry, Hans-Knöll-Straße 10, 07745 Jena, Germany

HIGHLIGHTS

- Canopy gaps influence microclimate in a temperate floodplain forest.
- Moderately higher temperature and soil moisture with more open over- and understorey
- Particularly strong influence of understorey density on soil temperature
- Soil biological activity not affected by different canopy openness levels
- Feeding activity increased with increasing soil temperature, despite moisture decline.

GRAPHICAL ABSTRACT

ARTICLE INFO

ABSTRACT

Forest canopy gaps can influence understorey microclimate and ecosystem functions such as decomposition. Gaps can arise from silviculture or tree mortality, increasingly influenced by climate change. However, to what degree canopy gaps affect the buffered microclimate in the understorey under macroclimatic changes is unclear. We, therefore, investigated the effect of forest gaps differing in structure and size (25 gaps: single tree gaps up to 0.67 ha cuttings) on microclimate and soil biological activity compared to closed forest in a European mixed floodplain forest. During the investigation period in the drought year 2022 between May and October, mean soil moisture and temperature as well as soil and air temperature fluctuations increased with increasing openness. In summer, the highest difference of monthly means between cuttings and closed forest in the topsoil was 3.98 ± 9.43 % volumetric moisture and 2.05 ± 0.89 °C temperature, and in the air at 30 cm height 0.61 ± 0.35 °C temperature. For buffering, both the over- and understorey tree layers appeared as relevant with a particularly strong influence of understorey density on soil temperature. Three experiments, investigating soil biological activity by quantifying decomposition rates of tea and wooden spatulas as well as mesofauna feeding activity with bait-lamina stripes, revealed no significant differences between gaps and closed forest. However, we found a positive significant effect of mean soil temperature on feeding activity throughout the season. Although soil moisture decreased during this period, it showed no counteracting effect on feeding activity. Generally, very few significant relationships were observed between microclimate and soil biological activity in single experiments.

Despite the dry growing season, decomposition rates remained high, suggesting temperature had a stronger influence than soil moisture. We conclude that the microclimatic differences within the gap gradient of our experiment were not strong enough to affect soil biological activity considerably.

1. Introduction

Climate change induces altered precipitation and temperature regimes and increases the frequency of climatic extremes (Fischer and Knutti, 2015; Stott, 2016; Zhang et al., 2013) influencing ecosystems worldwide (IPCC, 2022). In forests, macroclimatic changes may be mitigated via the buffering function of the closed canopy (Frey et al., 2016; Lombaerde et al., 2022). At the same time, silvicultural practices and disturbances associated with climate extremes may induce mortality of large trees and thereby disintegrate the canopy by gap formation. As climate change progresses, it is currently unclear whether forests with increasing canopy gaps will still be able to sustain their distinct microclimatic conditions and further ecosystem functions such as nutrient cycling (Davis et al., 2019; Dietz et al., 2020; De Frenne et al., 2021; Zellweger et al., 2020; Bright et al., 2017; Yan Li et al., 2015; Chen et al., 1999; Dominguez-Eusebio et al., 2021). Therefore, we investigate forest areas with different small-scale gap structures in the over- and understorey and their effect on microclimate as well as on soil biological activity over the vegetation period in the hot and dry year 2022 in a Central European floodplain forest.

The causes, sizes and structures of forest gaps are diverse. They can be generated by silvicultural activities, such as various thinning practices, shelterwood cutting, sanitation cutting and selective harvesting or dedicated forest conservation management with thinning for promoting stand structural complexity or particular tree species compositions (Duguid and Ashton, 2013; Li et al., 2020). As a consequence of climate change, there are worldwide also increasingly more gaps caused by tree mortality due to impacts such as droughts, storms, fires or infestations (Adams et al., 2009; Allen et al., 2010; Senf et al., 2021). In the years 2018–2020 we witnessed the most extreme drought period in Central Europe in terms of intensity and extent since climatic records began in 1766 (Rakovec et al., 2022) leading to severe canopy cover losses in forests (Thonfeld et al., 2022). In 2022, Europe again experienced a vegetation period with an above-average drought (Faranda et al., 2023; Rodrigues et al., 2022; Živaljević et al., 2023) and growing evidence predicts that climate change will increase the frequency and intensity of forest disturbance causing tree mortality in future years (Allen et al., 2010; Rakovec et al., 2022; Senf and Seidl, 2021).

The resulting reduction in tree canopy cover can lead to a loss of the buffering function altering the microclimate below the canopy and on the forest floor (Alkama and Cescatti, 2016; Lembrechts and Nijs, 2020; Zellweger et al., 2020). Under a closed undisturbed tree canopy, organisms experience a distinct microclimate: less direct sunlight and wind, leading to moderated temperature and moisture fluctuations compared to open areas (Arx et al., 2013; Aussenac, 2000; Didham and Lawton, 1999; De De Frenne et al., 2021). Effects of canopy gaps on microclimate, however, appear to be highly dependent on their spatial extent. The larger the canopy gaps the higher increases in soil and air temperature were observed (Abd Latif and Blackburn, 2010). In large forest gaps higher wind speed and radiation lead to increased evaporation and risk of drought (Londo et al., 1999). In smaller gaps, in contrast, soil moisture can even be increased compared to closed forests (Abd Latif and Blackburn, 2010; Kovács et al., 2020; Ritter et al., 2005). This can be attributed to reduced interception losses of precipitation and reduced transpiration of large trees, which normally exceeds evaporation from the exposed soil (Bauhus and Bartsch, 1995; Zhu et al., 2003; Zirlewagen and von Wilpert, 2001). While the impact of gap size on microclimate is well described, the exploration of how the structuring, encompassing density variations in both the over- and understorey, influences microclimate remains largely uncharted. However, it is plausible that the tree mortality in specific layers or the density of the regrowing understorey tree layer after a disturbance may significantly affect microclimatic dynamics (Meyer et al., 2022).

Not only can a sudden change in microclimate impact organisms adapted to a buffered forest microclimate (Hannah et al., 2014; McLaughlin et al., 2017) but also several ecosystem functions carried out by them (Arx et al., 2013). This is, for example, the case for decomposition which plays a key role in carbon sequestration and nutrient cycling in forest ecosystems (Chen et al., 1999; Dominguez-Eusebio et al., 2021; Royer et al., 2011). Climatic factors can directly influence the activity and biomass as well as species composition of soil microorganisms and invertebrate detrivores (Chen et al., 1999; Butenschoen et al., 2011; Petraglia et al., 2019; Prescott et al., 2003). These ectothermic organisms are in general expected to be more active under warmer conditions (Gillooly et al., 2001). However, this can be counteracted by thermal acclimatization and reduced soil water availability due to increased evapotranspiration and less precipitation in warmer summers (Crowther and Bradford, 2013; Bradford, 2013; Allison and Treseder, 2008). Overall, effects of microclimate on ecosystem functions, especially under climate change, are still widely unknown. Nevertheless, the high ecological relevance is clear and data are needed for more accurate predictions and targeted climate-sensitive and ecological forest management (Arx et al., 2013; De Frenne et al., 2021).

In this study, we investigate the effect of silvicultural and tree mortality-induced canopy openings on microclimate and soil biological activity as well as their relationship in a hardwood floodplain forest in Central Europe (Leipzig, Germany). The examined forest experiences massive alterations of its stand structure through forest management as well as pathogen-induced tree mortality intensified by the recent climate extremes. We exploit an established experiment, which provides a gradient of forest cover from heavily mortality-affected forest stands (*mortality+*) and only slightly disturbed forest stands (*mortality-*) each with and without understorey thinning. Additionally, small to intermediate (0.25–0.67 ha) silvicultural cuts (*femel cuttings*) are included in the experiment. Since soil conditions can also respond to forestry interventions (Latterini et al., 2023), which can affect soil biological activity, we control for bulk density, carbon-to-nitrogen ratio and pH of the soil in our study.

We ask what the influence is of mortality-caused and silvicultural-caused canopy gaps on microclimate and soil biological activity, and if this is additionally influenced by understorey thinning management practices.

We expect (a) *femel cuttings* to show larger temperature ranges and an increase in mean soil and air temperature, as well as a higher soil moisture content compared to plots in *mortality-* forest. Therefore, we expect the highest soil biological activity on *femel cuttings*. Microclimatic conditions and soil biological activity in *mortality+* forest stands are hypothesised to be intermediate between those of *femel cuttings* and *mortality-* forest. We further expect (b) that subplots with additional understorey thinning (treated subplots) show larger temperature ranges with warmer and also wetter conditions on average, and therefore higher soil biological activity than untreated subplots. However, we expect that the difference between untreated subplots and treated subplots is smaller than the difference between untreated subplots and *femel cuttings*. Finally, we ask what the relationship is between soil microclimate and soil biological activity at the study site. We expect (c) higher mean soil temperature and moisture as well as lower soil moisture fluctuation to be positively correlated with soil biological activity.

2. Material and methods

2.1. Study site

The study was conducted in a Central European floodplain forest in Leipzig, Germany. The forest is located in the transition zone between maritime and continental climates described by warm summers with an annual average temperature of 9.8 °C and an annual precipitation sum of 523 mm (DWD, station Leipzig/Halle, 1983–2023). The area stretches between the main rivers Weiße Elster, Pleiße and Parthe from the south to the northwest of Leipzig (Fig. 1). It contains four nature reserves and is also largely designated as a Special Protection Area EG Birds Directive, Natura 2000 FFH area and landscape conservation area. The floodplain forest grows on a loamy fertile vega, which is mainly the result of soil erosion following historical deforestation (Härdtle et al., 2020). Historically, regular spring floods created a hardwood floodplain forest (*Ficario-Ulmetum* KNAPP ex MEDWECKA-KORNAŚ) with the main tree species pedunculate oak (*Quercus robur* L.), common ash (*Fraxinus excelsior* L.), field elm (*Ulmus minor* ALL.), fluttering elm (*U. laevis* PALL) and Scots elm (*U. glabra* HUDS.; Härdtle et al., 2020). However, enhanced settlement, diking, and straightening of the rivers caused a loss of flooding dynamics and a lowering of the groundwater level (Haase and Gläser, 2009). The lack of a regular flooding regime promoted flood-intolerant species such as sycamore (*Acer pseudoplatanus* L.) and Norway maple (*Acer platanoides* L.) which currently account for the majority of the total regeneration (tree species composition on research plots Table S1; Scholz et al., 2022; Wirth et al., 2021). Without regular disturbance, this leads to darkening of the forest understorey, making it difficult for light-demanding tree species such as pedunculate oak to regenerate. This is a process that can be observed in many floodplain forests in Europe in the last decades (Härdtle et al., 2020). To increase the abundance of light-demanding species, so-called *femel cuttings*, small clear-cuts with a few individual remaining biotope trees, are established (Sickert, 2011). Oaks are sown or planted in these areas, protected from game browsing with a fence and competing vegetation is removed two to three times per season in the first years. The selected *femel cuttings* were between three and six years old when we established our experiment. Planted oaks were not higher than 2.5 m. Furthermore, the extremely dry years of 2018–2020 exacerbated mortality due to calamities, especially in ash (ash shoot dieback, bark beetles) and maple species (sooty bark disease), which prior to the drought jointly accounted for about 60 % of the trees in the upper stand (Wirth et al., 2021). Inventories in the Leipzig floodplain forest have not detected any healthy mature ash trees since 2020 (Wirth et al., 2021). Additionally, the elm species have been heavily affected by Dutch elm dieback since the mid-20th century. This prevents establishment in the upper canopy despite their shade tolerance and intensive vegetative regeneration (Martín et al., 2019; Niinemets and Valladares, 2006). An exception is the fluttering elm (*Ulmus laevis* PALL.), which shows a certain resistance (Mackenthun, 2004).

2.2. Experimental design

We selected five research plots of 0.25 ha both in forest stands with mostly healthy overstorey (*mortality-*) and forest stands severely disturbed by ash shoot dieback and sooty bark disease (*mortality+*, Fig. 1). All forest plots, evenly distributed across the northern and southern floodplain, consist of four 25 × 25 m quadrants, each with an 8 × 8 m subplot. In addition to the different levels of canopy openness,
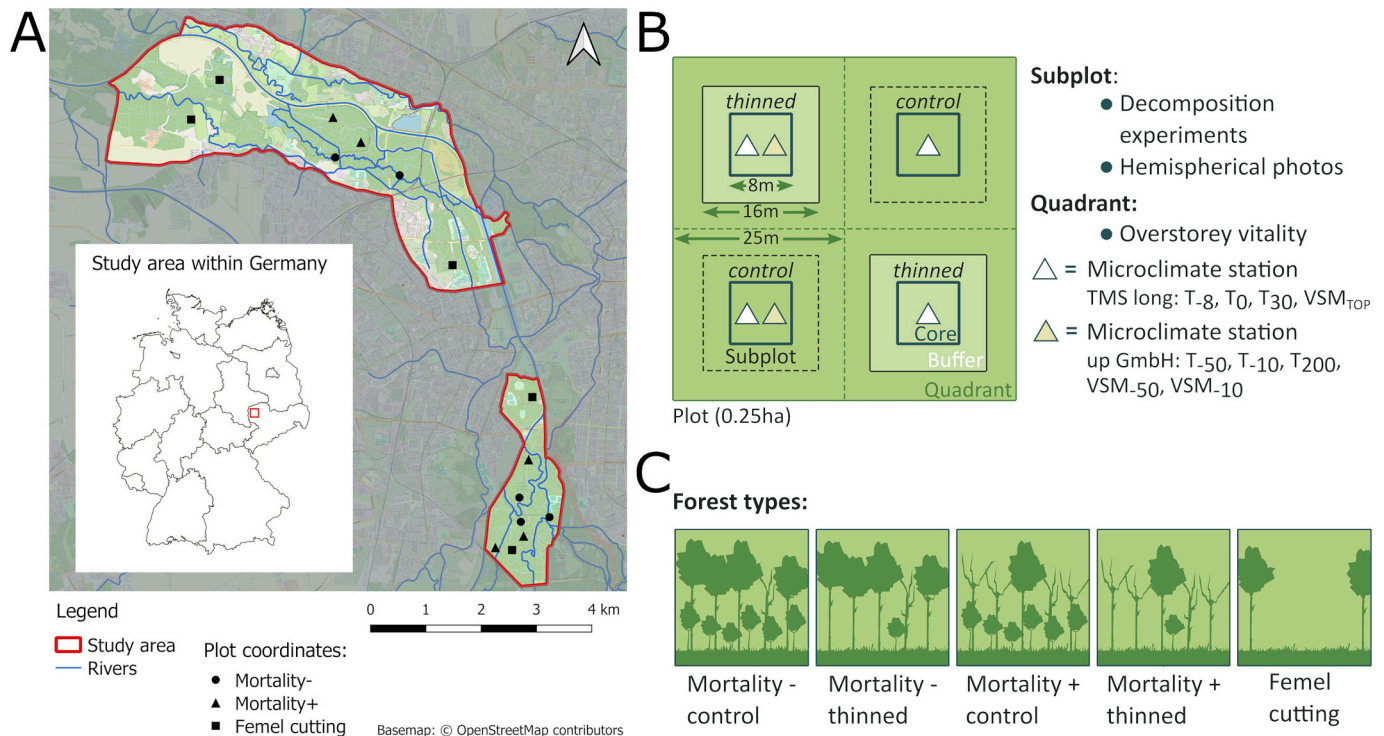
Fig. 1. Map and experimental design. (A) Map of the study area in the Leipzig floodplain forest with 15 research plots, five plots each in the forest with high mortality in the overstorey (*mortality+*), low mortality in the overstorey (*mortality−*) and on *femel cuttings*. (B) Each forest plot, 0,25 ha in size, comprises four 25 × 25 m quadrants, with an 8 × 8 m subplot. On and around the *thinned* subplots 16 × 16 m, the regeneration of sycamore, Norway maple and elder was cut in winter 2022. *Control* subplots stayed untreated. The plots on *femel cuttings* range from 0.25 to 0.67 ha in size, each containing two subplots, without an untreated *control*. On all subplots, a climate station (TOMST, Czech Republic) measuring temperature at 8 cm depth, at the soil surface and at 30 cm height, as well as soil moisture in the topsoil, was installed. On half of the subplots, an additional microclimate station (UP GmbH, Germany) measured soil temperature and moisture at 50 cm and 10 cm depth and air temperature at 200 cm height. Per subplot, decomposition experiments were carried out with each five wooden spatulas, tea bags and bait-lamina stripes- and hemispherical photos to estimate openness were taken at 0.9 m and 5 m height. (C) This design results in five categories, referred to as forest types: *mortality− control, mortality− thinned, mortality+ control, mortality+ thinned* and *femel cuttings*.

represented by the forest vitality status (*mortality−/mortality+*), we applied a treatment mimicking a management approach aimed at favoring the regeneration of light-demanding tree species. To this end, we removed small trees (diameter at breast height < 20 cm) of the flooding-intolerant tree species sycamore, Norway maple and elder on and around every second subplot on an area of 16 × 16 m leaving the cut wood on site (treatment: *thinned*). The two other subplots were established as untreated control (treatment: *control*). Furthermore, we established five research plots on *femel cuttings* of 0.25–0.67 ha in size, each with two quadrants and subplots, as there is no untreated control. This design results in five categories, which are referred to in the following as forest types: *mortality- thinned, mortality- control, mortality+ thinned, mortality+ control, femel cuttings*.

To account for plot variability in canopy density within forest types we measured openness at a height of 0.9 m and 5 m with hemispherical photos (Nikon Coolpix P5100 with fisheye converter Nikon FC-E20, Japan) on the subplot level. The images of the whole hemisphere were analysed with the software *WinSCANOPY* Pro *2009a* (Regent Instruments Inc., Canada). To calculate openness, each pixel was classified as open sky or canopy based on their RGB-values. Additionally, we recorded tree species composition based on the proportion of basal area covered by each species on all plots and estimated the vitality as the percentage of dead and dying trees in the overstorey (diameter at breast height > 20 cm) per quadrant.

On the total of 50 subplots (*mortality+* and *mortality-* with 5 replicates each with 4 subplots = 40 subplots, *femel cuttings* with 5 replicates each with 2 subplots = 10 subplots), we measured temperature and moisture from 50 cm depth up to 200 cm height, conducted decomposition experiments and analysed the soil abiotic parameters pH, carbon-to-nitrogen ratio (C/N) and bulk density.

2.3. Microclimate

A climate 'TMS Long' logger (TOMST, Czech Republic) was installed in the center of all subplots in May 2022. Temperature measurements were taken at 8 cm depth (T_{-8}), the soil surface (T_0), and 30 cm height (T_{30}), as well as moisture in the top 15 cm of the soil (VSM_{TOP}; Wild et al., 2019). The resulting raw soil moisture data (measured with the time-domain-transmission technique) was converted to volumetric soil water content (%), describing the volume of water (cm^3) per unit volume of soil (cm^3). This was done using the universal calibration equation for mineral soils (Kopecký et al., 2021), which is implemented in the R package *myClim* (Man et al., 2023). To further check whether results are also valid for different depths and heights we used per treatment on half of the subplots one additional microclimate station (UP GmbH, Germany) with YDOC data loggers (ML-417DS, YDOC, Netherlands) to measure soil moisture and temperature in 10 cm and 50 cm depth (VSM_{-10} and VSM_{-50}, WET 150, Delta-T Devices, UK) as well as air temperature at 200 cm height (T_{200}, BSHT05, TEKBOX, Vietnam). The WET 150 soil sensors convert a time-domain reflectometry signal via the implemented calibration equation for mineral soil (White et al., 1994) into volumetric water content.

All installed climate loggers measured in 15-min intervals (coordinated universal time) and were protected against irradiance with white plastic shields.

Data gaps (4.7 % of the data) which resulted from damaged climate loggers or technical defects were filled calculating an imputation PCA provided by the packages 'FactorMineR' (Lê et al., 2008) and 'missMDA' (Josse and Husson, 2016) using all measured microclimatic parameters. At the beginning of the measurement period, some YDOC loggers repeatedly stopped recording for a few hours due to an incorrect setting. For these cases, we smoothed the offsets between measured and imputed values introduced by imputation with a linear baseline correction, i.e. adjusting the trend of the imputed values to fit the measured data at both margins of the filled gaps.

2.4. Soil biological activity

Three different methods were employed to quantify soil biological activity (Fig. 2).

(1) Wooden spatulas: To estimate microbial wood degradation, we placed five wooden spatulas (NOBAMED Paul Danz AG, Germany; *Betula spec.*), 150 × 18 mm in size, evenly distributed per subplot in the soil for six months from 19/04/2022 to 24/10/2022. The spatulas were inserted vertically into the soil so that the top first centimeter remained above the surface. The spatulas were weighed beforehand in dry condition with an analytic balance, accurate to 0.01 g. After 6 months of exposure, they were carefully recollected with spades or soil corers, dried, cleaned and weighed again. Since the wooden spatulas sometimes broke during exposition or recovery and not all parts could always be found. Missing areas, most often below 10 % and always below 25 % of the complete area, were measured manually with millimeter accuracy and the calculated proportional weights of these areas were subtracted from the original weight (Gottschall et al., 2019). The percentage mass loss was calculated from the start and end weight of spatulas and averaged per subplot. Not all buried spatulas could be found at the end of the experiment, so that finally 65 % were used for the analysis. (2) Tea bags: To quantify microbial plant litter decomposition we followed the standardised method from Keuskamp et al. (2013) using fast decomposable green (*Camellia sinensis* (L.) KUNTZE) and slow decomposable rooibos (*Aspalathus linearis* (BURM.F.) R.DAHLGREN) tea in non-woven nylon bags that allow only microorganisms and fine roots to enter. For three months from 19/04/2022 to 15/07/2022, five green tea bags (Lipton, EAN: 8722700 05552 5) and five rooibos tea bags (Lipton, EAN: 8711327 5143 48) were buried in 8 cm depth evenly distributed per subplot. Previously, the dry weight per bag was determined with an analytic balance accurate to 0.01 g without string and label, subtracting an average bag weight (0.23 g). After exposure, the bags were buried out again, cleaned from adhered soil particles, dried and the tea was weighed again. The percentage mass loss was calculated from the start and end weight of the tea bags and averaged per subplot. Some of the tea bags were dug out by animals before the end of the experiment. However, 92 % of the tea bags of both tea types could finally be analysed. (3) Bait-lamina stripes: We used the bait-lamina test (Terra Protecta GmbH, Germany) to estimate mesofauna feeding activity (Kratz, 1998). The plastic stripes, 160 × 1 × 5 mm in size, have 16 holes of 15 mm diameter each with a spacing of 5 mm in between. The holes were provided by the
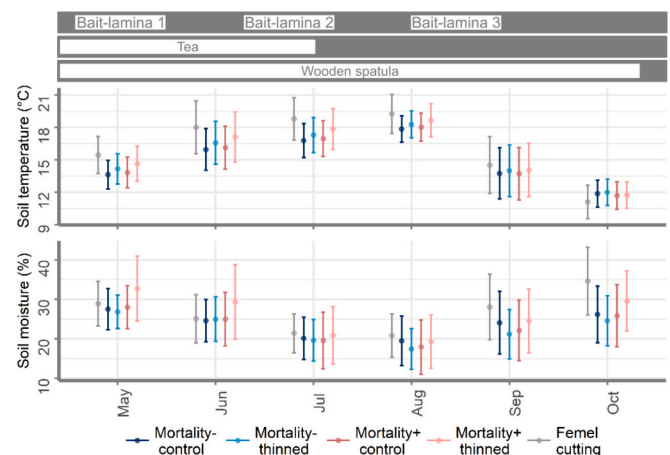
Fig. 2. Overview of the experimental periods and mean values with standard deviation of the temperature at 8 cm depth and the volumetric soil moisture of the topsoil (0–15 cm) per month and forest type. Wooden spatula experiment: 19/04/2022–24/10/2022, Tea bag experiment: 19/04/2022–15/07/2022, First bait-lamina campaign: 09/05/2022–31/05/2022, Second bait-lamina campaign: 27/06/2022–19/07/2022, Third bait-lamina campaign: 15/08/2022–06/09/2022.

company with a mixture of cellulose, wheat bran and activated carbon with a 70:27:3 ratio. Experimental studies reported, that this bait substrate is mainly consumed by mites, collembolans, enchytraeids, millipedes, and earthworms, whereas microbial degradation is of little relevance (Hamel et al., 2007). In three campaigns between May and September (09/05/2022–31/05/2022, 27/06/2022–19/07/2022, 15/08/2022–06/09/2022), five bait-lamina stripes were buried evenly distributed per subplot for three weeks each perpendicular to the soil surface with the top hole 1 cm below the surface and 6 cm without holes remaining above the surface. Exposure duration was determined by a pre-experiment until approximately half of the bait substrate was perforated. At the end of the experimental periods, the stripes were pulled out of the soil and the perforation was rated per hole as 100 % (completely perforated), 66.6 % (more than half perforated), 33.3 % (less than half perforated) and 0 % (not perforated). Mean percent feeding activity was calculated per stripe and per subplot. A few stripes were lost during the experiments. In the first campaign 86 %, in the second campaign 93 % and in the last campaign 96 % could finally be analysed.

2.5. Bulk density, pH, C/N

We took three soil samples per subplot in the centre, the northeast and the southwest corner with a stabbing cylinder (100 cm^2) after removing the top 10 cm soil layer and pooled these samples into one composite sample per subplot. If the sampling position was blocked by tree trunks, it was shifted towards the northwest or southeast corner. Care was taken to ensure that there were no larger roots than 2 mm in diameter or stones in the samples. The samples were dried at 40 °C for 3 weeks until the weight was stable. The dry samples were weighed again to determine the bulk density (g * cm^{-3}) as the ratio of dry weight and volume of the soil sample. Subsequently, the samples were sieved with a mesh size of 2 mm. We used 10 g of each soil sample to measure the pH value in 25 ml of 0.01 M CaCl$_2$ solution. The mixture was shaken for 6 min, left for 30 min and shaken again for 6 min. After the samples were left to rest for 1.5 h, the pH value was measured in the fluid fraction using a pH-meter testo 205 (testo GmbH, Germany). To quantify the carbon and nitrogen content another 0.5 g per soil sample was analysed with an elemental analyser (Elementar Vario EL III, Elementar, Germany).

2.6. Data analysis

All data analyses were performed with the software R version 4.2.2 (R Core Team, 2022). For the microclimatic data description and analysis, we used the daily means and ranges per logger of soil and air temperatures (T) as well as volumetric soil moisture (VSM) over the 24-h periods. The calculated relative differences between forest types (*mortality- thinned, mortality- control, mortality+ thinned, mortality+ control, femel cuttings*) are marked with the prefix "d" (dT, dVSM). To obtain representative values for the microclimatic differences between open areas and closed forest during summer, we calculated the highest difference of monthly means between *femel cuttings* and *mortality- control* and the standard deviation via error propagation based on the standard deviation per forest type of the subplot means of the respective month (Tables S2 and S3).

To analyse the effect of forest types on soil microclimate and soil biological activity we ran linear mixed-effect ANOVAs using the package 'lme4' (Bates et al., 2015). The day-based microclimate values and the pooled samples of the soil experiments per subplot were averaged for all models over the respective experimental period (Fig. 2) per subplot. This results in ten data points per model per forest type. Plot ID was set as random factor nested in block to account for the experimental design of placing multiple subplots per plot distributed into northern and southern forest areas (Fig. 1). Model assumptions were tested visually. If the ANOVA result was significant, a pairwise comparison was performed

using the *post-hoc* test Tukey HSD with the package 'emmeans' (Lenth, 2022). The applied significance levels are: $p > 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*). We did not control for the size of the *femel cuttings*, as we found no significant correlations between size and temperature or moisture (Fig. S1). To analyse the concrete effect of over- and understorey tree layers in the forest on microclimate, we additionally calculated linear mixed-effects models as described above with forest vitality status (*mortality-, mortality+*) and treatment (*thinned, control*) as separate categorical predictors including their interaction. For generalizing beyond the categories of our experiment, we repeated the same in an additional model with the continuous predictors openness at 5 m and 0.9 m height.

To estimate the main drivers of soil biological activity we used multiple linear mixed-effects models with the decomposed fraction of wooden spatulas, green or rooibos tea as well as the feeding activity of the bait-lamina campaigns as dependent variables and mean soil temperature and moisture as well as their ranges as independent variables. As further independent abiotic moderator variables, bulk density, pH and C/N were considered. Since pH and C/N can influence decomposition processes, but in turn are also dependent on decomposition processes, we decided to include them in the model only if there is a significant difference concerning the geographic distributions between northern and southern floodplain of our research plots. We tested the influence of the geographic location with a linear mixed-effects ANOVA as described above. For all models plot ID nested in block was introduced as random factor as explained earlier. The variables were scaled and model assumptions were visually proved. The fixed effects were tested by *t*-tests using the Satterwhaite method, the random effects by restricted likelihood ratio tests as implemented in the package 'lmerTest' (Kuznetsova et al., 2017). To show the relative influence of fixed and random effects (Nakagawa and Schielzeth, 2013), conditional and marginal R^2 were calculated per model with the package 'MuMIn' (Barton, 2022).

In order to examine the bivariate correlations of the individual environmental variables, we performed a Pearson correlation matrix for the longest experimental period with the package 'corrplot' (Wei and Simko, 2021).

3. Results

3.1. Effects of forest structure on microclimate

Forest structure strongly influenced understorey temperature but had only a minor impact on soil moisture. On average, more open sites were warmer and at the same time slightly moister.

Over the experimental period of the wooden spatula experiment (13/05/22–24/10/22) *femel cuttings* showed significantly warmer mean temperatures at 8 and 10 cm depth (dT = 0.83–1.36 °C) compared to *mortality- thinned* and *control* as well as *mortality+ control* plots (Fig. 3, Table S4). The conditions on *mortality+ thinned* were intermediate between *femel cuttings* and the other forest types, at 8 cm depth being significantly warmer than on *mortality+ control* (dT = 0.63 °C, Fig. 3). At 50 cm depth, *femel cuttings* were significantly warmer (dT = 0.55–1.06 °C) than all other forest types. The temperature ranges were significantly larger on *femel cuttings* in the topsoil (dT = 0.82–2.06 °C) and in the air at 30 and 200 cm (dT = 3.09–9.18 °C) compared to all other forest types.

The understorey thinning treatment was a significant predictor when analysing the effect of the over- and understorey on mean soil temperature in the forest without *femel cuttings* (Tables 1, S5). The vitality status showed no significant effect on soil temperature. When modelling the effects of the continuous variables, openness at 0.5 m and 0.9 m height, a similar result was obtained, namely that the openness of the understorey had a stronger influence on the soil temperature than the overstorey. This effect was not visible anymore for soil temperature at 50 cm depth (Table S5). The interaction between the openness at 0.5 m and 0.9 m
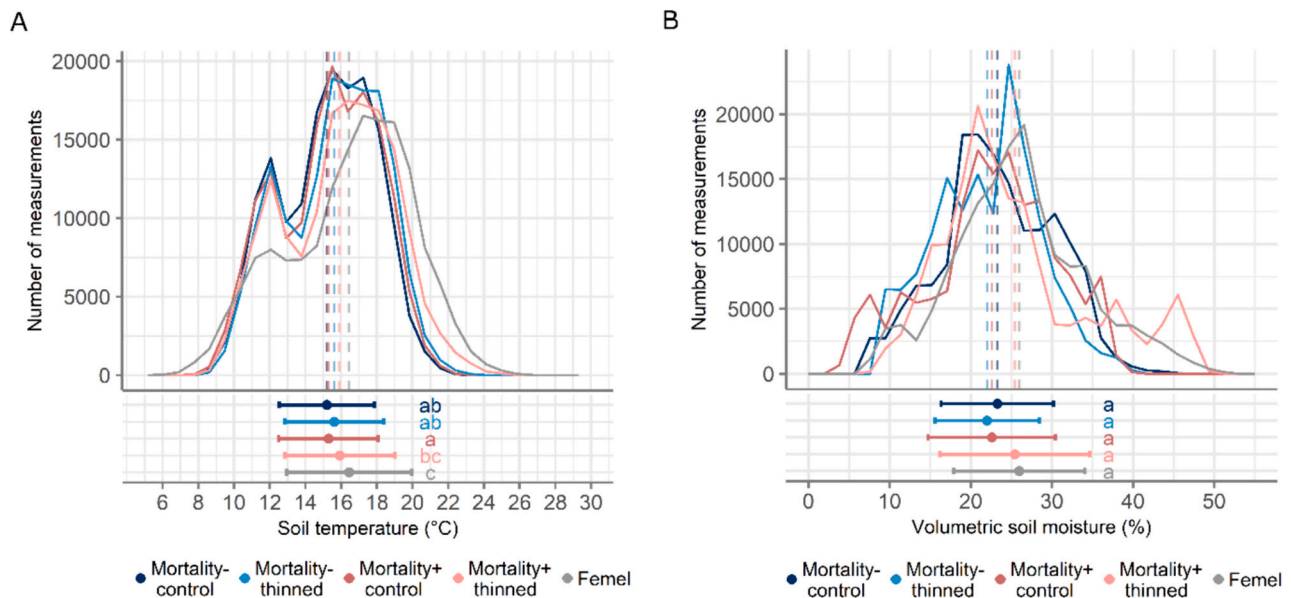
Fig. 3. Density plots of topsoil microclimate per forest type with mean and standard deviation during the wooden spatula experiment between 13/05/2022 and 24/10/2022. The letters indicate significant differences from pairwise multiple comparisons of the daily mean values per subplot between forest types. (A) Soil temperature at 8 cm depth, daily mean values (F = 11.27, $p < 0.001$) and ranges (F = 7.56, $p < 0.01$) averaged per subplot during the experimental period were significantly different between forest types (data for ranges not shown). The ranges of soil temperature were significantly higher on *femel cuttings* compared to *mortality− control*, *mortality− thinned* and *mortality+ control*. (B) Volumetric soil moisture in the topsoil (0–15 cm), mean values (F = 0.83, $p = 0.51$) were not, averaged daily ranges (F = 6.93, $p < 0.001$) were significantly different between forest types (data for ranges not shown). The ranges of soil moisture were significantly higher on *femel cuttings* compared to all other forest types.

showed a significant effect on the soil temperature range (Table 1, Fig. S2). In the air at 30 and 200 cm height, the temperature ranges were more strongly influenced by over- and understorey openness than the mean values (Table S5, Fig. S2).

On the day with the highest maximum temperature measured in the topsoil (19/06/2022, $T_{-8} = 26.56$ °C on a *femel cutting*), the difference between the average temperature maxima between *femel cuttings* (23.38 °C) and *mortality- control* (18.7 °C) was 4.68 °C. On the coolest plot on this day, the maximum topsoil temperature was 18 °C. Regarding the average diurnal variation between May and the end of October, *femel cuttings* showed the highest soil temperatures and the largest variations in all depths throughout the day, followed by *mortality+ thinned* (Fig. S3). Compared to the other forest types, the amplitude of the air temperatures in all heights on an average day on the *femel cuttings* displayed a higher maximum and lower minimum (Fig. S4). The seasonal pattern with warmer temperatures on more open sites was reversed in October when temperatures were coldest on these sites (Figs. 2, S5 and S6, Table S2).

Over the experimental period of the wooden spatula experiment in all depth layers, mean soil moisture was highest on *femel cuttings* followed by *mortality+ thinned* (Fig. 3, Table S4). Differences in soil moisture between forest types were not significant in the topsoil. However, at a depth of 10 cm, soil moisture was significantly higher on *femel cuttings* compared to *mortality- thinned* (dVSM = 12.11 %), and at 50 cm compared to *mortality- control* (dVSM = 9.84 %). The range of topsoil moisture was significantly higher on *femel cuttings* compared to the other forest types soil (dVSM = 0.77–0.97 %), but not so in deeper soil layers (Table S4).

We found no significant effect of over- and understorey openness in the forest on soil moisture, except for the interaction between openness at 0.5 m and 0.9 m, which showed a significant influence on the range of topsoil moisture during the period of the wooden spatula experiment (Tables 1, S5).

On the day with the lowest minimum in the topsoil (18/08/2022, $VSM_{TOP} = 3.69$ % on a plot of *mortality+ control*), the difference to the plot with the highest minimum on this day (plot of *mortality + thinned*,

$VSM_{TOP} = 32.6$ %) was 22.7 %. The highest differences on this day between averaged minima per forest type were between *femel cuttings* (17.73 %) and *mortality- thinned* (15.66 %) with 2.07 %.

Results for the other experimental periods on the microclimatic differences between the forest types (Figs. S3–S6) and the influence of over- and understorey on temperature and moisture of the topsoil (Tables S6–S9) are shown in the supplement. Similar findings were observed for deeper soil layers, but are not included. Monthly averages and ranges per forest type of all microclimatic parameters measured are provided in Tables S2 and S3. The size of the *femel cuttings* showed no significant effect on topsoil moisture, the temperature at 8 cm depth and the temperature at 30 cm height (Fig. S1).

3.2. Abiotic control variables

The pH values differed significantly between the northern and southern floodplain (F = 7.39, $p < 0.05$) with higher pH in the south $(\overline{pH}_{south} = 4.34 \pm 0.3, \overline{pH}_{north} = 3.94 \pm 0.45)$. The C/N ratio (F = 0.21, $p = 0.66$) showed no significant differences concerning the geographical distribution. An overview of the mean values per plot and treatment of openness, overstorey vitality, pH, C/N, bulk density, soil temperature and moisture is provided in Table S10. Among all bivariate Pearson correlations of abiotic parameters based on the longest experimental period from 13/05/2022 to 24/10/2022, significant positive correlations were found between and among microclimate, hemispherical openness, pH and bulk density (Fig. S12). Significant negative correlations occurred only between C/N and openness, microclimate as well as pH.

3.3. Differences in soil biological activity between forest types

Despite the differences in microclimate, no significant differences were found between forest types in the mean values of the decomposed fraction of wooden spatulas, green tea and the feeding activities during all three bait-lamina campaigns (Fig. 4). Only for rooibos tea, the result of the ANOVA was significant, but not in post-hoc pairwise comparison

Table 1
Effects of over- and understorey openness on microclimate.

	Estimates ± SE	t	*p*		Estimates ± SE	t	*p*
T-8 mean ; R²c = 0.43 ; R²m = 0.35				**T-8 mean; R²c = 0.58; R²m = 0.47**			
(Intercept)	-0.792 ± 0.209	-3.78	**	(Intercept)	0.638 ± 0.219	2.95	**
Status_Mortality+	0.135 ± 0.296	0.46	0.65	Openness_5m	-0.774 ± 0.515	-1.5	0.14
Treatment_thinned	0.661 ± 0.264	2.52	*	Openness_0.9m	1.712 ± 0.623	2.75	**
Status:Treatment	0.358 ± 0.371	0.96	0.34	Openness5m:0.9m	-1.975 ± 1.114	-1.77	0.09
T-8 range; R²c = 0.33 ; R²m = 0.19				**T-8 range; R²c = 0.44; R²m = 0.23**			
(Intercept)	-0.591 ± 0.212	-2.79	*	(Intercept)	0.169 ± 0.23	0.73	0.48
Status_Mortality+	0.175 ± 0.299	0.59	0.57	Openness_5m	-0.727 ± 0.532	-1.37	0.18
Treatment_thinned	0.163 ± 0.252	0.64	0.53	Openness_0.9m	0.466 ± 0.635	0.73	0.47
Status:Treatment	0.443 ± 0.357	1.24	0.23	Openness5m:0.9m	-2.345 ± 1.133	-2.07	*
VSM_TOP mean; R²m = 0.04				**VSM_TOP mean; R²m = 0.12**			
(Intercept)	-0.095 ± 0.33	-0.29	0.77	(Intercept)	0.621 ± 0.377	1.65	0.11
Status_Mortality+	-0.115 ± 0.466	-0.25	0.81	Openness_5m	1.352 ± 0.894	1.51	0.14
Treatment_thinned	-0.211 ± 0.466	-0.45	0.65	Openness_0.9m	1.31 ± 1.14	1.15	0.26
Status:Treatment	0.682 ± 0.659	1.04	0.31	Openness5m:0.9m	2.096 ± 2.054	1.02	0.31
VSM_TOP range; R²c = 0.11 ; R²m = 0.06				**VSM_TOP range; R²c = 0.17 ; R²m = 0.11**			
(Intercept)	-0.171 ± 0.188	-0.91	0.4	(Intercept)	-0.292 ± 0.219	-1.33	0.23
Status_Mortality+	-0.283 ± 0.239	-1.19	0.24	Openness_5m	-0.257 ± 0.47	-0.55	0.59
Treatment_thinned	-0.222 ± 0.237	-0.94	0.36	Openness_0.9m	-0.975 ± 0.591	-1.65	0.11
Status:Treatment	0.534 ± 0.336	1.59	0.12	Openness5m:0.9m	-2.259 ± 1.058	-2.14	*

Notes: In the models, the mean values and mean daily ranges (daily maximum - daily minimum) of soil temperature at 8 cm depth (T_{-8}) and moisture of the topsoil (0–15 cm; VSM_{TOP}) per subplot, averaged over the wooden spatula experiment (13/05/2022–24/10/2022), were calculated as dependent variables. On the left-hand side, the categorical variables forest vitality status (*mortality+*, *mortality-*) and treatment (*thinned*, *control*) as well as their interaction term were used as independent variables. The same models were repeated on the right-hand side with the z-transformed continuous variables openness at 0.9 m and 5 m height including their interaction term as independent variables. For all models plot identity nested in block was included as random factor. The conditional (R^2c) and marginal (R^2m) R squares are provided per model. If the variance of the random effect was estimated as zero, only the marginal R^2 is given. Estimates with standard error (SE), the results of the *t*-test and the *p*-values respectively the significance levels displayed by asterisks are shown.

between the forest types. We repeated the analysis for wooden spatulas, excluding those that were broken, yet observed no significant alteration in the outcome. The mean values of decomposition rates and feeding activities per plot and treatment are displayed in Table S11.

3.4. Predictors of soil biological activity

Soil microclimatic parameters barely mattered as predictors of decomposition rates or feeding activities, except for rooibos tea and when pooling all bait-lamina campaigns over the season (Figs. 5, 2, Table S12). In the joint model of all three bait-lamina campaigns feeding activity was significantly positively correlated to the mean soil temperature. For wooden spatula decomposition, the second and the third bait-lamina campaign no fixed effect was significant. Green tea decomposition showed a significantly negative relationship to pH and rooibos tea decomposition a significantly positive relationship to the range of soil moisture. The feeding activity of bait-lamina stripes in the first campaign was significantly positively correlated with pH. All

bivariate correlations of the respective models are displayed in the Figs. S13–S19.

4. Discussion

In this study, we aimed to investigate the effect of canopy structure on microclimate and soil biological activity including their relationship. We found that with increasing openness, especially in the understorey, the average microclimatic conditions during the growing season became significantly warmer and moderately moister. However, neither the degree of canopy openness nor the resulting microclimatic changes were found to have a strong effect on soil biological activity, which expressed normal rates despite the extremely dry summer.

4.1. Effects of forest structure

4.1.1. Temperature

As expected, we could demonstrate canopy gap effects on the
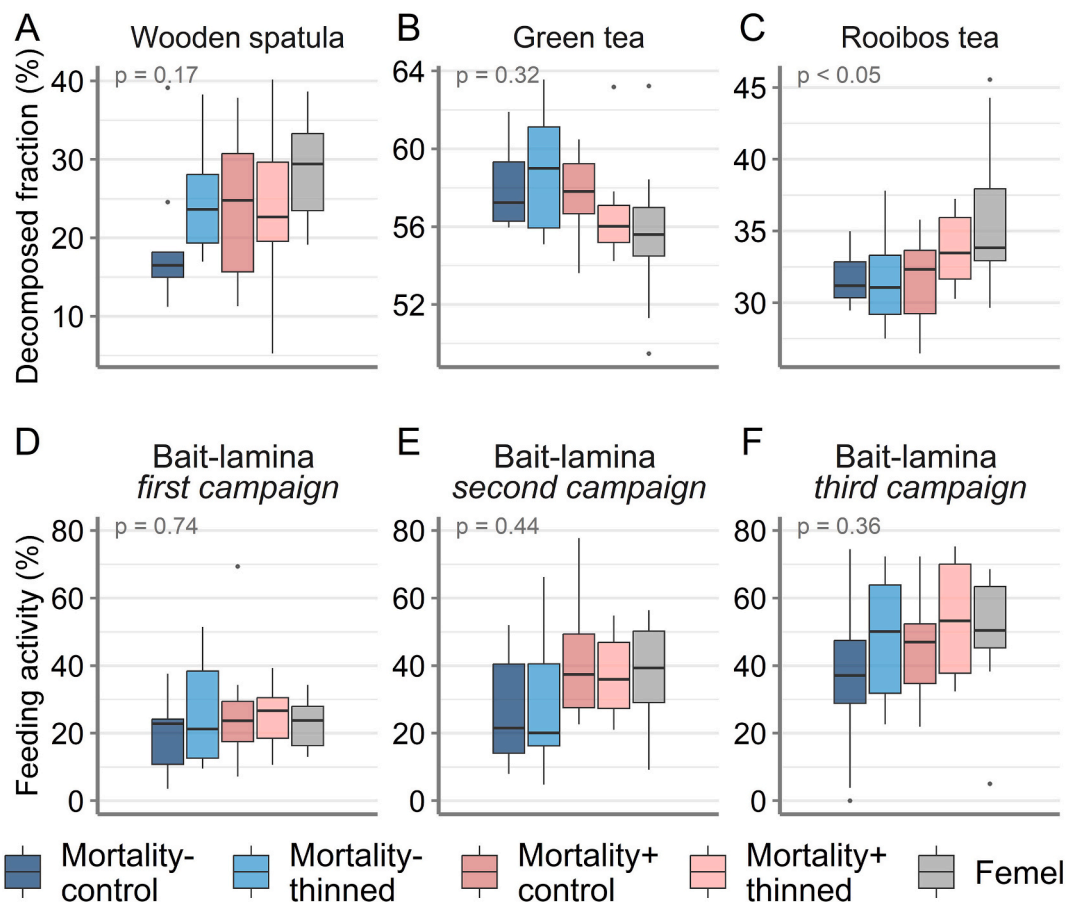
Fig. 4. Differences in fractions of decomposed materials and feeding activities between forest types. The boxplots represent the mean values from five samples per subplot, with a total of 10 subplots for each forest type. The *p*-values of calculated ANOVAs are shown in the fig. (A) Wooden spatula experiment (19/04/2022–24/10/2022), F = 1.8, (B) tea bag experiment green tea (19/04/2022–15/07/2022), F = 1.3, (C) tea bag experiment rooibos tea, F = 3.05, (D) first bait-lamina campaign (09/05/2022–31/05/2022), F = 0.5, (E) second bait-lamina campaign (27/06/2022–19/07/2022), F = 0.98, (F) third bait-lamina campaign (15/08/2022–06/09/2022), F = 1.17.

microclimate, which is in line with other studies measuring microclimate in different gap sizes and closed forest conducted in temperate deciduous forests (Abd Latif and Blackburn, 2010; Horváth et al., 2023; Kovács et al., 2020). Sites with more open conditions, especially *femel cuttings* and *mortality+ thinned*, were exposed to higher temperature fluctuations (Table S4, Figs. S3–S6). On the one hand, this can be explained by less absorption and reflection as well as transpirative cooling by trees leading to hotter temperature maxima. On the other hand, cooling at night or in colder months is also more pronounced as the heat retention effect via the shielding of trees is reduced, which results in lower minima during these periods (Abd Latif and Blackburn, 2010). The soil, though, is characterised by higher inertia than the air (Ashcroft and Gollan, 2013; Lu et al., 2009; Verstraeten et al., 2006). The extremes are less pronounced and changes occur more slowly than in the air, which is mainly due to the higher mobility and mixing of air (Arx et al., 2013).

The slower soil temperature changes persist longer, potentially leading to shifts in soil biota compositions, and impacting ecosystem functions (Glassman et al., 2018; Feng et al., 2022). Ectomycorrhizal fungi, for instance, are more sensitive to temperature changes compared to pathogenic fungi (Větrovský et al., 2019). Especially temperature maxima, highlighted by Rijkers et al. (2023) and Gleason et al. (2005), can drive changes in soil biota communities. The maxima in soil and understorey air temperature are also where we observed the highest temperature offset between closed forest and open areas (Table S2). However, previous studies showed, that the offset between maximum temperature in buffered sub-canopies and open areas only increases with increasing macroclimatic temperatures, as long as the water availability does not limit evapotranspiration (Davis et al., 2019; Zhang et al., 2020, Greiser et al., 2024). This effect is confirmed in our data: temperatures increased from May to the end of August (Table S2), but moisture decreased (Table S3). An increase in offsets in temperature maxima could only be observed in the air up to and including June and slightly shifted in the soil up to and including July (Table S2). The order of the group means of topsoil temperature remained the same over all experimental periods (Figs. 3, S8–S11). The highest mean, maximum and minimum soil temperatures were always measured on *femel cuttings*, followed by *mortality+ thinned*, *mortality- thinned* and the lowest soil temperatures were measured on *mortality+ control* and *mortality-control*. Thus, understorey density appears to play a considerable role in buffering temperatures in addition to overstorey canopy cover. Correspondingly, the mean soil temperature was more strongly influenced by the treatment in the understorey than by the vitality status of the overstorey during all experimental periods (Tables 1, S5–S9). Overstorey vitality and openness at five meters showed no significance in the models. This may be due to two main reasons: Firstly, there was no fully closed overstorey left in our study area, limiting the range of overstorey openness, despite significant differences between forest types (Fig. S21). Secondly, measurements at five meters were sometimes affected by taller understorey trees, especially on *control* subplots, not fully reflecting overstorey openness. However, over- and understorey openness were moderately strongly correlated (R = 0.61) and did not act independently (Tables 1, S5 and S9). In the air the interaction of over- and understorey canopy showed an amplifying effect on the temperature
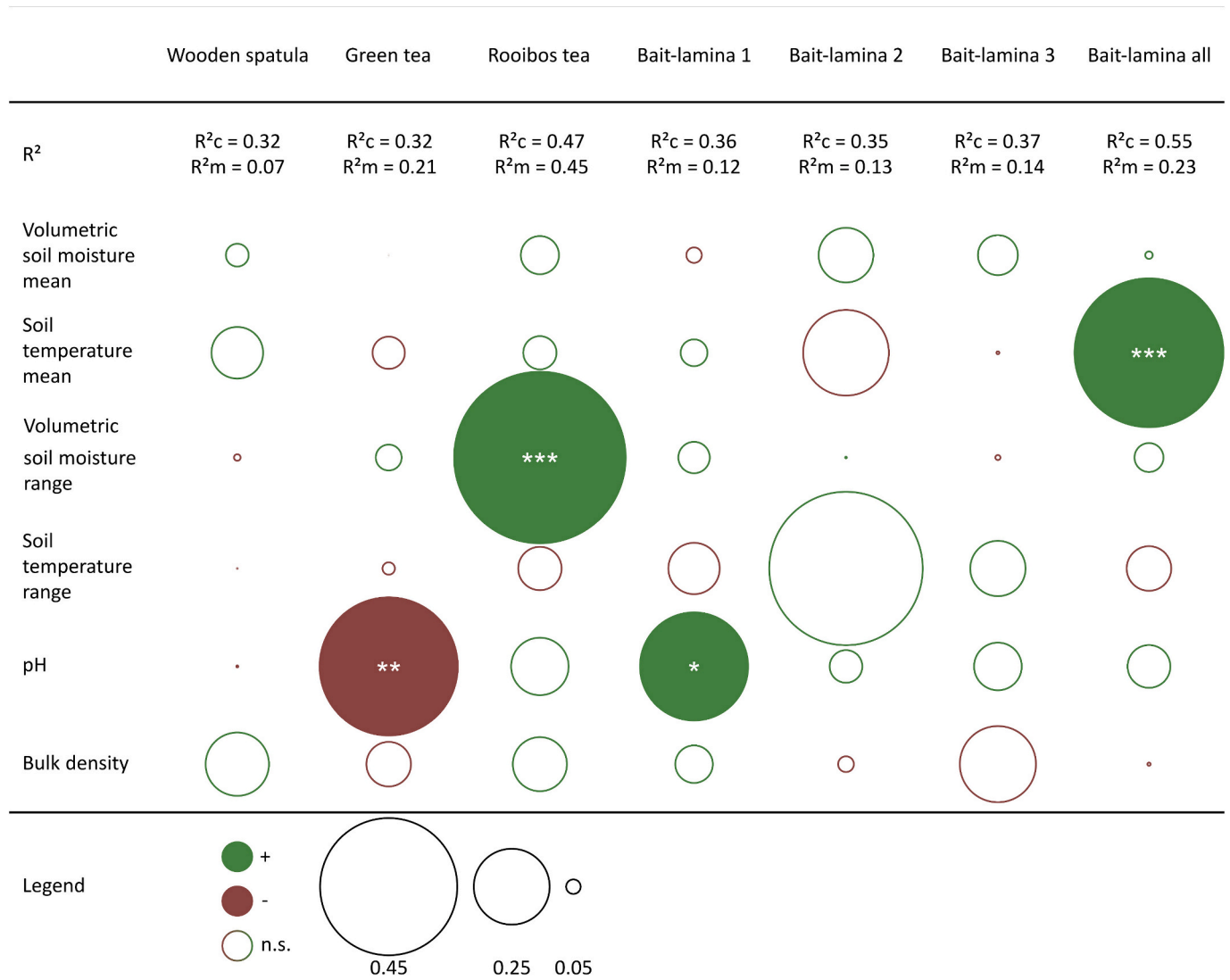
Fig. 5. Graphical representations illustrating the estimated effect sizes of abiotic conditions on soil biotic activity, derived from multiple linear mixed-effects models. Dependent variables were the mean values per subplot from respective decomposition experiments, while independent variables included mean soil temperature at 8 cm depth and moisture of the topsoil (0–15 cm), alongside the mean daily range of soil temperature and moisture, pH, and bulk density per subplot. Random effects accounted for plot identity nested within blocks. In the 'bait-lamina all' model with repeated measures per subplot, the random factor was specified as subplot identity nested in plot, further nested in block. Circle diameters represent the magnitude of the estimated effect size of the predictor variables on the outcome variable: green for positive and red for negative relationships, filled for statistical significance. Detailed model results can be found in Table S12 in the supplement.

range, indicating, as expected, stronger fluctuations on more open sites (Figs. S2 and S4). In the soil, however, the interaction showed a weakening effect on the soil temperature range (Fig. S2). This difference may again point to the higher inertia of the soil compared to the air and the larger offset between more open and closed sites in temperature maxima, compared to the minima. In general, the range of soil temperature increased with increasing openness, but the subplots with the highest openness at 0.9 m and 5 m experienced a faster cooling between September and October of the maxima than of the minima, which reduced the range in these periods compared to the summer (Table S2).

Lower mean soil temperatures and reduced extremes during the season in denser forest clearly show the buffer function provided by trees although 2022 was an above-average warm and dry growing season in the study area (Fig. S20). The extraordinarily warm weather conditions of this season, however, could be a reason why the temperature differences we measured between the treatments were slightly higher than in comparable studies investigating gaps with similar light conditions during the same month. Whereas in our study the daily mean soil temperature on *mortality+ thinned* was on average between May and

September 0.8 °C warmer and the daily maximum 1.2 °C warmer compared to the *control* forest subplots, studies measuring topsoil temperatures in similar gap sizes and/or light conditions in comparison to control forest plots reported lower differences (e.g. difference of means 0.31 °C and of daily maxima 0.71 °C in Horváth et al. (2023), mean differences of 0.3–0.6 °C in Abd Latif and Blackburn (2010)). Likewise, the soil temperatures on *femel cuttings* (0.25–0.67 ha) compared to forest control subplots, exhibited an average difference of 1.5 °C higher mean and 2.3 °C higher daily maximum, surpassing values reported by other studies with similar gap sizes (compared to closed forest e.g. mean differences 0.4–0.6 °C on clear-cuts of 0.8 ha in Hashimoto and Suzuki, 2004, mean difference of 1 °C on a clear-cut of 0.27 ha in Carlson and Groot, 1997). Larger temperature differences could, on the one hand, indicate comparatively stronger warming in the forest gaps. On the other hand, they may signal a stronger buffering in the forest, which we consider more likely due to the multi-layered, dense stand structure in our study area. It is also conceivable, that the low soil moisture all over the season even reduced the temperature difference between forest types due to reduced evapotranspirative cooling (Arx et al., 2013; Richter

et al., 2022). Comparing the measurements with other studies it is to say, that next to different macroclimatic conditions, in our experimental gaps not all trees were removed. On the *femel cuttings* single biotope trees remained and the forest gaps are characterised by the mortality status of the overstorey and a partial removal of the understorey regarding the tree species. On similar gap sizes as our *thinned* treatment, but with markedly higher openness of 43.5 % (compare Table S10; openness 5 m: 12.03–27.44 %; openness 0.9 m: 10.3–19.68 %) Abd Latif and Blackburn (2010) reported considerably higher differences of mean daily soil temperatures up to 2.3 °C compared to neighbouring closed forest. Similar mean temperature differences up to 2.5 °C and maximum differences up to 5 °C in depths of 5 to 50 cm were measured in studies comparing microclimate on larger clear-cuts of 1 to 2.2 ha size with control forest sites (Carlson and Groot, 1997; Hashimoto and Suzuki, 2004; Radler et al., 2010). The measured temperature data of our study reflect this reported gradient between different gap sizes respectively openness and fit in the global observations of Zellweger et al. (2019), which indicate that buffering properties decrease strongly below 75 % canopy cover (see openness in Table S10). Overall, our results show not only the importance of the gap size for the microclimate, but particularly of its vertical structuring in terms of density in the over- and understorey.

4.1.2. Soil moisture

Even during periods with lower than average precipitation (climate chart see Fig. S20), values for mean soil moisture were similar or higher on *femel cuttings* and *mortality+ thinned* compared to the other forest plots (Fig. 3, Tables S3 and S4, Figs. S8–S11). The fact that soil moisture can be higher in forest gaps than in closed forest despite higher solar radiation refers to the greater proportion of precipitation falling through and the lower proportion of transpiration from old trees (Kovács et al., 2020; Abd Latif and Blackburn, 2010; Zirlewagen and von Wilpert, 2001). With increasing gap size, the soil moisture level typically rises (compare *mortality- thinned*, *mortality+ thinned* and *femel cuttings*; Abd Latif and Blackburn, 2010; Kovács et al., 2020; Gray et al., 2002) until the gap is so large that the wind causes stronger air turbulence and lead to drying processes (Chen et al., 1999). However, a trend towards warmer and moister soil conditions was even visible with increasing size of the *femel cuttings* despite the small sample size and sometimes large small-scale microclimatic site variations on the same *femel cutting* (Fig. S1). At 50 cm depth, *mortality+ thinned* showed a more stable seasonal pattern and higher soil moisture than *femel cuttings* between mid-July and the beginning of September (Fig. S7). Here, potentially the hydraulic lift is an underlying mechanism, through which trees passively spend water from moister soil layers into soil layers with low water potential (Caldwell et al., 1998). An effect that is unlikely to be important on *femel cuttings* due to the almost complete absence of large trees. The decline in moisture of the topsoil, however, was particularly pronounced on *mortality+ thinned* while it became steadily drier between May and September (Fig. S7, Table S3). Presumably, when it rained at the beginning of the season, more moisture reached the soil than on plots with closer canopy. However, when drought occurred the higher evaporation of the most often less covered soil compared to *femel cuttings* resulted in a higher loss of soil moisture in the upper soil (Arx et al., 2013). Higher evaporation of the bare soil might also explain why the topsoil of *mortality- thinned* was most often drier than the respective *control* (Fig. F6). Overall, the differences between the treatments and vitality status within the forest were not very relevant for the soil moisture during this dry season (Tables 1, S5–S9). The only significant effect, the interaction term of openness at 5 m and 0.9 m on the range of topsoil moisture, should be carefully interpreted because of its single appearance during the wooden spatula experiment and the overall very small differences in the soil moisture ranges (Table 1). Higher differences were visible compared to *femel cuttings*, although also often not significant (Table S4). In very small gaps, the effect of reduced transpiration and interception can sometimes hardly contribute to higher

soil moisture, because roots of neighbouring trees protrude into the gap and withdraw the soil water (Baker et al., 2013). Nevertheless, *mortality+ thinned* showed, as expected, consistently higher soil moisture levels in all depths than the *control*. The effect was most pronounced at a depth of 50 cm, where it was also visible on *mortality-thinned* compared to *control* (Table S4, Fig. S7). Under warmer and drier conditions as predicted under climate change, this knowledge can be particularly important for the management of multi-layered forest stands, as targeted interventions like thinning in the understorey can reduce competition for soil water and may create resilience against drought stress in the overstorey (Meyer et al., 2022).

4.1.3. Soil biological activity

The highest mean decomposition rates or feeding activities per experimental period were always quantified on *femel cuttings* or *thinned* treatments (Fig. 4). However, in none of the experimental periods, the differences in decomposition rates or feeding activities were significant in pairwise comparison between the forest types. Despite the very dry season, the decomposition rates and feeding activities were comparable to the results of other studies from temperate forests (Desie et al., 2023; Thakur et al., 2018). Losses of the wooden spatulas were relatively high with 35.2 %. We do not assume that the wooden spatulas were so strongly decomposed that they could not be found. Rather, they were dug up by animals or broken off above ground and were then difficult to find in the forest soil. However, it is unlikely that this loss introduced a bias, as the distribution of missing spatulas is fairly equal between the forest types (28–44 %). Furthermore, we assume birch wood decomposition results represent most tree species in the study area, supported by comparable wood degradation rates of prevalent plant families (Pietsch et al., 2014).

4.2. Relationship of microclimate and soil biological activity

Microclimate played only a minor role as predictor for soil biological activity in our multiple linear regression models (Fig. 5, Table S12). Apparently, the gradient of soil moisture and temperature in our experimental design was too small to evoke differences in decomposition rates or feeding activities considerably. However, it was striking, that the feeding activity quantified with bait-lamina tests increased between the three experimental periods. During this time, from mid-May till the beginning of September, the average temperature got warmer and the average soil moisture lower (Fig. 2, Tables S2 and S3). A highly significant positive correlation could be calculated for mean soil temperature and feeding activity encompassing the three bait-lamina campaigns (Fig. 5). This relationship aligns with expectations, as warmer temperatures typically enhance soil biological activity due to heightened resource use efficiency and metabolic rates (Gillooly et al., 2001), supported by various experimental studies (Gongalsky et al., 2008; Wang et al., 2010; Hobbie et al., 2006; Melillo et al., 2002; Conant et al., 2011). It can even trigger a trophic cascade effect that increases activity across different trophic levels driven by increased resource availability or altered soil biotic diversity (Hobbie et al., 2006; Mueller et al., 2016, Brown et al., 2004). However, it is interesting that the results show no counteracting effect concerning soil moisture. Especially in forest ecosystems it is known, that reduced soil moisture lowers soil fauna abundance (Blankinship et al., 2011). Thakur et al. (2018) showed an interaction effect between soil temperature and moisture with lower feeding rates at warming and reduced precipitation. In this treatment, however, the temperature increase (+ 3.4 °C) and the precipitation reduction (mean soil moisture at 20 cm depth in summer months around 10 %) were even more extreme than the microclimate measured in our study. Similar results were observed in experimental studies, where litter decomposition increased with rising temperatures under high soil moisture conditions but decreased under low moisture conditions (Butenschoen et al., 2011; Aerts, 2006; Bontti et al., 2009). In this particularly dry year, the mean soil moisture in the topsoil was in the

summer often below 20 % (on *mortality- control* also at 50 cm depth, Table S3), which is below availability for many plant species on clayey soils (Saxton and Rawls, 2006). Nevertheless, the soil moisture was apparently not limiting for soil biological activity. As described in Liang et al. (2022), decomposition processes can be still active below the wilting point. Perhaps we also do not see an effect of mean soil moisture over our multi-period model of bait-lamina tests because the mesofauna, which should be primarily responsible for the degradation, is more mobile and can move to wetter microsites after feeding. Collembola and mites move, furthermore, in airspaces and can therefore stay active in drier soils. Also, fungi can use wetter microsites over a wide range via their hyphae and are thus less susceptible to desiccation than bacteria (Vries et al., 2018; Sun et al., 2017). However, it can also matter whether the moisture conditions are constant or fluctuate (Huhta and Hänninen, 2001; Kamczyc et al., 2022). We had expected changing soil moisture to be negatively correlated with soil biological activity, as fluctuating water availability can lead to osmotic stress and restricted nutrient and transport availability of microorganisms (Schimel, 2018). Moreover, also for mesofauna that live in a soil water matrix e.g. nematodes, it is reported that they are sensitive to moisture fluctuations, although some of them can survive desiccation by going dormant (Alpert, 2005). However, in our study, the range of daily soil moisture was a significant positive predictor of the decomposition of rooibos tea (Fig. 5). Varying soil moisture and also temperature could potentially increase species richness via a wider range of spatio-temporal microhabitats since each decomposer species has its own optimal microclimatic conditions for growth and reproduction, which even may change between developmental stages (Mueller et al., 2016; Huston, 1979; Hättenschwiler et al., 2005). Higher species richness in turn may increase activities. Unfortunately, we cannot make any statement about the diversity of the decomposers in our study.

Besides microclimatic variations that can cause changes in the diversity and activity of soil biota, many other factors concerning the physical and biochemical soil properties can be of relevance (Fierer et al., 2009; Mulder et al., 2005).

Differences in pH can favour different species, which in turn decompose different substrates. While for example earthworms and many bacteria prefer more basic soils, many fungi grow better under acid conditions (Rousk et al., 2011; Mueller et al., 2016). This may be a reason why pH is a key predictor in some of our models, although it does not act in the same direction (Fig. 5).

In the meta-analysis of Latterini et al. (2023) decomposition rates increased with more light and higher soil temperatures in areas where only some trees were removed, contrasting with decreased rates in clear-cut areas. This difference may be due to greater soil disturbance in clear-cuts compared to less invasive forestry practices. While soil compaction from logging can affect soil properties and microbial communities (Schnurr-Pütz et al., 2006; Frey et al., 2009; Shestak and Busse, 2005), its impact on decomposition remains inconclusive in recent literature (Latterini et al., 2023). In our study, the bulk density, slightly higher but not significantly on *femel cuttings* (Fig. S22), is not a significant predictor for soil biological activity (Fig. 5). In a meta-analysis of soil compaction from Nazari et al. (2021) bulk density of compacted forest soils differed on loamy soils by 6.4 % and on clayey soils by 12.6 % to control forest sites, which is more than in our study with a difference of 5.5 % between *femel cuttings* and the other forest types. While recovery of bulk density is slow, studies indicate that noticeable differences in microbial activity are typically seen only in the first few years after harvesting (summarised in Lewandowski et al., 2015). The older age of the *femel cuttings* in our study, ranging from three to six years, may explain the lack of such differences in soil biological activity, as vegetation has re-established. This is consistent with findings showing no significant difference in nutrient cycling between gaps with re-established vegetation and control forest (Schliemann and Bockheim, 2014; Prescott et al., 2003; Hope et al., 2003).

Decomposition processes can thus change due to many microclimatic and physico-chemical soil-related factors. These factors, in turn, are influenced by a variety of environmental factors that can be subject to human interventions, such as the amount of over- and understorey vegetation, soil texture and the actual macroclimatic conditions (Lewandowski et al., 2015; Scharenbroch and Bockheim, 2007; Vilhar and Simončič, 2012).

5. Conclusion and application

The results show that closed forest canopies serve as climatic buffer. The resulting reduction in climatic extremes is gaining significance for biodiversity, ecosystem functions and human well-being, in a warming world with an increasing range and frequency of climatic extremes (De De Frenne et al., 2021). As this study shows, it seems important assessing the forest buffering function to address over- and understorey dynamics, since both influence the microclimatic conditions. The influence of the openness of the understorey on the soil temperature was particularly strong. This indicates that under the given conditions with high mortality in the overstorey due to drought stress and pathogens, understorey thinning has a major influence on soil microclimate. It is to be expected that the microclimate reacts to canopy openings also in other forest ecosystems in a similar way as in our study, but this may not necessarily lead to negative effects on ecosystem functions. In our study, despite the extreme dry season in 2022, soil biological activity was quite little influenced by the microclimatic differences of the treatments and vitality status of the forests. Nevertheless, it can be seen that soil biological activity increased with increasing temperatures. Increased decomposition rates, can become problematic for the ecosystem via elevated CO_2 and CH_4 fluxes leading to positive feedback loops (De Frenne et al., 2019; Allison and Treseder, 2008; Conant et al., 2011; Ofiti et al., 2021). Conversely, but not visible in our study, a decrease of soil biological activity at low soil moisture, which often accompanies high temperatures, can lead to less carbon sequestration (Thakur et al., 2018; Butenschoen et al., 2011; Londo et al., 1999). Due to such imminent disturbances of decomposition processes and thereby the nutrient cycle, when planning forestry measures the soil microclimate should be taken into account in its potentially important role in maintaining biodiversity and ecosystem functions. For a better understanding of how a certain loss of buffering capacity and subsequent microclimatic changes affect soil biological activity, more research is needed to re-evaluate the ecosystem consequences of forest management practices in times of climate change. To support this and gain a more holistic perspective considering a broad range of environmental conditions, it would certainly be helpful to include measurements of microclimate and soil biological activity in large-scale biodiversity monitoring programmes as they are currently planned as part of national or European biodiversity monitoring programmes (e.g. Bolte et al., 2022, European Commission, 2023).

CRediT authorship contribution statement

Annalena Lenk: Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ronny Richter:** Writing – review & editing, Software, Methodology. **Lena Kretz:** Writing – review & editing, Supervision, Methodology. **Christian Wirth:** Writing – review & editing, Supervision, Resources, Methodology, 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.

Open research statement

Data and R code are available on zenodo (https://doi.org/10.5281/zenodo.11445629).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.173572.

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