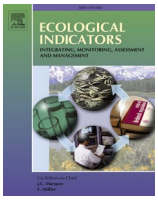
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Beech buffers: Microclimate regulation in temperate old-growth forests, surroundings and forest edge

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ABSTRACT

Central European forests are increasingly threatened by the climate crisis. Microclimatic and hydrological self-regulation are key to forest stability, with old forests especially effective. This study analysed the microclimatic performance of old beech forests in Germany, component parts of a UNESCO World Heritage Site. Four component parts (Grumsin, Hainich, Kellerwald, and Serrahn) were monitored for about one year from May/June 2022 using data-loggers to assess maximum temperature (Tmax) and water vapor pressure deficit (VPDmax) across core and buffer zones, forest edges, and open land. Tmax in beech forests approached 40 °C, while non-forests exceeded 46 °C. The highest VPDmax was recorded in non-forests, exceeding 7 kPa, whereas forest interiors maintained lower atmospheric dryness. Denser canopy cover near the forest edge correlated with lower Tmax, higher humidity, and reduced VPDmax. A collapsing spruce stand in Kellerwald was 4.5–6 °C warmer than the neighboring old-growth beech forest, showing the cooling role of intact forests. The reduction in VPDmax, a key factor in tree survival during dry periods, underscores the importance of maintaining mature forests. Dense canopy, understorey, and wide buffer zones are essential for stabilizing microclimate under climate change. Expanding and preserving old-growth forests mitigates climate-related stresses and sustains ecological functionality.

1. Introduction

Central European Forests are showing serious effects of recent heat and drought extremes (Buras et al., 2018; Knutzen et al., 2025; Rohner et al., 2021; Schuldt et al., 2020; Seidl et al., 2017; Senf et al., 2020). Increased levels of tree mortality are likely due to extreme heat, insufficient precipitation, reduced soil moisture, and atmospheric drought (Schiefer et al., 2024). Since 2018, there has been a coupling of various anomalies in many regions, such as central Germany, consisting of, for example, warm and dry winters, significant precipitation decreases, and record-breaking heat waves (van der Woude et al., 2023; Xoplaki et al., 2025). Under the current climate trajectory, events such as the unprecedented drought of 2018–2019 might be part of a new normal in the future (Hari et al., 2020; Rousi et al., 2023). Warmer temperatures lead to a non-linear increase in water vapour pressure deficit (VPD) leading to plant desiccation and damage (Grossiord et al., 2020; Hatfield & Prueger, 2015). Higher VPD, also called atmospheric drought, increases the transpiration rate and therefore reduces the water potential of plants (Martin-StPaul et al., 2023). This further induces a decline in tree growth and thus carbon sequestration (Rohner et al., 2021; Smith et al., 2020; Thom et al., 2020; van der Woude et al., 2023; Vieira et al., 2020).

In addition to heat and drought extremes, frost days represent another critical climatic stressor for forest ecosystems, particularly in temperate regions (Vitasse and Rebetez, 2018; Weigel et al., 2018). Sudden late-spring frosts can damage emerging leaves, buds, and flowers, leading to reduced photosynthetic capacity and growth for the rest of the season. Frost-induced damage also increases tree vulnerability to pests and diseases and can amplify mortality under repeated or combined stress events (Lamichhane, 2021; Menzel et al., 2020).

Forests are likely impacted not only by individual extreme events but also by the cumulative effects of multiple stressors, exacerbated by reduced functionality and insufficient recovery time. Structurally poor conifer plantations with low biodiversity are particularly at risk (Spiecker & Kahle, 2023). Between 2018 and 2021, more than half a million hectares have already been affected by the loss of tree cover across Europe (Thonfeld et al., 2022). The situation is intensified by the

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loss of tree cover due to bark beetle infestation, disease outbreaks and salvage logging, which exacerbates the severe fragmentation of forest remnants in the cultural landscape. This fragmentation contributes to increased forest warming and a decline in overall forest vitality (Adhikari et al., 2024; Mann et al., 2023).

Given these escalating challenges, there is an urgent need for climate-adapted forest management strategies. One of the fundamental debates concerns the role of non– or low- versus high-intervention strategies in securing forest functions and adaptive resilience (Luick et al., 2021; Popkin, 2021). Anthropogenic land-use has altered forests' structures, composition and extent worldwide. This has severe implications for the provision of ecosystem services (Foley et al., 2005), and forest management has been shown to contribute to local warming and vulnerability (Blumröder et al., 2021; Blumröder et al., 2020; Norris et al., 2012). There is evidence for more effective microclimatic regulation by old forests during climate extreme periods (Adhikari et al., 2024; Lindenmayer et al., 2022; Menge et al., 2023; Wolf et al., 2021). Yet, especially in the more intensively used forest landscape, their relative buffering capacity under current climatic conditions has been little studied. One of the reasons may be that old forests have become rare. Only about 0.7 % of forests in Europe have remained untouched by intensive use or conversion and represent primary forests (Sabatini et al., 2018).

Starting from the Ukrainian and Slovak Carpathians in 2007, including German forest areas in 2011, and then becoming pan-European as from 2017, a growing group of European countries established a serial UNESCO World Heritage Site (WHS) dedicated to the "Ancient and Primeval Beech Forests of the Carpathians and Other Regions of Europe" (Ibisch et al., 2017). This World Heritage Site conveys the story of the post-glacial expansion of European beech (*Fagus sylvatica*), an ecological process that is still ongoing and will be accompanied by range shifts in the current climate change. This unique setting of well-protected, relatively old beech forests provide special conditions for studying their importance, not only as anchors of old-growth biodiversity, but also in terms of their landscape ecological functions. Adhikari et al. (2024) used remote sensing to analyze temperature regulation and tree greenness trends in the same region during recent years of temperature extremes. Based on detailed empiric observation, this study provides a more comprehensive and in-depth assessment of microclimate regulation focusing on the influence of canopy structure and edge effects on temperature and VPD across and between different forest stands that go beyond the capabilities of remote sensing.

We studied four of the UNESCO World Heritage beech forests in Germany (Grumsin, Hainich, Kellerwald, and Serrahn). Our focus was on heat and drought extremes, as they present a crucial threat to forest vitality and functionality. Previous research, including studies by Adhikari et al. (2024), Norris et al. (2012), Blumröder et al. (2021) and Li et al. (2015) highlighted significant variations in the temperature regulation capacity of forest stands, with these differences becoming more pronounced under higher temperature thresholds.

Based on existing literature and preliminary findings, we hypothesize that maximum temperatures (Tmax) and water vapor pressure deficit (VPDmax) will be lower in the core zones of old-growth forests compared to non-forests and open-canopy stands, and that higher canopy cover as well as greater distance from the forest edge will enhance this cooling effect, leading to increased humidity and reduced atmospheric dryness. We also expect fewer frost days in the forest core zones due to the thermal buffering effect of the closed canopy, which moderates temperature extremes and reduces the risk of freezing events. This study aims to i) quantify the temperature difference between the older beech forest in the core zone and the surrounding more or less open stands in the buffer zone and non-forests; and to ii) map the temperature profile along the transition from non-forests open areas across the forest edge into the buffer and core zones using microclimatic data-loggers. The study provides far-reaching insights for forest management with regard to climate change adaptation. It furthermore permits statements on the importance of protected old forests and forests.

2. Materials and methods

2.1. Study sites

Four of the five German component parts of the pan-European UNESCO World Heritage site "Ancient and Primeval Beech Forests of the Carpathians and Other Regions of Europe" served as research sites for this study (Fig. 1).

All four research sites were included in the UNESCO serial World Heritage property in 2011 because they fulfilled certain criteria such as older trees and a strict protection status. Still, all considered beech forests show a clear and individual signature of anthropogenic impacts such as timber harvesting, hunting or even military training activities until the 1980 s (Table 1). With regard to average and maximum tree ages, biomass stocks, forest structure and biological composition, all studied forests differ from pristine beech forests as they exist e.g., in some parts of the Carpathians.

The zonation with core and buffer zones, as according to the requirements for inscription as UNESCO World Heritage property, does neither represent the current management regime nor the past or recent management intensity. At most sites, both in the 'UNESCO' core and buffer zones, there is no active forest management anymore. Mainly, the core zones are under legal protection for a longer time compared to the buffer zones, but forestry operations were absent in the entire sites for the last 20–30 years. The spatial design of core and buffer zones across the four sites is diverse and reflects topography and local forest (conservation) history.

At each of the four studied component parts, different setups of microclimatic data-loggers were implemented (Table 2, Fig. 1). These depended on the site characteristics such as forest type and zonation, and in some cases also limitations such as permissions provided by the responsible authorities and administrations influenced the setup. Despite heterogeneity in setup, the overarching aim was to capture microclimatic transitions at different spatial scales.

After an initial screening using available satellite data, site visits and consultation with site managers, sampling plots with microclimate data-loggers were installed in May and June 2022 and left in place for recording data for approximately one year.

Fig. S4 illustrates the study sites with orthophotos and shows the spatial distribution of plots across different forest categories. The definitions of forest categories and their abbreviations are provided in Table S1. Table S2. presents the number of plots and their arrangement across sites and categories.

In Grumsin forest, a total number of 64 plots were installed. A line of 20 sampling points spaced about 20–30 m apart was installed in the core zone in close proximity (20–30 m) to a road that crosses the forest, and two lines of 10 points each spaced about 20–30 m apart were installed in the adjacent buffer zone. Two lines of 12 points each (5 m, 10 m, 15 m, 20 m, 25 m, 30 m, 40 m, 50 m, 75 m, 100 m, 150 m from the edge) were installed outside the forest on an agricultural field (Fig. 1a).

In Hainich National Park, two transects with a total of 72 plots were distributed from the non-forest open field (a total of 15 plots arranged in 5 m, 10 m, 15 m, 20 m, 25 m, 30 m, 40 m, …; 100 m, 150 m, 200 m distance from the forest edge into the open field) through the forest edge and the buffer zone to the core zone (a total of 19 plots arranged in 5 m; 10 m; 15 m; 20 m; 25 m; 30 m; 40 m; …; 100 m; 150 m; …; 300 m; 400 m; 500 m from the forest edge into the forest) (Fig. 1b). One transects included only one plot at the edge of the forest, where a clear and open boundary was found between the open field and the forest. Within the second transect, the edge could not be assigned to one specific location as shrubs and trees extended into the grassland, and therefore three sampling points were established within the forest edge. In addition, five points were placed within the core zone on existing permanent sampling plots defined and maintained by the National Park authority.

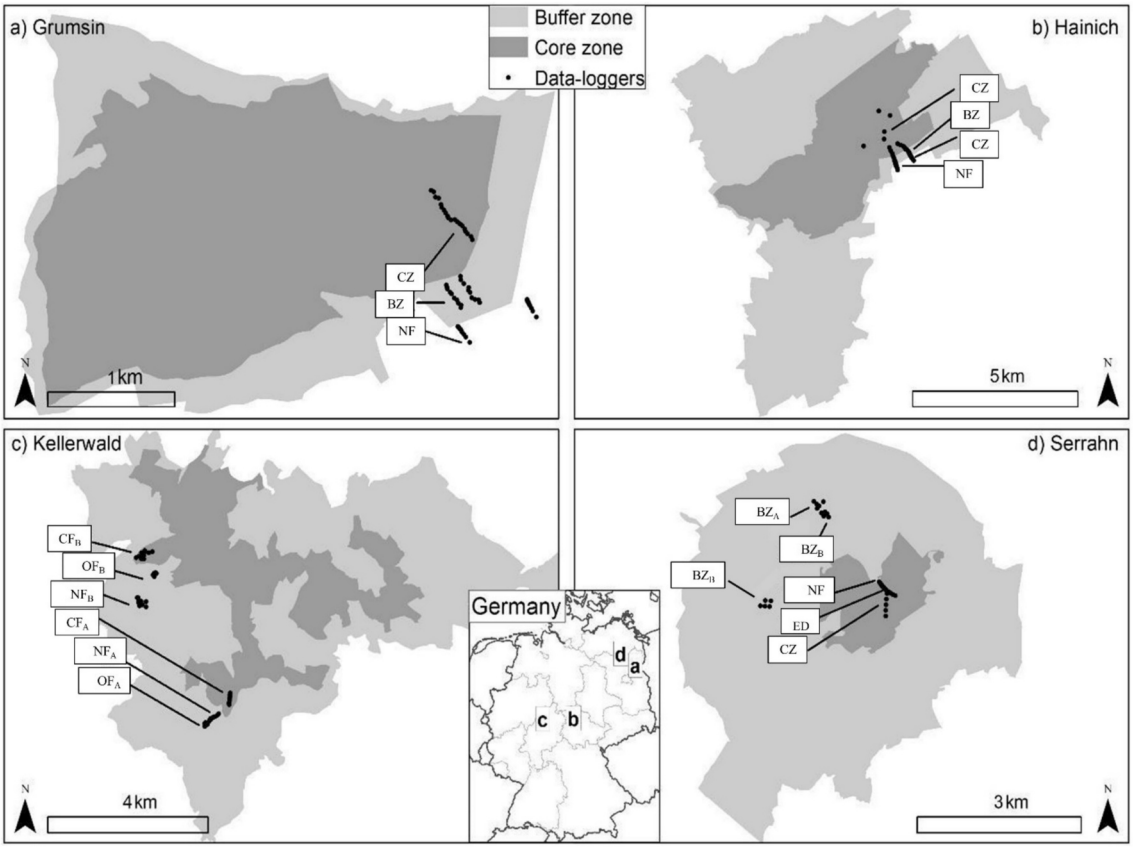


Fig. 1. Overview map showing the four investigated German component parts of the serial UNESCO World Heritage site "Primeval Beech Forests of the Carpathians and Ancient Forests of Other Regions in Europe" and the location of sampling plots: a) Grumsin (CZ = core zone, BZ = buffer zone, NF = non-forest); b) Hainich (CZ = core zone, BZ = buffer zone, ED = forest edge, NF = non-forest agricultural land); c) Kellerwald (CZ_A = core zone A, CZ_B = core zone B, OF_A = open forest A (dead spruce stand), OF_B = open forest B (open beech stand), NF_A = non-forest A, NF_B = non-forest B); d) Serrahn (CZ = core zone, BZ_A = pure pine stand, BZ_B = pine stand mixed low broadleaved understorey, BZ_C = pine stand with dense beech understorey, ED = forest edge, NF = non-forest) for each height level (in ca. 1.3 m and 0.1 m above ground).

In Kellerwald National Park, six different locations were identified as sampling sites and ten plots were set up in each site (Fig. 1c). Two of the sites were within the core zone, where data-loggers were placed on existing permanent sampling plots under the supervision of the National Park Authority. Two sites represent 'open' forest, one a collapsing spruce stand (due to bark beetle infestation) and the other an open beech stand characterised by scattered old trees. The two non-forests represent grassland with encroaching shrubs and early successional tree cover.

In Serrahn, 49 plots were distributed (Fig. 1d). A linear transect consisting of a total of 29 sampling plots, ranged from non-forest grassland (10 plots) through the forest edge (3 plots) to the core zone (16 plots). Five additional sample plots were selected in the core zone at existing permanent monitoring plots. In addition, three stands with five sampling plots each were selected in the surrounding pine plantations. These were a pure Scots pine stand, a Scots pine stand with a low broadleaved understorey and a Scots pine stand with a dense understorey of Fagus sylvatica, all plots together representing the gradual transformation of pine plantations into relatively self-willed beech forests.

Each sampling plot was classified according to its location and a spatio-structural category, such as forest in the core zone or buffer zone, open forest, non-forest and forest edge. The forest edge was defined as the canopy edge of the outermost tree, while plots 5 m from the edge were also considered as forest edge. Distance from the forest edge was measured either in the field using a tape measure or using GPS coordinates and the ruler function in ArcMap 10.8.2 (Esri, 2020). The plots assigned to specific forest stands, such as pine stands, where no transect line structure was adhered in the setup of the plots, were not included in the analysis related to the influence of the distance from the forest.

2.2. Microclimatic measurements and analyses

A total of 250 data-loggers measuring temperature (Onset HOBO-Pendant) and 125 data-loggers measuring relative humidity and temperature (HOBO Pro v2) were installed across the four sites. The relative humidity loggers were strategically placed across key microclimatic gradients (forest core, edge, and open areas), ensuring representative coverage despite their lower number compared to temperature loggers. A wooden stake of 2 m in length was anchored in the ground at each of the designated measurement locations. Temperature loggers were mounted on the stake at a height of approximately 1.3 m above ground, and relative humidity loggers were mounted at a height of approximately 0.1 m. The loggers faced north and were protected from direct sunlight by a white protective cover (see Blumröder et al., 2021). All data-loggers were programmed to take measurements simultaneously every ten minutes and store the data locally, which were manually downloaded every four to eight weeks.

Records were taken from the day after the loggers were installed in the field until the day before the loggers were removed from the sites. Within this sampling period, days with incomplete or erroneous data were excluded from the analysis. These include days when logger data were downloaded and recording was interrupted, and days with non-simultaneous recordings due to incorrect programming. In addition, some data-loggers had to be excluded from the dataset, or at least for a period of time, because they were temporarily on the ground outside the protective casing. This was particularly the case for the temperature

Table 1
Characteristics of the four component parts used as study areas. [Grumsin; (BGR, n.d.; MLUK, 2000; Luthardt et al., n.d.); Hainich (*BGR*, n.d.; Nationalpark Hainich, 2010., 2010; Großmann et al., 2018; Wartena & Ewald, 2020); Kellerwald (Bretón Pérez, 2016; *BGR*, n.d.; *Kellerwald-Edersee National* Park 2021, n.d.; Nationalpark Kellerwald-Edersee, n.d.) Serrahn (BGR, n.d.; Härdtle & Oheimb, 2009; Oheimb et al., 2004; Spieß, 2015)].

	Grumsin	Hainich	Kellerwald	Serrahn
Conservation status	UNESCO WHS (2011); Schorfheide Chorin Biosphere Reserve core zone (1990); Nature Reserve (1990); Special Area for Conservation and Special Protected Area (EU) (2000)	UNESCO WHS (2011); Hainich National Park (1997); Special Area for Conservation (EU) (2004)	UNESCO WHS (2011); Kellerwald Edersee National Park (2004); Nature Park (2001); Special Area for Conser- vation (EU) (2000)	UNESCO WHS (2001); Müritz National Park (1990); Special Area for Conservation (EU) (2004); Nature reserve (1952)
Size	590 Core Zone (CZ); 274 Buffer Zone (BZ)	1573 (CZ); 4085 (BZ)	1467 (CZ); 4271 (BZ)	268 (CZ); 2568 (BZ)
Elevation(m.a. s.l.)	84–139	225–490	245–626	80–124
Relief	Staunch set moraine, depres- sions and elevations	Shelly limestone ridge, interrupted by shallow wet ravines/ clefts	Hetero- geneous relief, steep slopes	Hetero- geneous relief (upsetted moraines), frost sinks
Forest type	Milio- Fagetum	Horde- lymo- Fagetum	Luzulo- Fagetum	Melico- Fagetum
Soil type	Clay sands and boulder clay/ loam	Shelly lime- stone and silty clays	Poor gray- wacke soil, rich in silica, and clay silt	Clay sands
Landscape	Clay sands and boulder clay/ loam	Forested mountain range surrounded by pastures and agricultural areas	Forest mid- elevation mountains bordered by the Edersee reservoir	Lake-forest rich region
Historical use	Between 1985 and 1989, single-trunk use; extensive use only in the NW of the core zone around 1950	Since 1965 single hardwood tree harvesting; since 1998 no timber extraction; last extraction of conifers in 2003; last forestry management activity in 2007	Since 1980: selected tree removal; since 2004: no silvicultural interventions in core zones; since 2009: no timber harvesting in buffer zones; removal of conifers	Since 1960 s: no silvicultural interventions in the core zone; since 2013: no silvicultural interventions in buffer zone

Table 2
Main characteristics of the study sites. [Sources: Personal communication with site managers.].

Component Parts	Forest Category	Approx.max. tree age [years]	Main tree species	Structure	Last timber harvesting activities
Grumsin	Core Zone (CZ)	180	*Fagus sylvatica*	Old-growth forest	Between 1985 and 1989, single-stem use
	Buffer zone (BZ)	180	*Fagus sylvatica*	Mature stand with dense understorey	Between 1985 and 1989, single-trunk use (extensive use only in the extreme NW of the core zone around 1950)
	Non-forest (NF)	–	–	Agricultural field (rapeseed, wheat)/pasture	–
Hainich	Core zone (CZ)	200	*Fagus sylvatica*	Old-growth forest	Since 1965 single hardwood tree harvesting; since 1998 no timber extraction;last extraction of conifers in 2003;last forestry management activity in 2007
	Buffer zone (BZ)	200	*Fagus sylvatica*	Mature stand with relatively dense understorey	Since 1965 single hardwood tree harvesting; since 1998 no timber extraction;last extraction of conifers in 2003;last forestry management activity in 2007
	Non-forest (NF)	–	–	Pasture	–
Kellerwald	Core zone A (CZ_A)	190	*Fagus sylvatica*	Old-growth forest	2004
	Core zone B (CZ_B)	150	*Fagus sylvatica*	Old-growth forest	2004
	Open forest A (OF_A)	65	*Picea abies*	Dead/dying spruce stand	2009
	Open forest B (OF_B)	165	*Fagus sylvatica*	Solitary old beech trees	2004
	Non-forest A(NF_A)	–	–	Pasture	–
	Non-forest B (NF_B)	–	–	Pasture with fenced cultivation of Arnica montana	–
Serrahn	Core zone (CZ)	205	*Fagus sylvatica*	Old-growth forest	around 1960
	Pine with beech understorey (BZ_C)	177	*Pinus sylvestris* & *Fagus sylvatica*	Pine stand with dense beech understorey	1995
	Pine with little broadleaved understorey (BZ_B)	60	*Pinus sylvestris*	Pine stand with little broadleaved understorey	2004
	Pure pine (BZ_A)	52	*Pinus sylvestris*	Pine monoculture	2013
	Forest edge (ED)	207	*Fagus sylvatica*	Forest edge between the old growth core zone and non-forested pasture	around 1960
	Non-forest (NF)	–	–	Pasture	–

data-loggers, which were initially located 1.3 m above the ground. In addition, few devices were damaged or stolen during the sampling season. As a result, the total number of data-loggers varied over time (Fig. S1).

2.3. Canopy cover

At each measuring point, canopy cover was estimated using a spherical crown densiometer with a convex mirror (Model A, Forestry Suppliers, Inc., Mississippi, USA) once during the growing season in 2022 (Lemmon, 1956). Canopy cover represents the portion of sky that is covered by tree canopies looking vertically upwards (see also Blumröder et al., 2021).

2.4. Data analyses and statistics

All data preparation and analyses were conducted with RStudio, R version 4.0.3 (R Core Team, 2020). For each of the four testing sites, daily mean temperature was calculated as average of all recordings per day of all distributed data-loggers. A subset of data measured during the 20 days with the highest daily mean temperature was used to calculate Tmax by extracting and averaging the five maximum temperature recordings on these days per sampling height.

Water vapor pressure deficit (VPD) was calculated using the temperature and relative humidity data of the loggers located in 0.1 m above-ground with the RH to VPD function in R included in the plantecophys (Duursma, 2015). For each of the four testing sites, daily mean VPD was calculated as average over all values per day. A subset of the 20 days with the highest daily mean VPD was used to calculate VPDmax by extracting and averaging the five maximum VPD recordings on these days per plot.

The number of frost days was calculated as the total number of days per plot with a minimum temperature of less than or equal 0 °C within a defined time interval. The time interval was chosen depending on the availability of measurements, e.g., constant number of data-loggers and readings available (Table 3).

For the comparisons between groups, the data was tested for normal distribution by conducting Shapiro tests. As normal distribution was not given, non-parametric Kruskal-Wallis tests were conducted and subsequent pairwise Wilcox tests with Bonferroni adjustments to test for differences between the groups or forest categories.

For the data retrieved from the data-loggers, we applied linear mixed-effects models (Table 4) to analyze the effects of canopy cover and distance from the forest edge on mean maximum temperature (Tmax) and mean maximum vapor pressure deficit (VPDmax) using lme4 package in R (Bates et al., 2015). To improve interpretability and reduce multicollinearity, continuous predictors were mean-centered before model fitting.

As previous studies have demonstrated that edge effects on forest microclimate often exhibit a non-linear response to distance (e.g., Cadenasso et al., 1997; Ewers & Banks-Leite, 2013; Slater et al., 2024), we retained the non-linear spline model for inferring the relationship between distance from the forest edge and Tmax. Specifically, we fitted the model *Tmax ~ Canopy cover + s(Distance) + (1 | Forest category)* where *s(Distance)* represents a spline term for distance, and forest category was included as a random effect.

Table 3
Period and days considered for the analysis of frost days, e.g., days with daily minimum temperature of no more than 0 °C.

	Nov	Dec	Apr/May
Grumsin	2022-11-01–2022-11-30	2022-12-01–2022-12-31	2023-04-13–2023-05-13
Hainich	2022-11-11–2022-11-27	2022-12-01–2022-12-31	2023-04-13–2023-05-13
Kellerwald	2022-11-01–2022-11-23	2022-12-01–2022-12-31	2023-04-12–2023-05-12
Serrahn	2022-11-01–2022-11-30	2022-12-01–2022-12-31	2023-04-04–2023-05-04

Table 4
List of linear mixed-effect models employed. *Tmax* and *VPDmax* represents mean maximum temperature and mean maximum VPD respectively, *Canopy cover* represents mean canopy cover based on densiometer data, *Distance* represents distance from forest edge. *Forest category indicates* for; a) Grumsin (CZ = core zone, BZ = buffer zone, NF = non-forest); b) Hainich (CZ = core zone, BZ = buffer zone, ED = forest edge, NF = non-forest agricultural land); c) Kellerwald (CZ_A = core zone A, CZ_B = core zone B, OF_A = open forest A (dead spruce stand), OF_B = open forest B (open beech stand), NF_A = non-forest A, NF_B = non-forest B); d) Serrahn (CZ = core zone, BZ_C = pine stand with dense beech understorey, BZ_B = pine stand mixed low broadleaved understorey, BZ_A = pure pine stand, ED = forest edge, NF = non-forest).

Model	Equation
i	Tmax ~ Canopy cover * Distance + (1 | Forest category)
ii	VPDmax ~ Canopy cover * Distance + (1 | Forest category)

3. Results

The data assessed in this study reached temperature peak records of more than 40 °C in all component parts (Kellerwald: 46.74 °C; Hainich: 43.95 °C; Grumsin: 43.84 °C; Serrahn: 43.72 °C) (Table S3) and VPD of more than 7 kPa (Kellerwald: 9.03 kPa; Hainich: 7.47 kPa; Grumsin: 7.38 kPa; Serrahn: 7.06 kPa) (Table S4). In each of the four component parts, the highest daily mean temperature exceeded 27 °C (Kellerwald: 28.32 °C; Grumsin: 28.01 °C; Hainich: 27.69 °C; Serrahn: 27.09 °C) and the VPD 2 kPa (Kellerwald: 2.58 kPa; Hainich: 2.39 kPa; Grumsin: 2.24 kPa; Serrahn: 2.02 kPa) (Table S4). The highest average temperature over the 20 warmest days of the respective component part was measured in Grumsin (24.16 °C), followed by Serrahn (23.27 °C), Kellerwald (22.70 °C) and Hainich (22.54 °C). Maximum temperatures exceeded 30 °C and went up to almost 40 °C in the beech forests and were above 40 °C and up to more than 46 °C in the non-forest. The highest average mean VPD per component part was recorded in Kellerwald (1.46 kPa), followed by Grumsin (1.45 kPa), Hainich (1.38 kPa) and Serrahn (1.34 kPa).

3.1. Maximum temperature (Tmax)

The highest Tmax were measured in the non-forests of all four study areas (Fig. 2, Table S5- S8, Fig. S2 (a – d)) (see Fig. 3).

In Grumsin, significant differences in maximum temperature (Tmax) were observed among the zones. At 1.3 m height, Tmax in the buffer zone (BZ) was 0.46 °C lower than in the core zone (CZ), with this difference being statistically significant ($p < 0.05$). At 0.1 m, the temperature difference between BZ and CZ was 0.53 °C, though this was not statistically tested. Compared to the non-forests (NF), Tmax in BZ was approximately 6 °C lower ($p < 0.001$) at both measurement heights, with highly significant differences (Fig. 2a, Table S5).

In Hainich, the zones differed significantly from each other, with the exception of the core zone (CZ) and the buffer zone (BZ), both near the ground (Fig. 2b, Table S6). The core zone recorded the lowest temperature values, remaining more than 7 °C cooler ($p < 0.001$) near the ground than the non-forest (NF). The forest edge (ED) was 3.03–4.96 °C ($p < 0.001$) warmer than the core and buffer zones and 1.84–2.15 °C cooler ($p < 0.001$) than the NF area.

In Kellerwald, the two analyzed core zones (CZ_A, CZ_B) showed no significant difference in maximum temperatures, but all other sites differed significantly ($p < 0.001$) from each other and from the two core zones (Fig. 2c). The core zones were 5.15–9.31 °C cooler ($p < 0.001$) than the two non-forests (NF_A, NF_B) where the highest maximum temperatures were measured (Table S7).

In Serrahn, the core zone (CZ) and the pine stand with dense beech

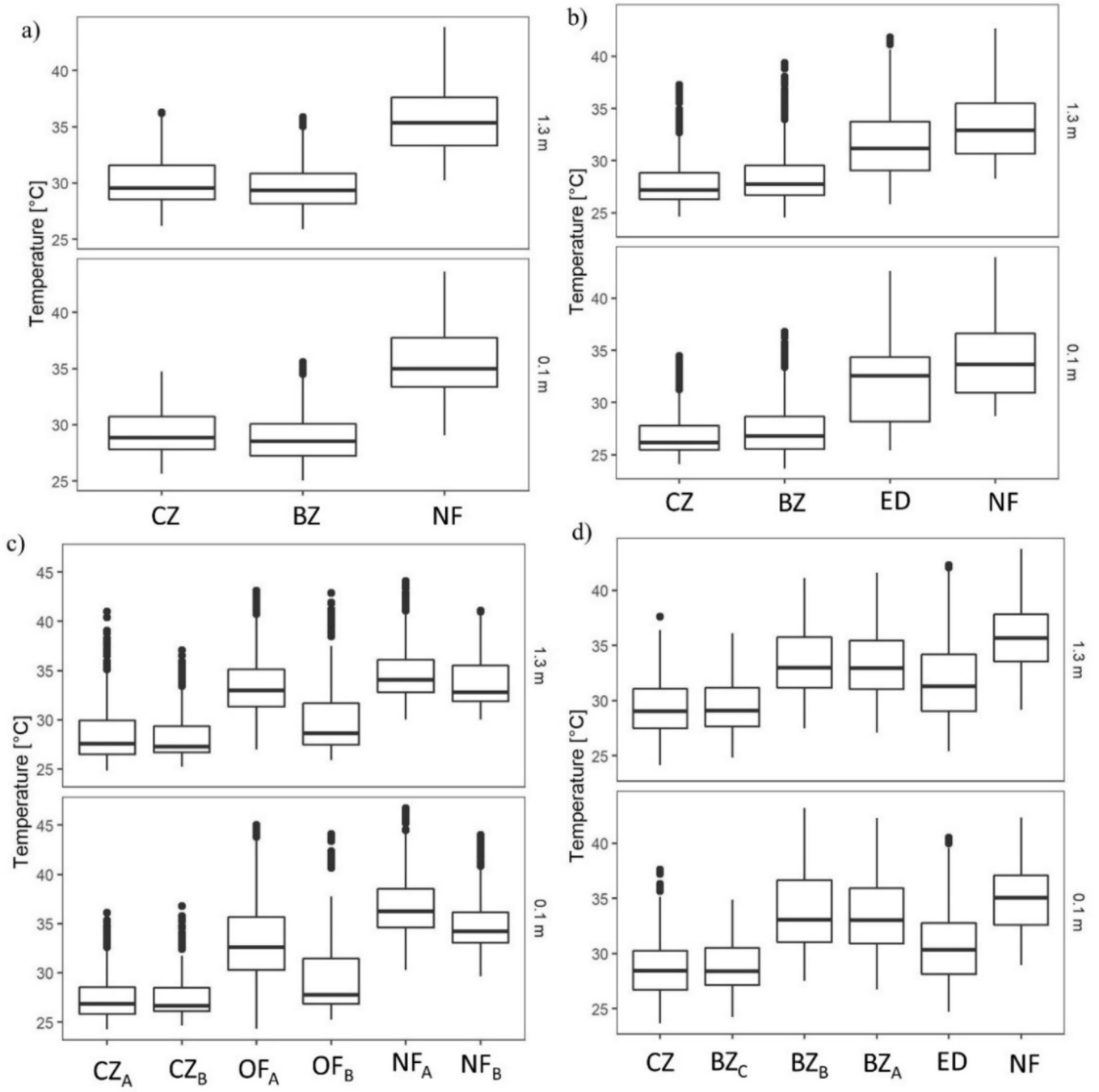


Fig. 2. Boxplots showing median (horizontal line) maximum temperature in a) Grumsin (CZ = core zone, BZ = buffer zone, NF = non-forest); b) Hainich (CZ = core zone, BZ = buffer zone, ED = forest edge, NF = non-forest agricultural land); c) Kellerwald (CZ_A = core zone A, CZ_B = core zone B, OF_A = open forest A (dead spruce stand), OF_B = open forest B (open beech stand), NF_A = non-forest A, NF_B = non-forest B); d) Serrahn (CZ = core zone, BZ_A = pure pine stand, BZ_B = pine stand mixed low broadleaved understorey, BZ_C = pine stand with dense beech understorey, ED = forest edge, NF = non-forest) for each height level (in ca. 1.3 m and 0.1 m above ground).

(BZ_C) layer did not differ from each other and both had significantly lower maximum temperatures (up to 7.32 °C, $p < 0.001$)) compared to the other areas (Fig. 2d, Table S8). The two pine stands with low understorey vegetation (BZ_B, BZ_A) showed almost similar high temperatures (33.24–33.79 °C) as the non-forest (NF) (35.07–36.02 °C).

The results of the linear mixed-effects model i showed that the effect of canopy cover on mean maximum temperature (Tmax) varied across the four component parts (Table S9). In Hainich, Kellerwald, and Serrahn, canopy cover was significantly associated with a reduction in Tmax ($p < 0.001$), and models showed high marginal R^2 values (>0.80), indicating that fixed effects accounted for a substantial proportion of the variance. In Grumsin, however, the effect of canopy cover was not statistically significant ($p = 0.076$), with a low marginal R^2 (0.10) and a high conditional R^2 (0.946), suggesting that most of the variation in Tmax was attributable to differences among forest category (ICC = 0.94). Based on the non-linear model, distance from the forest edge showed a significant, site-dependent effect on Tmax, with the strongest reductions in Tmax occurring close to the edge and diminishing with increasing distance, particularly in Hainich and Kellerwald. This pattern reflects a non-linear, saturating relationship, where edge effects weaken

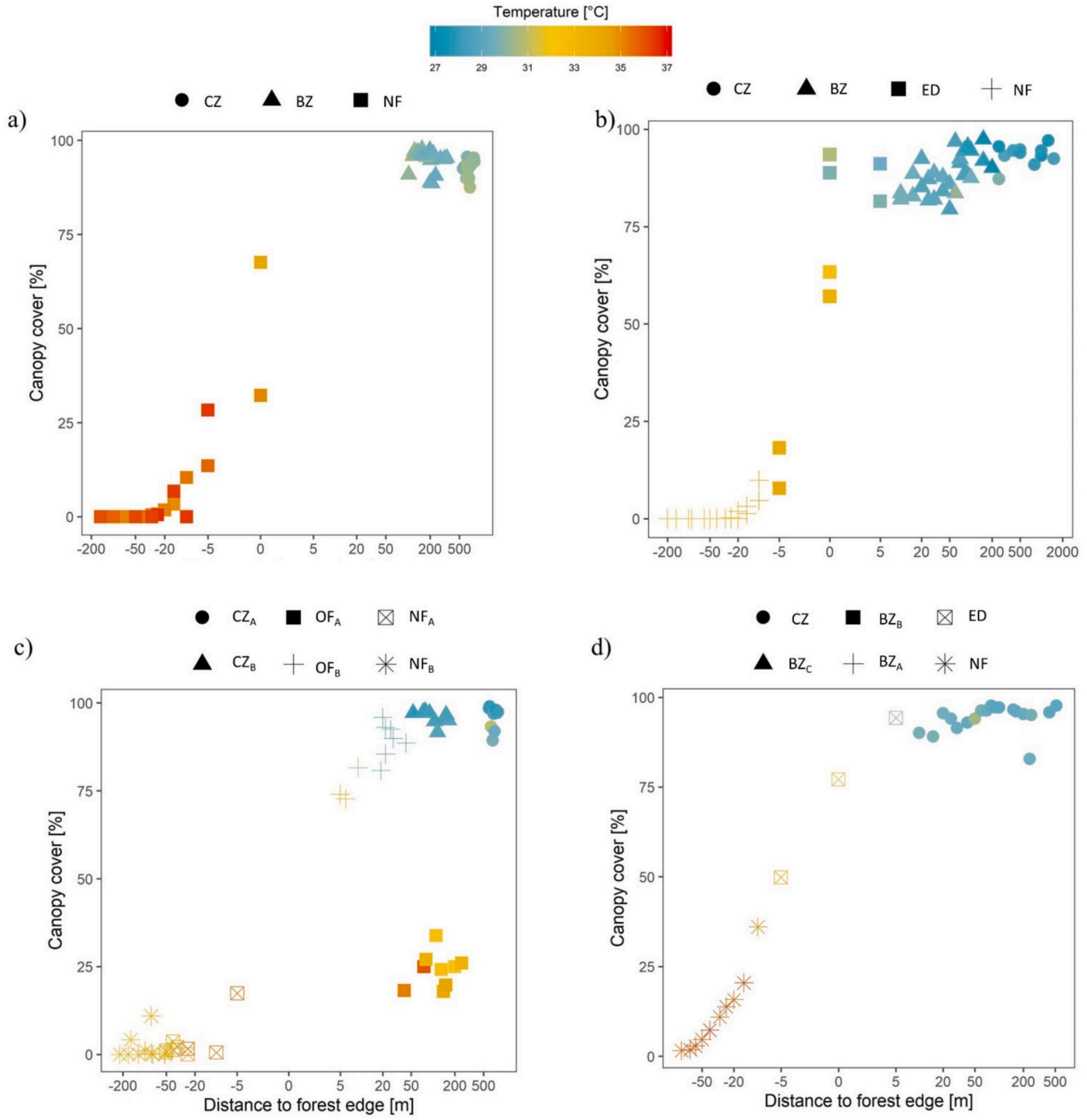


Fig. 3. Interrelation of Tmax in 1.3 m above ground with canopy cover and distance to forest edge in a) Grumsin (CZ = core zone, BZ = buffer zone, NF = non-forest); b) Hainich (CZ = core zone, BZ = buffer zone, ED = forest edge, NF = non-forest agricultural land); c) Kellerwald (CZ_A = core zone A, CZ_B = core zone B, OF_A = open forest A (dead spruce stand), OF_B = open forest B (open beech stand), NF_A = non-forest A, NF_B = non-forest B); d) Serrahn (CZ = core zone, BZ_A = pure pine stand, BZ_B = pine stand mixed low broadleaved understorey, BZ_C = pine stand with dense beech understorey, ED = forest edge, NF = non-forest) for each height level for each height level (in ca. 1.3 m and 0.1 m above ground). Each point represents one sample plot; the colour of a point indicates Tmax; the shape of each point corresponds with the forest category of the sampling plot.

deeper into the forest interior (Table S10).

3.2. *Vapour pressure deficit (VPD)*

In all investigated component parts, the highest VPDmax was measured in a non-forest zone, where mean VPDmax on the driest days was above 4 kPa, while maximum values were about 7 kPa (Fig. 4, Table S11-S14).

In Grumsin, all zones differed significantly from each other, with VPDmax in the buffer (BZ) and core zones (CZ) being 1.82 kPa and 1.64 kPa lower than in the non-forest (NF) respectively (both $p < 0.001$) (Fig. 4a, Table S11).

In Hainich, the largest significant difference in VPDmax (1.87 kPa, $p < 0.001$) was found between the core zone (CZ) and the non-forest (NF).

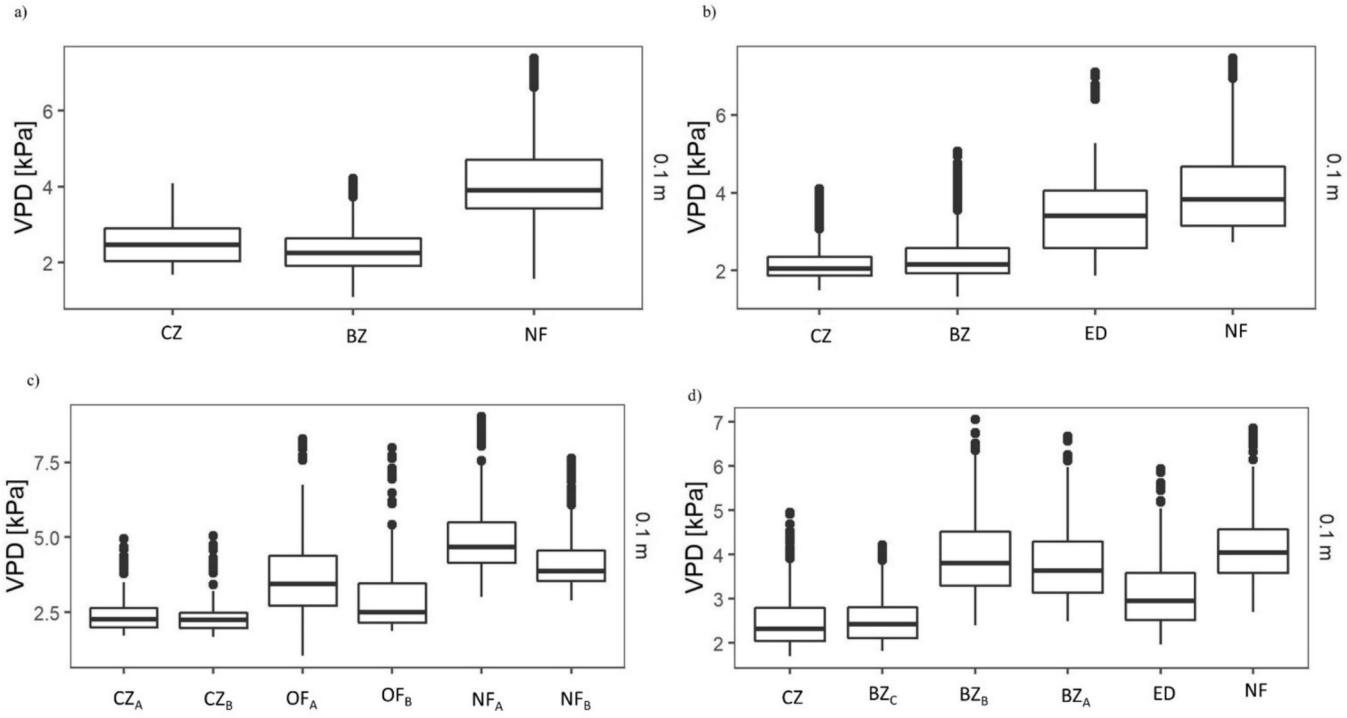


Fig. 4. Boxplots showing median (horizontal line) maximum VPD in a) Grumsin (CZ = core zone, BZ = buffer zone, NF = non-forest); b) Hainich (CZ = core zone, BZ = buffer zone, ED = forest edge, NF = non-forest agricultural land); c) Kellerwald (CZ_A = core zone A, CZ_B = core zone B, OF_A = open forest A (dead spruce stand), OF_B = open forest B (open beech stand), NF_A = non-forest A, NF_B = non-forest B); d) Serrahn (CZ = core zone, BZ_A = pure pine stand, BZ_B = pine stand mixed low broadleaved understorey, BZ_C = pine stand with dense beech understorey, ED = forest edge, NF = non-forest) for each height level for 0.1 m above ground.

The difference between buffer and core zone was 0.15 kPa ($p < 0.05$) and between forest edge and non-forest 0.63 kPa ($p < 0.05$) (Fig. 4b, Table S12).

In Kellerwald, the two core zones (CZ_A, CZ_B) studied showed no signiicant difference in VPDmax, but all other sites differed significantly from each other and from the two core zones (Fig. 4c, Table S13). The highest VPDmax was found in the non-forests. In non-forest (NF_A), the VPDmax value was more than twice as high as in the two core zones ($p < 0.001$). In the spruce forest affected by severe forest dieback (OF_A), VPD max was 0.57–1.35 kPa lower than in the non-forests and 1.18–1.22 kPa higher than in the core zones ($p < 0.001$).

In Serrahn, the core zone (CZ) and the pine stand with dense beech (PF) understorey did not differ from each other and had significantly lower VPDmax of 1.67–1.78 kPa compared to the non-forest plots ($p < 0.001$). (Fig. 4d, Table S14). The two pine stands with low understorey cover did not differ significantly from the non-forests (NF), where the VPDmax was more than 4 kPa and thus highest.

The results of linear mixed-effects model ii showed that the effect of canopy cover on mean maximum VPD (VPDmax) varied across the four component parts (Table S15). In Hainich, Kellerwald, and Serrahn, canopy cover was significantly associated with a reduction in VPD ($p < 0.001$), and models showed high marginal R^2 values (≥ 0.72), indicating that fixed effects explained a substantial portion of the variance. In Grumsin, however, the effect of canopy cover was not statistically significant ($p = 0.705$), with a low marginal R^2 (0.092) and a high conditional R^2 (0.951), suggesting that most of the variation in VPD was attributable to differences among forest category (ICC = 0.95). Distance to the forest edge did not have a significant effect on VPD at any of the component parts. (Table S15, Fig. 5).

3.3. Frost

During the study period, the first frost days were observed in November 2022. In Grumsin, five frost days were recorded in all plots out of the 30 days considered (Fig. 6). In Hainich, frost was observed on five to six days in the core and buffer zones, and on five to seven days in the forest edge and non-forests, out of the 17 days considered. In Kellerwald, frost was recorded on three to four days in the core zones and non-forests, and on four to five days in the open forest areas.

In December, 16 frost days (out of 30 days considered) were recorded in all plots in Grumsin, with one additional day recorded in three out of nine plots in the core zone (Fig. S3a). In Hainich, 16 to 17 frost days were observed in the core zone, and up to 18 frost days were recorded in all other zones (out of 31 days considered) (Fig. S3b). In Kellerwald, the lowest number of frost days (17 out of 31 days considered) was recorded in the open beech forest, followed by 18 frost days in the CZ_B and 18–19 frost days in the non-forest B. In all other plots, 20 frost days were observed (Fig. S3c). In Serrahn, 11 to 12 frost days were recorded in all zones, with 13 frost days observed in two plots in the pine forest (Fig. S3d).

The last frost days were recorded in April 2023. In Grumsin, no frost was recorded on nine days in the core zone (in seven out of eleven plots) and in the buffer zone (in eight out of eleven plots), while frost was observed on one or two days in the non-forests. In Hainich, no frost was recorded in one of the three core zone plots, and in eight out of 14 plots in the buffer zone; frost was recorded on one day in the remaining plots and up to three days in the other zones. In Kellerwald, one frost day was recorded in the two core zones and in the open beech forest, two to three days in the dead spruce forest, and up to six days in the non-forests. In Serrahn, five to seven frost days were recorded in the core zone, six to seven days in the non-forest and mixed beech–pine stands, and eight to twelve days in the pure pine stand and the pine stand with low beech understorey. Overall, no clear difference in frost days was detected between forest types (Table S16).

4. Discussion and conclusions

We provide evidence that mature, well-protected beech forests

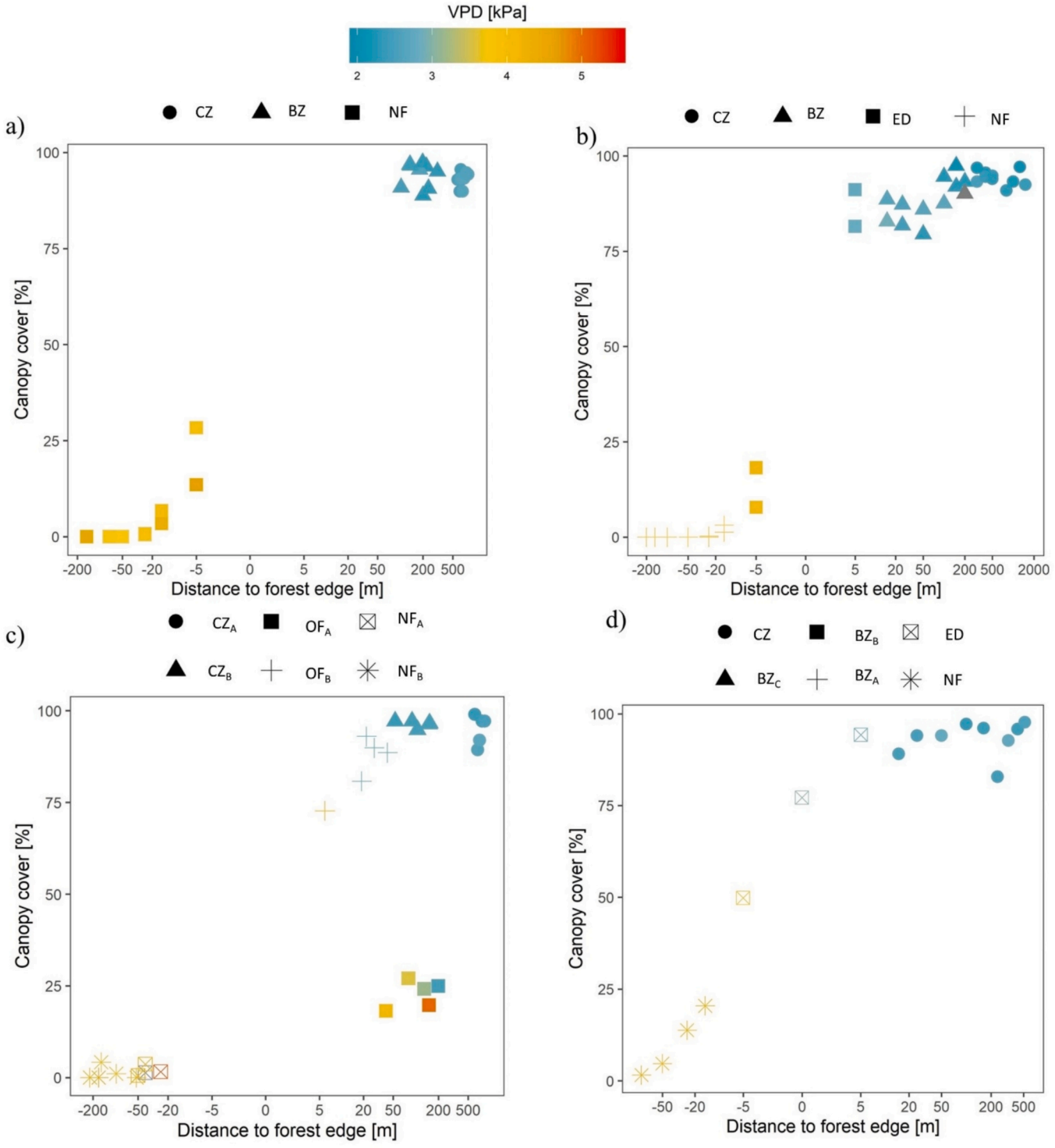


Fig. 5. Interrelation of VPDmax at ground level with canopy cover and distance to forest edge in a) Grumsin (CZ = core zone, BZ = buffer zone, NF = non-forest); b) Hainich (CZ = core zone, BZ = buffer zone, ED = forest edge, NF = non-forest agricultural land); c) Kellerwald (CZ_A = core zone A, CZ_B = core zone B, OF_A = open forest A (dead spruce stand), OF_B = open forest B (open beech stand), NF_A = non-forest A, NF_B = non-forest B); d) Serrahn (CZ = core zone, BZ_A = pure pine stand, BZ_B = pine stand mixed low broadleaved understorey, BZ_C = pine stand with dense beech understorey, ED = forest edge, NF = non-forest) for each height level. Each point represents one sample plot; the colour of a point indicates VPDmax; the shape of each point corresponds with the forest category of the sampling plot.

provide strong microclimatic buffers, significantly reducing maximum temperatures (Tmax) and water vapor pressure deficits (VPDmax) during hot-days, when compared to adjacent open, non-forests. Several studies have also documented that mature, old-growth forests serve as effective buffers, stabilizing local microclimatic conditions (Adhikari et al., 2024; Betts et al., 2018; Frey et al., 2016; Lindenmayer et al., 2022; Thom et al., 2020; Wolf et al., 2021). However, the effect of forests on frost is less clear. Frost as such should not be a problem in temperate forests, but especially late frosts after warm winters could increase vulnerability (Meyer et al., 2022). In this context, it is important to note that in the studied forests the core and buffer zones with dense vegetation had the lowest number of frost days. Even within well-

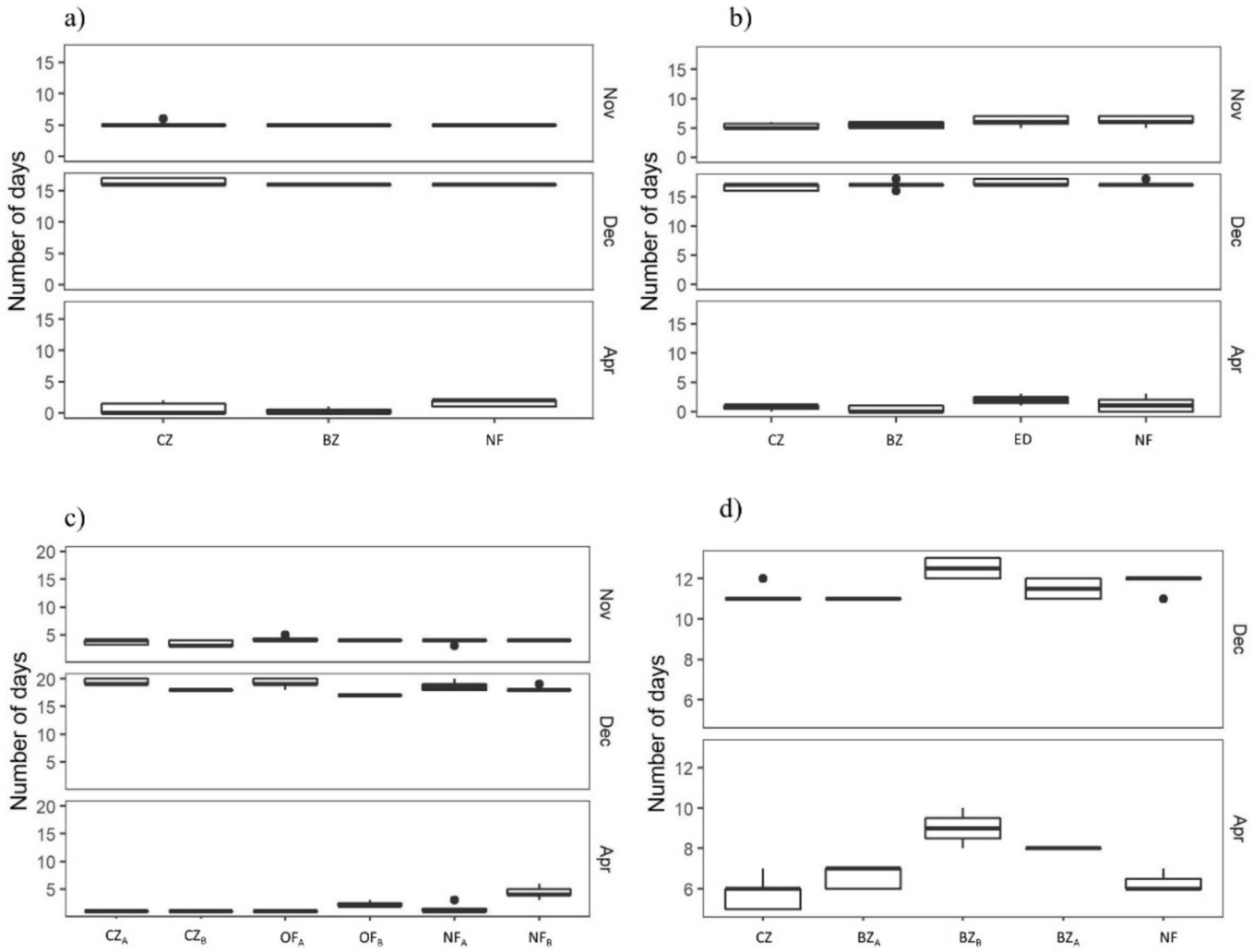


Fig. 6. Number of frost by forest category and time period in a) Grumsin (CZ = core zone, BZ = buffer zone, NF = non-forest); b) Hainich (CZ = core zone, BZ = buffer zone, ED = forest edge, NF = non-forest agricultural land); c) Kellerwald (CZ_A = core zone A, CZ_B = core zone B, OF_A = open forest A (dead spruce stand), OF_B = open forest B (open beech stand), NF_A = non-forest A, NF_B = non-forest B); d) Serrahn (CZ = core zone, BZ_A = pure pine stand, BZ_B = pine stand mixed low broadleaved understorey, BZ_C = pine stand with dense beech understorey, ED = forest edge, NF = non-forest).

buffered old-growth forests, relatively extreme temperatures and VPD values can be recorded on extreme days.

Our findings show canopy cover has a significant cooling effect, reducing both VPDmax and Tmax during the hot and dry days. Based on some data from older studies (Brantley et al., 2017; Ferchaw et al., 2013; Sohn et al., 2016), there are silvicultural recommendations to apply thinning and increase canopy openness in the forests in order to promote their adaptation to climate change, but the results of microclimatic measurements during the recent extreme years do not support this approach (Blumröder et al., 2021; Blumröder et al., 2022). Extreme maximum temperatures and atmospheric drought have become very relevant risk factors for forests and can be controlled by vegetation density.

Protecting old forests effectively requires the establishment of wide, vegetated buffer zones (Adhikari et al., 2024). These buffers should be as wide as possible, particularly where they border non-forested or even unvegetated areas, and should consist of dense vegetation forming a closed canopy. There is an increased risk of damage to trees on unbuffered boundaries between open land and forest with extreme microclimatic differences. Previous studies have shown that the strongest changes in microclimate, vegetation structure, and tree mortality occur within the first 15–100 m from the forest edge, with canopy openness and edge-driven tree mortality declining beyond this zone (Laurance et al., 1997; Williams-Linera, 1990). Consistent with this, our findings show that maximum temperatures were elevated near forest edges and declined with distance into the forest interior, reflecting a strong edge-to-interior gradient in thermal conditions. This pattern was most pronounced in Hainich and Kellerwald, whereas at the other sites the gradient was weaker or not statistically significant, supporting the conclusions that microclimatic buffering by forests is context-dependent and more effective where vegetation structure and buffer zones are intact. Forest gaps increase the risk of heat and VPD penetrating the core of old forests. In landscapes where buffer zones are narrow, degraded, or fragmented – as is often the case in managed forests, the forest's ability to moderate such extremes is significantly reduced. (Ewers & Banks-Leite, 2013). In contrast, forests surrounded by wide, dense and structurally complex buffer zones experience less penetration of heat and drought conditions. This helps to maintain cooler and more stable microclimates at their centres (Adhikari et al., 2024)." As climate change advances, it will become increasingly important to maintain and even strengthen the microclimatic buffering effect of the forest. It is therefore sensible to allow succession and the development of shrubby structures into the open and to avoid abrupt edges.

Besides the canopy cover, cooling and buffering also depend on the understorey structure (Thrippleton et al., 2018). In Grumsin, the dense regeneration of the beech forest in the buffer zone resulted in even lower

temperatures than in the core zone. This is also related to the recent history of the core zone, as windthrow events have caused openings in the canopy, at least temporarily, resulting in higher temperatures. In Kellerwald, some areas characterised by old trees still show a long-lasting legacy of earlier forest management, as the density of old trees was reduced before protection several decades ago. This may negatively affect the microclimatic regulation capacity. In Serrahn, dense beech understorey in pine plantations was found to increase the reduction of maximum temperatures and VPD. Comparable effects have also been shown in other studies (Blumröder et al., 2021; Blumröder et al., 2022; Díaz-Calafat et al., 2023). In comparison, the two pine stands with little or no broadleaf understorey were only about 1 to 2.5 K cooler than the non-forest. In general, the conifer stands studied had higher temperatures and VPD than the beech stands likely due to higher canopy openness and lower structural complexity in the conifer stands. This aligns with findings from Adhikari et al. (2024) where coniferous forests also exhibited higher temperatures and lower vitality in and around all five old growth forests during recent hot years. This has important management implications, as it shows that even a structurally poor plantation can become more heat and drought tolerant in a relatively short period of time if the development of a broadleaved understorey is supported. In this context, the management of large herbivores in regions dominated by conifer plantations is expected to reduce forest vulnerability. It's important not to overlook the understorey structure when studying how forests respond to climate change, as it can significantly influence temperature and drought impacts. In this study, only canopy cover was measured as an indicator of forest structure, while other important attributes such as understorey vegetation cover, height, and species composition were not quantified. This limited our ability to fully evaluate the contribution of the understorey to microclimate buffering, particularly at sites such as Serrahn and Grumsin, where this contribution could be considerable. Future research should include quantitative understorey measurements using standardized field methods or remote sensing approaches, including cost-effective methods such as UAV-based observations, which have been successfully applied to characterize complex forest structures, including understorey layers (Solano et al., 2022; Zellweger et al., 2019). As prolonged exposure to extreme maximum temperature and vapor pressure deficit can significantly increase plant stress and mortality (Chawla et al., 2022), future research should focus on quantifying also the duration of conditions exceeding critical ecological thresholds to provide a more comprehensive understanding of their ecological impacts.

Certain conifer plantations (particularly Scots pine) are warmer than broadleaved forests, and their contribution to the risk of forest landscape warming increases significantly as they degrade and collapse (Adhikari et al., 2024). The collapsing spruce stands in Kellerwald, where dead and dying trees were not salvage logged and remained on site are classified as open forest (OF_A). The site was about 4.5–6 °C warmer than the old beech forest in the core zone, but only up to 2 °C cooler than the non-forest. In contrast, the open beech forest (OF_B) was only about 1–2 °C warmer than the old-growth stands. As the conifer plantations degrade and collapse, broadleaved forest patches surrounded by them are increasingly threatened and further amplifies the risk of landscape warming and ecosystem changes. Given the importance of microclimate, these calamity areas should not be (temporarily) converted to open land by clear cutting and salvage logging. These areas show much higher Tmax and VPDmax, comparable to open land. Warming and drying soils as well as suffering vegetation are involved in positive feedbacks that can self-propagate droughts (Li et al., 2023; Vicente-Serrano et al., 2020) and it is increasingly understood that soil heat can outpace air temperature extremes (García-García et al., 2023). Maintaining a high amount of deadwood in the forest is important to protect soil moisture and natural regeneration (Jouy et al., 2023). This contributes to the mitigation of further warming and declining ecosystem functionality.

A recent study by Krüger et al. (2025) showed that strict forest reserves in Germany experienced lower disturbance rates and severities than managed forests, especially during years of climatic extremes. Their findings support our conclusion that protected, structurally intact forests are more resilient to both microclimatic stress and large-scale natural disturbances, strengthening the case for integrating protected forest reserves into landscape management. Our findings also highlight that less disturbed and less stressed forests are more resilient to extreme weather conditions, emphasizing the urgent need for stronger protection of old-growth forests Unfortunately, in Germany, these forests have been reduced to small relics, and even have a more or less intensive history of utilization and silvicultural management. Currently, the forestry sector is advocating for more intensive forest management as a strategy for climate change adaptation. Our findings question the scientific basis of such approaches in the context of old-growth forest conservation. Our study demonstrates that forests with less human intervention perform better under recent extreme weather conditions, reinforcing the importance of preserving their natural state. Our study also proves once again the scientific value of well-protected ancient forests and especially the pan-European UNESCO World Heritage Site of ancient beech forests. These forests are valuable for research because of their function as reference areas and as learning sites especially for nature-based climate adaptation. Appropriate efforts were and are necessary to protect these forests from exploitation and degradation so that they can develop in a 'wilder', largely self-organized manner – and so that a scientific evaluation of their performance is also possible in the future. However, it is deeply concerning that these old-growth forests are in small, isolated fragments within an unfavorable landscape. The German government must take urgent action to fulfill its national and international commitments, including those under the Federal Climate Action Act (Luick et al., 2025a), the EU Nature Restoration Regulation (Luick et al., 2025b) and the Global Biodiversity Framework (CBD, 2024). This involves not only enhancing the protection of existing forests but also prioritizing their restoration and expansion. To safeguard these ecosystems, we must draw lessons from old forests and allow them the space and time needed to develop.

5. Uncertainties and limitations

Among the five UNESCO World Heritage beech forests in Germany, Jasmund was not included in this study due to its location on the Baltic Sea coast in northern Germany, as the maritime influence on the peninsula was expected to dominate over the microclimatic differences caused by the forest structure. The plot network was heterogeneous across the four study sites due to differences in local conditions, permissions, and historical management practices. Although this complicates direct cross-site comparisons, linear mixed-effects models explicitly accounted for site variability by including site-specific random effects. This allowed for a clear analysis of how canopy cover and distance from the forest edge influenced mean maximum temperature (Tmax) and mean maximum vapor pressure deficit (VPDmax). Additionally, the studied beech forests are located at relatively low altitudes, mostly below 500 m, with minimal topographical variations (Adhikari et al., 2024), thereby reducing the potential for significant influences on microclimate. The comparatively lower amount of relative humidity sensors compared to temperature sensors limited the spatial resolution of humidity data and therefore VPD.

CRediT authorship contribution statement

Yojana Adhikari: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation. **Jeanette Silvin Blumröder:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Caroline Meier:** Writing – review & editing, Project administration, Investigation, Funding acquisition, Formal analysis. **Pierre L. Ibisch:** Writing – review & editing,

Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.114111.

Data availability

Spatial locations of data loggers are at https://zenodo.org/records/15352367, and corresponding microclimatic data are available at https://zenodo.org/records/10409712.

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