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# Higher soil moisture increases microclimate temperature buffering in temperate broadleaf forests

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ABSTRACT

Forest canopies can buffer the understory against temperature extremes, often creating cooler microclimates during warm summer days compared to temperatures outside the forest. The buffering of maximum temperatures in the understory results from a combination of canopy shading and air cooling through soil water evaporation and plant transpiration. Therefore, buffering capacity of forests depends on canopy cover and soil moisture content, which are increasingly affected by more frequent and severe canopy disturbances and soil droughts. The extent to which this buffering will be maintained in future conditions is unclear due to the lack of understanding about the relationship between soil moisture and air temperature buffering in interaction with canopy cover and topographic settings. We explored how soil moisture variability affects temperature offsets between outside and inside the forest on a daily basis, using temperature and soil moisture data from 54 sites in temperate broadleaf forests in Central Europe over four climatically different summer seasons. Daily maximum temperatures in forest understories were on average 2 °C cooler than outside temperatures. The buffering of understory temperatures was more effective when soil moisture was higher, and the offsets were more sensitive to soil moisture on sites with drier soils and on sun-exposed slopes with high topographic heat load. Based on these results, the soil–water limitation to forest temperature buffering will become more prevalent under future warmer conditions and will likely lead to changes in understory communities. Thus, our results highlight the urgent need to include soil moisture in models and predictions of forest microclimate, understory biodiversity and tree regeneration, to provide a more precise estimate of the effects of climate change.

## 1. Introduction

Forest canopies can buffer understory microclimate and biodiversity against temperature extremes and drought (De Frenne et al., 2021; Geiger et al., 2012). Compared to open fields with short vegetation, temperatures under forest canopies often show dampened diurnal and even seasonal fluctuations with less extreme hot and cold temperatures during day and night, respectively. This dampening or moderation of temperature extremes is often referred to as the "buffering" function of forests (De Frenne et al., 2021; Lenoir et al., 2017) and as "cooling" function when specifically referring to buffering of warm extreme temperatures. Survival, performance and distribution of many forest organisms, including seedlings of late-successional shade-tolerant tree species and cold-adapted understory plants, are dependent on buffered understory microclimates (Greiser et al., 2020; Hylander, 2005; Löbel et al., 2018; Scheffers et al., 2014). As the climate is warming, the frequency and severity of heat waves and soil droughts have been increasing and will likely increase in the future (IPCC, 2021). Therefore, the capacity of forests to buffer heat will become increasingly important for forest biodiversity and functioning. Nevertheless, the future buffering function of forests is at risk because it depends on stable canopy cover and sufficient soil water content (De Frenne et al., 2021).

Buffering of daily maximum temperatures in forest understories is the net result of canopy shading, soil water evaporation and plant transpiration (the latter two together referred to as *evapotranspiration*), as well as soil thermal inertia, in turn dependent on soil moisture, due to the high heat capacity of water (Ashcroft and Gollan, 2013; Davis et al., 2019; De Frenne et al., 2021). Evapotranspiration is a very efficient

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surface cooling mechanism as the latent heat flux of water evaporation is high. Forests with a more closed canopy provide a stronger buffering effect because the denser canopies can reflect and absorb more radiation and transpire or intercept and evaporate more water (Al-Kaisi et al., 1989; Wei et al., 2018). Dense broadleaf canopies are also better capable to separate air masses below and above the canopy.

The buffering capacity of forests can be quantified by the temperature offset, i.e., the difference between the temperature inside and outside the forest (below the canopy and in open areas respectively). The offset has been measured and modelled at different spatial and temporal scales, often with a focus on monthly or seasonal average offsets (Frey et al., 2016; Kašpar et al., 2021; Von Arx et al., 2012; Zellweger et al., 2019). Based on statistical models, offsets have also been extrapolated in space (Frey et al., 2016; Greiser et al., 2018; Haesen et al., 2021; Jucker et al., 2018) and/or in time (De Lombaerde et al., 2022). However, these extrapolations often disregard changes in the local water balance and the effects of overcast skies, moist air and dry soils, which would limit evaporative cooling (Davis et al., 2019; Seneviratne et al., 2010). Importantly, the role of soil moisture and its fluctuations has been overlooked in microclimate modelling. Existing models often use spatially variable but temporally static soil moisture estimates (e.g., topographic wetness indices, as in Fridley, 2009; Greiser et al., 2018; Macek et al., 2019; Vanwalleghem and Meentemeyer, 2009; Wolf et al., 2021a). Continuous time-series of in-situ measured soil moisture are, therefore, needed to investigate the potential importance of soil moisture in temperature buffering.

The coupling of near-ground temperatures to soil moisture has been demonstrated at local and global scales and the physical principles behind it are well understood (Campbell and Norman, 1997). In the relationship between soil moisture and evaporative fraction (defined as the ratio between latent heat flux and available energy at the land surface), we can expect three contrasting regimes: wet, transitional, dry (Seneviratne et al., 2010). In the dry and wet regimes, changes in soil moisture do not lead to changes in the evaporative fraction (and thus surface temperature), because it is either too dry for plant roots to effectively take up water and support evaporative cooling (dry regime, usually only found in deserts), or the system is energy-limited and a further increase in water availability would not enhance evapotranspiration (wet regime). Only in the transitional regime we can expect a coupling of soil moisture and surface temperature via changes in the evaporative fraction (Schwingshackl et al., 2017; Seneviratne et al., 2010). Therefore, non-linear responses of surface temperature to soil moisture can be expected when the system shifts between regimes. This may happen for one and the same forest location when soil moisture increases from dry or mesic (moisture-limited) to wet (energy-limited), and as both soil moisture regimes and energy input via solar radiation varies across topographically complex landscape and canopy gradients, we would expect spatial variations in the shape of the temperature – soil moisture relationship. This has, however, not been explored explicitly.

Global-scale analyses (e.g., Seneviratne et al., 2010; Schwingshackl et al., 2017) have laid valuable groundwork in this field. Nevertheless, they operate at spatial resolutions of several kilometers, a limitation particularly relevant when studying variables like soil moisture, which can exhibit strong variation over short distances (Ali et al., 2010; Kaiser and McGlynn, 2018; Tague et al., 2010; Vergopolan et al., 2022). Indeed, the work of Von Arx et al. (2013) and Davis et al. (2019) has provided significant insights on local scales, investigating the relationships between microclimate buffering, canopy cover, and locally measured or modelled soil moisture. Von Arx et al. (2013) provided understanding of the mechanisms linking soil moisture, canopy and understory temperature during periods of homogeneous weather conditions by focusing on time-integrated buffering capacity in forests with varying Leaf Area Index (LAI). However, spatiotemporal heterogeneity in soil moisture and microclimate temperature underscores the need for daily field-collected data to disentangle the interactive effects of canopy openness, topography, and soil moisture on forest microclimatic buffering.

Mechanistic models describing the coupling of energy and water exchange among the soil, canopy and the atmosphere could in principle account for the key mechanisms at a fine spatial resolution. Nevertheless, they require detailed information on canopy structure, soil properties and atmospheric conditions to generate accurate landscape-scale predictions (e.g., Maclean and Klinges, 2021) and have seldom been validated with empirical data over a wide range of conditions (e.g., Luan and Vico, 2021). As such, they may not provide reliable estimates of the spatial relationships between temperature offset, soil moisture, canopy and topography.

In summary, despite attempts to quantify the coupling between soil moisture and near-ground temperature, we know little about the *shape* of this relationship in forest understories as well as about the *interaction* with canopy cover and topographic setting at the landscape scale. This knowledge gap has been emerged, among others, from data and model limitations (Babaeian et al., 2019; Dorigo et al., 2011). The increasing availability and use of consumer-grade microclimate sensors has just recently allowed the continuous monitoring of in situ understory temperature and soil moisture with appropriate spatial replication and at a sub-daily resolution (e.g., Wild et al., 2019). With these novel data, we can investigate how soil moisture drives forest microclimate buffering at scales that are relevant for modelling carbon and nutrient balances (Humphrey et al., 2021), for predicting the impact of climate change on species distribution and population dynamics (Woods et al., 2015), and for identifying climate change refugia for threatened species (Greiser et al., 2020; Krawchuk et al., 2020; Wolf et al., 2021a). Studying soil-atmosphere feedbacks at many locations across a heterogeneous landscape is also most appropriate for climate change mitigation as well as regional and local forest management adaptation to a changing climate (Hylander et al., 2021).

In this study, we analyzed 54 time series of in-situ temperature and soil-moisture measured during four growing seasons in temperate forest understories in Central Europe. We explored if and how soil moisture fluctuations drive temperature differences between maximum temperatures outside and inside the forest by linking daily maximum temperature offsets to daily average soil moisture in interaction with canopy openness and topographic heat load, while accounting for daily weather conditions. We ask, whether and when soil moisture drives forest buffering and under which conditions forests can lose their buffering function.

Generally, we expect:

(H1) Offsets are more negative (i.e., there is more buffering/cooling) with increasing soil moisture.

(H2) This relationship (H1) holds true up to a soil moisture level, beyond which a further increase in soil moisture does not lead to a stronger cooling due to an energy limitation (Fig. 1a; Seneviratne et al., 2010).

(H3) The sensitivity of temperature offsets to soil moisture is higher on sites with high topographic heat load, where more solar energy is available to evaporate water (Fig. 1b), and under denser canopies, because they may more efficiently evaporate soil water due to a larger leaf area (Fig. 1c).

Emerging from the specific hypotheses above, we expect that forests can lose their buffering function when soils get too dry on sites that receive a lot of incoming solar radiation (sunny slopes with more open canopy, Fig. 1).

## 2. Materials and methods

### 2.1. Study area

The study area lies at the dry edge of forest distribution in Central Europe, in the Bohemian Karst (Fig. 2). The climate is continental temperate with long warm summers, moderately cold winters and a mean annual temperature of 9.8 °C (Neumětely weather station,

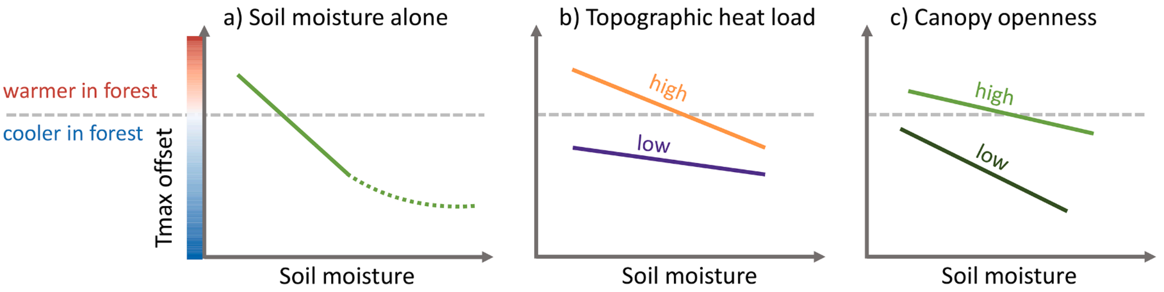

**Fig. 1.** Hypothesized relationship between daily soil moisture and daily maximum temperature offsets in temperate forest understories. We expect a cooling and non-linear effect of soil moisture (a), as well as interactions of soil moisture with topographic heat load (b) and canopy openness (c).

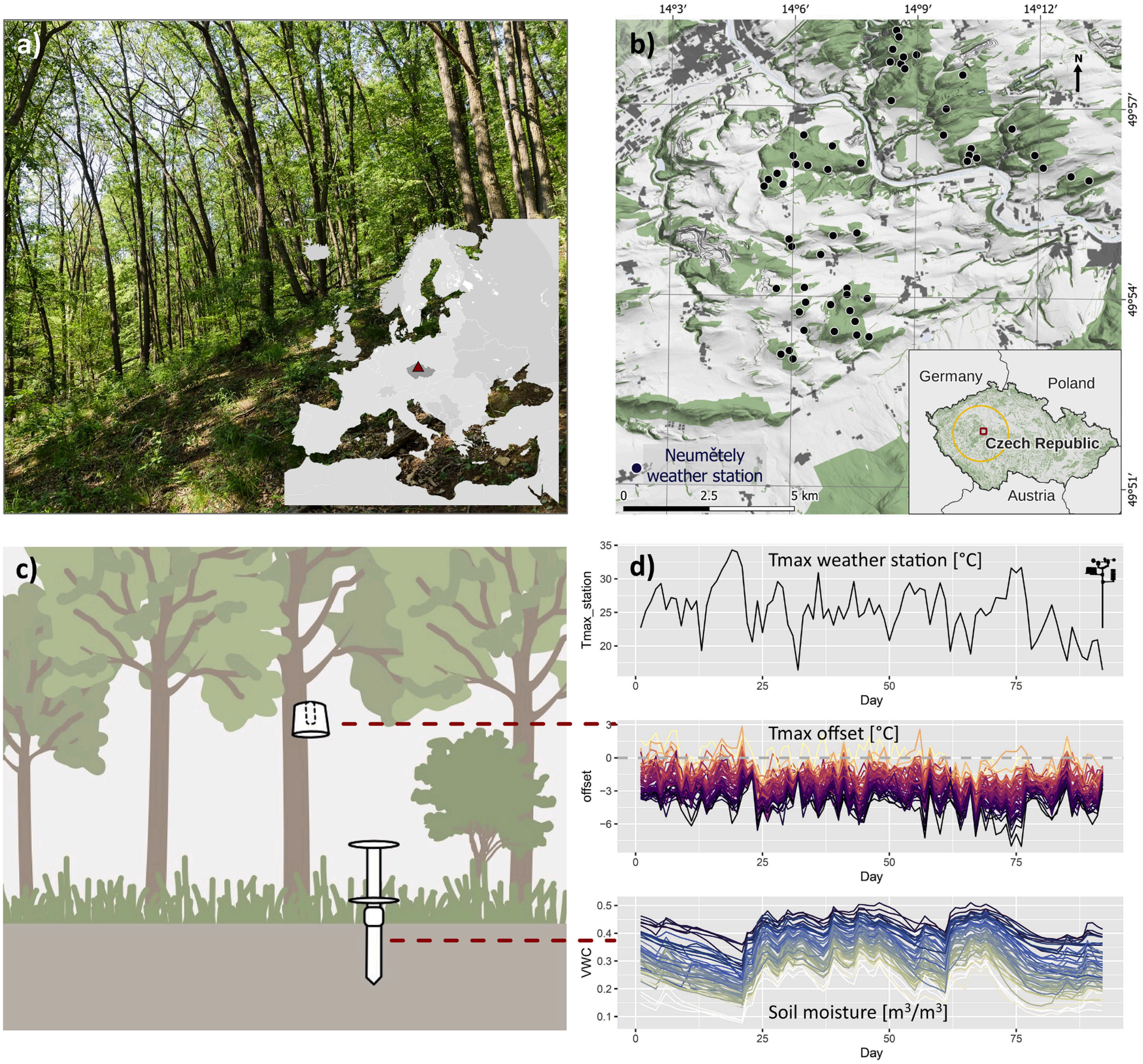

**Fig. 2.** Overview of the study area, sampling design and microclimate data. a) Typical forest in the Bohemian Karst and its location in Europe. b) Terrain in the study area with 54 logger locations (black dots), reference weather station in Neumětely, forests and villages (green and grey patches, respectively). The inset map shows the location of the Bohemian Karst within the Czech Republic (red square) and the area with 35 weather stations used to calculate regional temperature lapse rates (yellow circle). c) Sampling design used at each measurement site with one logger measuring understory temperature at weather station height (2 m above ground) and one logger at the forest floor measuring soil moisture in the soil between 0 and −15 cm. d) Time series of daily maximum temperature at weather station, daily temperature offsets in the forest understoreys and daily soil moisture (VWC = volumetric water content) for all logger sites in the summer 2021 (1st June–31st August).

2012–2021 period). The total annual precipitation over this period was 546 mm and fell mainly as rain. Elevation of the study area ranges from ca. 250 m near the Berounka river up to 500 m a.s.l. on the top of highest hills. The topographic relief represent undulating karst plateau intersected by the Berounka river and its tributaries (Fig. 2).

Dominant forest soils are Cambisols and Leptosols derived from underlying limestones and mudstones (Šamonil et al., 2009). The soils are shallow (<0.5 m) with thin humus layer and predominantly silt-loam texture. The soils are mineral, often well drained and calcareous (Hofmeister et al., 2002).

The combination of a complex karst terrain with varying soil types creates a mosaic of contrasting forest types with high plant species diversity. Forests cover ca. 35 % of the area and are interspersed with grasslands, fields and villages (Fig. 2). Depending on soil conditions and topographic position, the dominant canopy trees are the broadleaf deciduous species *Quercus pubescens, Fagus sylvatica, Quercus petrea* agg., *Carpinus betulus, Fraxinus excelsior, Tilia cordata* and *Acer platanoides.*

### 2.2. *Temperature and moisture measurements*

For microclimate measurement, we selected 64 forest plots from ongoing vegetation monitoring schemes in the study area (Kopecký and Čížková, 2010; Šipoš et al., 2020). The selected plots extended over ca. 50 km$^2$ and cover the vegetation and environmental heterogeneity of the region (Table 1). To reduce potential microclimatic edge effects, all selected plots are situated at least 30 m from the nearest forest edge.

At each plot, we measured understory air temperature at 2 m height with a TOMST Thermologger and soil moisture content of the upper 15 cm of soil with a TOMST TMS logger (Wild et al., 2019). The temperature logger at 2 m was attached to the north side of a tree within maximum 3 m horizontal distance to the TMS logger on the ground. Loggers were protected with standardised white plastic shields blocking direct sunlight and rain. TMS loggers were placed inside wire cages protecting them from wildlife (Wild et al., 2019). Loggers were installed during May 2018 and data were downloaded twice a year, before and after the growing season. Only summer data from each year were used (1st June – 31st August for the years 2018–2021). After filtering out potentially problematic measurements and the loggers with incomplete time series, we restricted the analysis to 54 sites with complete measurements across all four studied summer seasons (Fig. 2b).

As a reference, we used the standard weather station of the Czech Hydrometeorological Institute located in the Neumětely village (Lat 49.8542 °N, Lon 14.0375 °E, Elevation 322 m a.s.l.), ca 5 km SW from the study area (Fig. 2). To account for the elevation differences between the weather station and the forest sites (up to 165 m; Table 1), we adjusted daily maximum temperatures measured at weather station with a regional maximum temperature lapse rate calculated through linear regression between daily maximum temperatures and elevation of 35 standard weather stations operating up to 70 km from the Neumětely weather station (Fig. 2). As a result, temperatures of each forest plot were compared with slightly different temperatures outside the forest, depending on plot elevation and daily temperature lapse rate (see Supporting Information for details).

**Table 1**
Range of environmental variables covered by the 54 logger sites in the Bohemian Karst. Soil moisture represents mean volumetric soil water content over four summer seasons (1st June–31st August in years 2018–2021). Elevation, canopy openness, topographic heat load and mean soil moisture summaries are based on site-averaged values, whereas daily temperature and offset summaries are based on daily values at each site.

| Variable | Unit | Min | Mean | Max | Source |
|---|---|---|---|---|---|
| Elevation | m | 288 | 387 | 487 | Lidar DTM |
| Canopy openness (summer 2018) | % | 3.9 | 10.1 | 23.7 | Hemispherical photographs |
| Topographic heat load | – | −0.48 | 0.04 | 0.45 | Lidar DTM |
| Mean soil moisture | m$^3$/m$^3$ | 0.12 | 0.22 | 0.34 | TMS logger |
| Daily maximum air temperature at 2 m in forest understories | °C | 12.0 | 24.3 | 39.4 | Thermologger |
| Daily temperature offset (forest understory – free-air) | °C | −8.2 | −2.0 | 3.9 | Thermologger and weather station (elevation-corrected) |

Daily offsets (in °C) were calculated by subtracting the daily maximum temperature at weather station (elevation-corrected, see above) from the daily maximum temperature inside the forest measured by the logger at 2-m height.

Daily soil moisture (volumetric soil water content, VWC, in m$^3$/m$^3$) for each site was measured every 15 min by a TMS logger using soil moisture sensor based on Time Domain Transmission principle (Wild et al., 2019). To convert raw measurements into VWC, we used the universal calibration equation for mineral soils (Kopecký et al., 2021) as implemented in the R package *myClim* (Man et al., 2023). From the resulting time-series of VWC, we calculated average VWC for each day and site.

To approximate daily evaporative demand of the atmosphere – which is directly related to the evapotranspiration and hence evaporative cooling – we calculated the daily maximum vapour pressure deficit, VPD, at the reference weather station from daily maximum temperature and daily minimum relative air humidity using an approximation of the Clausius–Clapeyron equation (Magnus equation) implemented in R package *plantecophys* (Duursma, 2015).

### 2.3. *Canopy openness and topographic heat load*

We characterized the sites based on the forest canopy openness and topographic exposure and hence potential incoming solar radiation. The effect of forest density on temperature offsets was approximated by the canopy openness for each site, as estimated from hemispherical photographs. At each site, we captured three upward-facing hemispherical photographs during July 2018, using centre-weighted exposure mode and three different exposures (+0. 33, −0.66, −1.66 EV) using a Canon 40D camera with a Sigma 4.5 mm F2.8 EX DC Circular fish-eye lens levelled at 1 m height. Subsequently, from each exposure set, we selected the exposure maximizing the contrast between canopy and sky pixels, converted the selected RGB image to grayscale with 2BG algorithm, classified canopy and sky pixels using intermodes thresholding method (Chianucci and Macek, 2023), and finally calculated canopy openness at the 100° angle of view (Hederová et al., 2023).

The potential incoming solar radiation was characterized by topographic heat load for each site calculated with the SAGA GIS Diurnal Anisotropic Heating function (Böhner and Antonić, 2009) from a LiDAR digital terrain model (DMR 5G, provided by the Czech Office for Surveying, Mapping and Cadastre) resampled to 10 m resolution using SAGA GIS (Conrad et al., 2015). This index accounts for slope gradient and orientation effects on received solar energy, but contrary to solar radiation, topographic heat load accounts also for the asymmetrical heating of the slopes, with the highest heat load realized at South-Southwest, 202.5° (Böhner and Antonić, 2009). Topographic heat load is a unitless index, with values ranging from −1 (coolest) to +1 (warmest).

While offset, soil moisture and VPD were used as daily fluctuating variables, canopy openness and heat load remained static variables, i.e., the values did not change from day to day or year to year.

### 2.4. *Statistical models*

In our analyses, we allowed non-linear responses, which are expected e.g., for soil moisture (Seneviratne et al., 2010) and canopy openness (Zellweger et al., 2019), and accounted for the random effect of site and measurement year by using generalized additive mixed models (GAMMs) and identity-link functions under the assumption of a Gaussian distribution of errors. Generalized Additive Models (GAMs) are a flexible extension of linear models, designed to capture non-linear relationships in data. While linear models assume a strictly linear relationship between predictors and the response, GAMs allow for the incorporation of smooth, non-linear functions of individual predictors. Importantly, GAMs employ regularization techniques that penalize model complexity, encouraging a simpler linear response when the data suggests linearity, thus striking a balance between capturing non-linearities and adhering to the principle of parsimony.

Before modelling, we reduced possible temporal autocorrelation by using only every 4th day (Davis et al., 2019), which resulted in a dataset with 23, instead of 92, daily values for each summer season. We used this reduced dataset to model temperature offsets as a function of daily soil moisture, canopy openness and topographic heat load (Fig. 3). We included also their three-way interaction to explore under which conditions (in terms of potential energy input modified by canopy openness and topographic heat load) soil moisture drives temperature offsets. To account for the air evaporative demand, we included daily maximum vapour pressure deficit, VPD, at the reference weather station. Due to a limited sample size, we could not include an interaction term of VPD with soil moisture. As random factors, we used year (to account for differences in general weather patterns among years) nested in plot ID (to account for repeated measurements from the same sites). The model included all predictors as non-linear terms:

$$offset = te(soil\_moisture, canopy\_openness, heat\_load) + s(VPD)$$

where *offset* is the daily maximum temperature offset, *te()* is a tensor product capturing interaction among predictors and *s()* is a smooth term capturing potentially non-linear effect of a predictor (Wood, 2017). We fitted the smooth terms and tensor product with restricted maximum likelihood, REML (Wood, 2011), and used thin plate regression splines with extra shrinkage. This extra shrinkage allows the GAMM to set the smooth term to 0 and therefore to effectively exclude from the final model the predictor with no effect on the response variable (Marra and Wood, 2011). We specifically tested for non-linear responses, fitting a linear version of the full-year model using the same model structure and function as above, where both AIC values and model residual distribution supported the non-linear model (AIC.linear = 13,702.91, AIC.nonlinear = 13,027.74). Previous to fitting the full model, we also tested and confirmed the significance of the three-way interaction separately from the single model terms by fitting a model that separated the single model smooth terms from the interaction captured in a *ti()* tensor product (Wood, 2017).

We checked model diagnostics with the function *appraise*() from the R package *gratia* (Simpson, 2022). We repeated the analysis for each of the four years separately, using only plot ID as a random effect and the same thinned dataset (23 days per year).

We performed all statistical modelling in R version 4.2.0 (R Core Team, 2022) using the *tidyverse* suit of packages for data compiling and cleaning (Wickham et al., 2019), the function *gamm()* from the package *mgcv* to fit GAMM models (Wood, 2017) and the package *gratia* (Simpson, 2022) and *ggeffects* (Lüdecke, 2018) for visualizing model outputs.

## 3. Results

### 3.1. Temperature buffering in the forest understory

Summer season averages as well as the temporal distribution of maximum temperatures (at weather station), vapour pressure deficits (at weather station), temperature offsets (at forest sites) and soil moisture (at forest sites) differed in each year (Fig. 4). When considering average values, the years ranked in chronological order with 2018 being the hottest and driest year and 2021 being the coolest and wettest year (Fig. 4).

Forests had on average a cooling effect, with maximum daily temperatures in the forest understory being on average 2 °C colder than maximum temperature outside the forest (Table 1, Fig. 4). The observed temperature offsets considerably varied across sites, days and years (Fig. 4d). In all years, there were also days when temperatures in forest understories were *higher* than temperatures outside forests (positive offsets, Fig. 4d). Daily temperature offsets were related to daily soil moisture in interaction with canopy openness and topographic heat load (effective degrees of freedom, edf = 18.38, $F = 48.49$, $p < .001$; total variance explained by the GAMM: 47 %; Fig. 5; Table S1). Daily vapour pressure deficit, VPD, also contributed to the explained variation, but did not show a consistent pattern (edf = 8.87, $F = 78.24$, $p < .001$; Fig. 6).

### 3.2. Higher soil moisture cools the forest understory

Temperature offsets became on average more negative (i.e., the cooling effect was stronger) when soil moisture was higher (Fig. 5a). As soil moisture at any given site generally fluctuated only over a part of the entire observed gradient (Fig. S2), the effect of daily soil moisture on daily temperature offsets included also the (intercept) effect of generally wetter sites producing generally cooler temperatures. Temperature

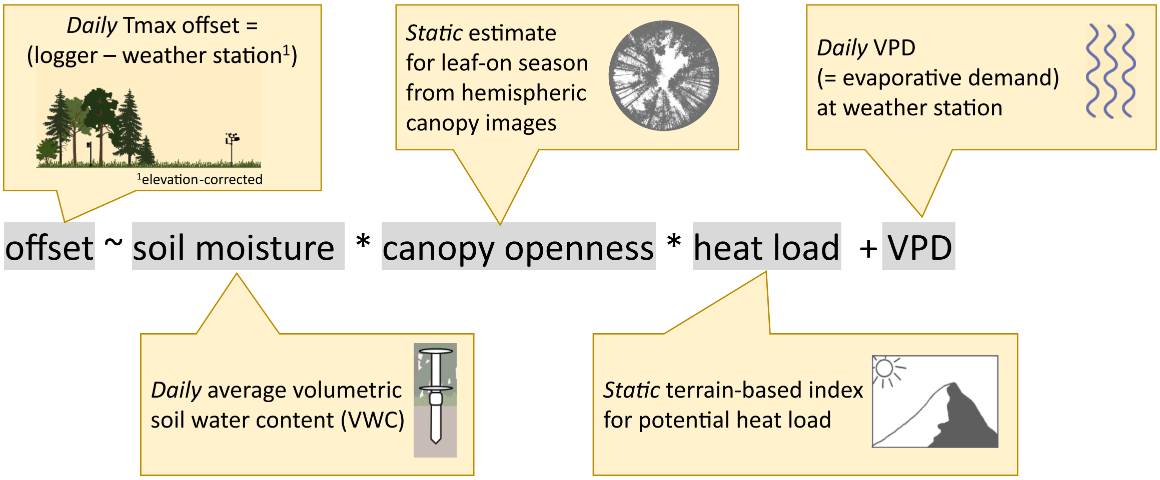

**Fig. 3.** Conceptual figure of the model structure. Daily maximum temperature offsets (Tmax inside forest–Tmax outside forest) were modelled as a function of daily soil moisture, canopy openness, topographic heat load, their three-way interaction and daily maximum vapour pressure deficit, VPD.

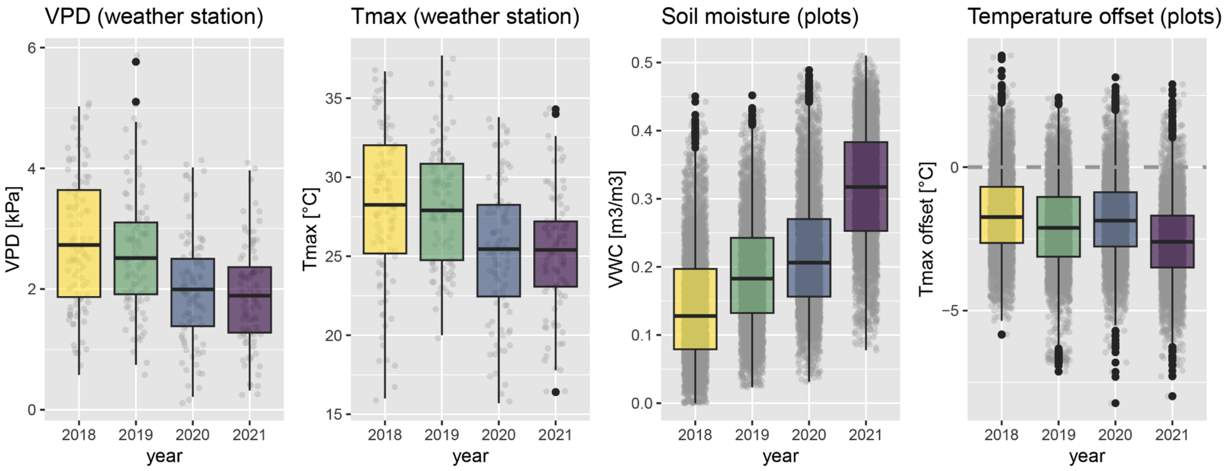

**Fig. 4.** Overview of summer daily values (grey points) of a) VPD and b) Tmax measured at weather station outside forest and c) soil moisture and d) temperature offset measured at 54 forest plots over four years. VPD = vapour pressure deficit, Tmax = daily maximum temperature, VWC = daily soil volumetric water content, Tmax offset = difference between daily maximum temperature inside the forest (measured by a TOMST Thermologger) and outside the forest (elevation-corrected daily weather station data).

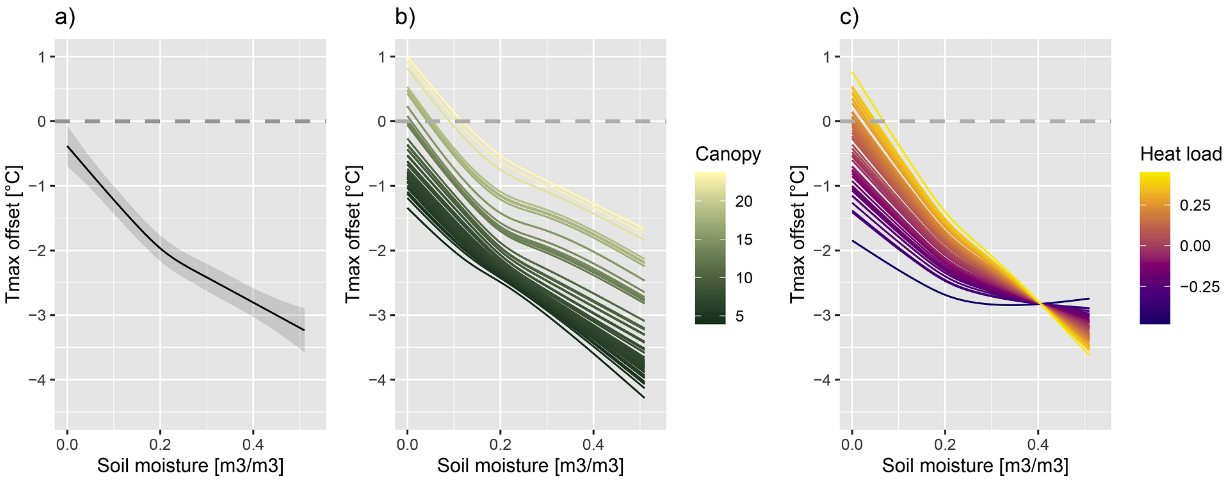

**Fig. 5.** Partial response curves for soil moisture (volumetric soil water content, VWC) averaged over all other predictors (a), and in interaction with canopy openness [%] (b) and topographic heat load (c) where southwest-facing slopes have highest values. Responses are plotted for average random effects and average fixed effects, if not explicitly displayed, e.g., responses in b) are plotted for average topographic heat load (fixed), average VPD (fixed) and averaged over plots (random) and years (random). The shaded area around the GAMM curve represents the 95 % confidence interval. Below the grey dashed line, temperature offsets are negative and forests have a cooling effect. Above the line, offsets are positive and forests are warmer than free-air temperatures.

offsets responded in a non-linear way to soil moisture, where the sensitivity of temperature offsets to soil moisture was often higher in drier than in wetter soils (Fig. 5). In other words, the slopes were steeper at lower soil moistures and shallower at high soil moistures (Fig. 5a), a pattern which was strongest for sites with low topographic heat load values (all other variables held constant, Fig. 5c).

### 3.3. *Canopy openness and topographic heat load effects on forest buffering*

Canopy openness generally reduced the average cooling effect of a forest site, i.e., temperature offsets were less negative under open canopies compared to more closed canopies (for average heat load, Fig. 5b). Similarly, the average cooling effect decreased (i.e., less negative, sometimes even positive offsets occurred) with higher topographic heat load (Fig. 5c). Together, these results confirm that forest understorey temperatures are generally warmer at sun-exposed slopes and more open forests.

We also found significant three-way-interactions, where the relationship between soil moisture and temperature offsets was contingent on canopy openness and topographic heat load (Fig. 6, Fig. S4). Specifically, offset-to-soil-moisture slopes were consistently steeper at sites with higher heat loads compared to topographically shaded sites with lower heat loads (for average canopy openness, Fig. 5c). In fact, sites with low heat loads showed a more pronounced non-linear response to soil moisture with decreasing soil moisture-offset coupling under moister conditions (for average canopy openness, Fig. 5c). For canopy openness, interaction patterns were generally weaker (i.e., offset-to-soil-moisture slopes were more similar across canopy gradients for average heat load; Fig. 5b).

When analyzing each year separately, we found differences in the strength of soil moisture- temperature offset coupling with 2019 and 2020 generally showing weaker effects of soil moisture and 2018 and 2021 showing strong effects (Supporting Information, Fig. S5).

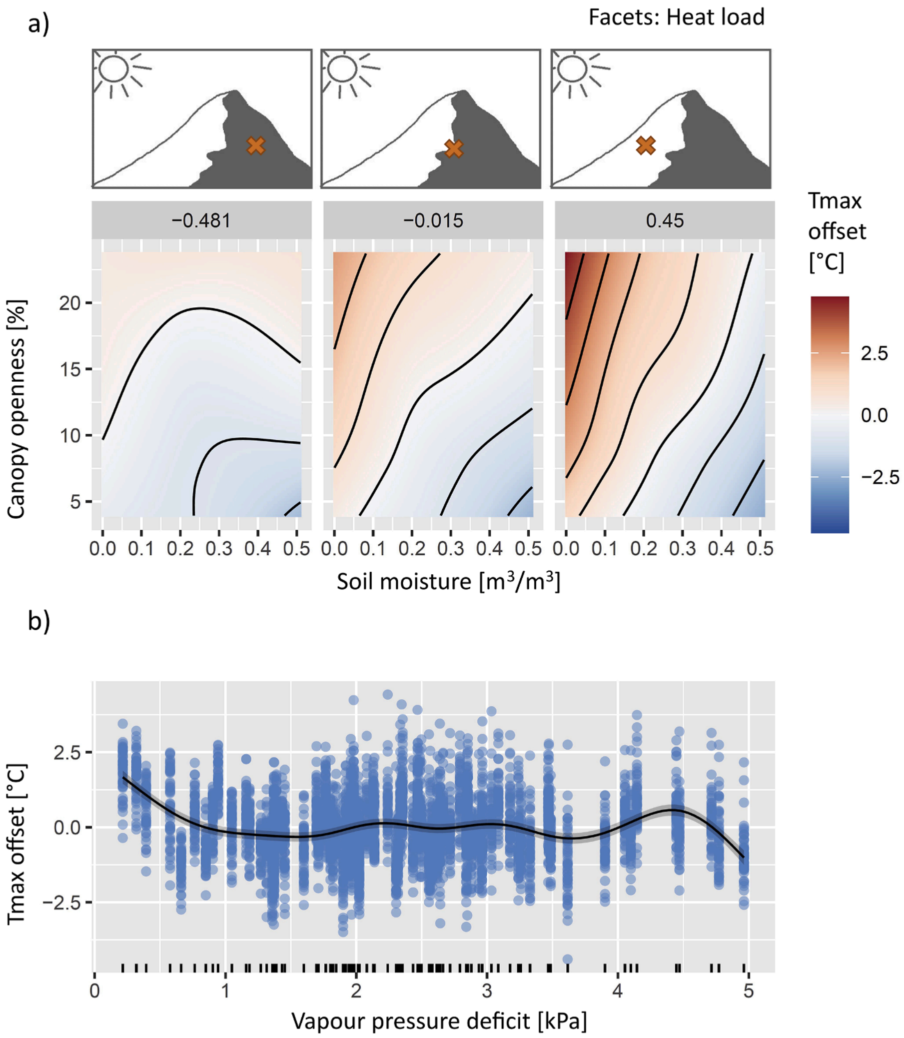

**Fig. 6.** Partial response plots of the three-way interaction between soil moisture, canopy openness and topographic heat load (a) and of vapour pressure deficit, VPD (b) explaining spatio-temporal variation in temperature offsets. Tmax offset = difference between daily maximum temperature inside the forest (measured by a TOMST Thermologger) and outside the forest (elevation-corrected daily weather station data). Contours in (a) are isolines with one-degree Celsius interval.

## 4. Discussion

### 4.1. *Higher soil moisture cools the forest understory*

We quantified the relationships between daily forest understory temperature buffering and soil moisture along canopy openness gradients in a topographically complex landscape in Central Europe, at high temporal (daily) resolution while also covering a high spatial replication (54 sites across 50 $\mathrm{km}^2$). Across sites, we found an average cooling effect in forest understories of ca. 2 °C, which is comparable to the cooling effects reported from other temperate forests (Haesen et al., 2021; Von Arx et al., 2012; Zellweger et al., 2019). However, we found large variability in offsets from site to site, day to day and year to year (Figs. 4d and S3). These spatio-temporal dynamics in forest microclimate buffering were strongly linked to spatio-temporal dynamics in soil moisture, where moister soils cool the understory more effectively than dry soils, confirming hypothesis H1 (Figs. 5 and 6). Furthermore, the relationship between soil moisture and the offset was non-linear, i.e., the sensitivity of the offset to soil moisture changed along the soil moisture gradient and was generally higher in drier soils, holding the other factors constant. This change in sensitivity confirms hypothesis H2. The shape of the relationship is such that buffering capacity decreases rapidly in drier soils. The reduced buffering capacity likely results from combined reduction of soil water evaporation and plant transpiration. At the other extreme, the reduced sensitivity at high soil moisture suggests an energy limitation (Campbell and Norman, 1997; Pieruschka et al., 2010; Schwingshackl et al., 2017; Seneviratne et al., 2010). This explanation is further supported by the pattern of decreasing moisture–temperature coupling being predominant on topographically shaded sites with lower incoming solar energy, which in turn likely limits evaporative cooling. The non-linearity was, however, not very strong and varied across the years (Fig. S5), indicating that, in our study region, soil moisture, on average, is currently driving understory temperatures along the entire moisture gradient ("transitional regime" *sensu* Seneviratne et al., 2010).

As we identified a strong water limitation on understory cooling, especially at the dry end of the soil moisture gradient, we can expect a threshold behavior of the cooling function. We anticipate the cooling effect to decline more rapidly as soils dry out even further, reducing evapotranspiration due to low water availability, up to a point where some forests lose their cooling function completely, and understories become *warmer* than open areas. (Figs. 5, 6, S3, S8). Thus, forest microclimate can shift from being supportive for buffering-dependent tree seedlings and other understory organisms to being unsupportive or even harmful for them (Von Arx et al., 2013), depending on soil moisture fluctuations alone.

The revealed patterns are robust to the chosen reference temperature (here elevation-corrected weather station data) because they are based on temporal dynamics of offsets and soil moisture and their coupling.

However, the absolute values of the offsets are affected by the chosen reference temperatures and therefore need to be interpreted with caution. In our models, we used empirically measured soil moisture, which is also a result of forest vegetation, topography and previous evapotranspiration rates, in turn driven by vapour pressure deficit (VPD). As such, feedbacks between these components are inherently included in our model results, but should also be studied explicitly (He et al., 2013; Sohn et al., 2016).

Interactions among soil moisture, canopy openness and topographic heat load together with daily VPD explained around half of the variation in the temperature offset. The unexplained variation as well as the inconsistent responses to VPD are likely the result of complex mechanisms and interactions between soil, plants and the atmosphere that we could not capture in our statistical models (Grossiord et al., 2020; Lendzion and Leuschner, 2009; Massmann et al., 2019; Nalevanková et al., 2020; Oren et al., 1999). The limited effects of VPD might be the result of opposite mechanisms at play. Higher VPD values should lead to higher evapotranspiration and thus to a stronger cooling in the understory, but plants have the ability to reduce evapotranspiration when faced with elevated VPD by closing their stomata, aiming to conserve water (Oren et al., 1999) and thus limiting the cooling. Other uncertainties are caused by the VDP estimate. Our daily VPD estimates are determined based on daily maximum temperature and minimum air humidity at the weather station, and hence correspond to the highest daily demand and conditions outside the canopy, whereas understory evapotranspiration is controlled by sub-daily fluctuations of VPD values below the canopy.

### 4.2. *Canopy openness and topographic heat load effects on forest buffering*

Consistent with earlier findings, the average cooling effect of forest canopies is stronger under more closed canopies (Greiser et al., 2018; Kašpar et al., 2021; Zellweger et al., 2019) and at topographically shaded sites (Dobrowski, 2011; Macek et al., 2019; Meineri and Hylander, 2017).

These factors also interacted with soil moisture, confirming our third hypothesis H3 (Figs. 5 and 6). The interaction of soil moisture with canopy openness was, however, relatively weak (Fig. 5b) and inconsistent among the years (Figs. S5 and S7). Denser canopies reduce incoming solar radiation leading therefore to generally cooler maximum temperatures in the understory (intercept effect in Fig. 5b). Dense canopies with a higher Leaf Area Index (LAI) may also evaporate water more efficiently, thus leading to a stronger coupling of understory cooling to soil moisture (as we found for 2018 and 2021, Fig. S5). At the same time, dense canopies reduce the wind velocity and mixing of air from above and below the canopy, thereby reducing the VPD below the canopy (not measured), which actually decreases understory evapotranspiration. This mechanism in turn could explain the opposite direction of the soil moisture – canopy openness interaction that we found in years 2019 and 2020, where soil moisture had a stronger effect on understory cooling when canopies were more open (Fig. S5). The variation in coupling strength and interactions between years may also be caused by time lags in vegetation responses to growing conditions. Time lags in plant transpiration are to be expected, for example when vegetation is recovering from a dry spell, and can extend across growing seasons (Gutierrez Lopez et al., 2021; Wu et al., 2022). Furthermore, we built our models on the assumption that canopy openness is closely related to LAI and constant over time, but there are likely changes in the overstory and understory vegetation during the summer season and between years. For example, the continuous leafing of deciduous trees throughout the growing season can change the understory microclimate and its responses to soil moisture (Von Arx et al., 2013). As short-term and long-term changes in understory and overstory LAI affect transpiration rates in forests and thereby the cooling potential of forest canopies, inclusion of these temporal dynamics and the intricate timing of LAI with fluctuating soil moisture and general atmospheric conditions might improve our understanding of forest microclimate.

We found that topographic heat load increased understory temperatures in general and strongly modified the coupling between soil moisture and temperature offset. Sun-exposed sites with a high topographic heat load were on average less buffered (i.e., warmer), but received more energy (solar radiation) for evapotranspiration, hence responded also strongest to soil moisture fluctuations (Fig. 5). Conversely, shaded slopes and terrain depressions were generally cooler as they received less direct radiation. Nevertheless, in these topographical settings the offset did not respond as strongly to soil moisture as in sun-exposed sites, supporting the hypothesis of an energy limitation for evapotranspiration, especially at higher soil moisture levels (Figs. 1, 5c). Our findings are thus consistent with earlier studies from mixed-coniferous forests in western North America, where local moisture availability interacted with topographic heat load in driving understory temperatures (Wolf et al., 2021b). The interactions of soil moisture with canopy openness and topographic heat load show how important the incoming energy (modified by terrain and canopies) is in addition to soil moisture to drive and predict forest buffering in topographically complex landscapes.

### 4.3. *Implications for forest ecosystems in a changing climate*

Climate change is threatening forests in various ways. Under rising summer temperatures, forest buffering is increasingly important to avert heat stress for understory biodiversity (Sanczuk et al., 2023; Zellweger et al., 2020). Whether forests can continue to fulfil that function will depend on water availability, which is under threat from increasingly frequent and severe droughts (Meusburger et al., 2022). In north-western United States, projections of forest microclimate buffering based on climate change and changes in water balance show that the predominantly coniferous forests become increasingly water limited and lose their buffering capacity (Davis et al., 2019). The 2018–2020 multi-year drought was probably the most intensive soil drought experienced in Central Europe over the last centuries and similar or even more intensive soil droughts are predicted to become more frequent in all of central Europe (Rakovec et al., 2022). The temperate forests in Europe are particularly vulnerable to these droughts (Lindner et al., 2010). The loss potential loss of buffering capacity may be exacerbated by drought-induced crown dieback, pest outbreaks, as well as active drainage and stream regulation following human land use. As a consequence, the buffering capacity of forests as an important ecosystem function is currently threatened and its loss can involve failure in tree regeneration, losses of forest biodiversity and therefore large changes in forest ecosystem structure and functioning.

Climate change refugia - locations in the landscape with locally favourable microclimates for threatened cold-adapted species or communities in a surrounding matrix of harmful and deteriorating climate conditions - will therefore be more and more tightly linked to stable and sufficient water supply, as previously suggested (e.g., McLaughlin et al., 2017). We show that the sufficient supply of water may not only affect refugia populations directly (because species depend on water) but also indirectly via local cooling effects. We can therefore imagine two types of climate change refugia that provide cool microclimates during the warmest period of the year: one type where stable and sufficient soil water provides evaporative cooling on sites with high energy input (e.g., springs on sunny slopes) and another type where soil moisture and cooling are decoupled due to generally low energy inputs (here, local temperature buffering arises predominantly from topographic and canopy shading). Both types of forest stands with abundant soil water supply and/or with limited energy input (topographically shaded slopes or depressions) may become crucial in harbouring a relatively large proportion of forest biodiversity in a hotter and drier future (Andrew and Warrener, 2017; Hampe and Petit, 2005; McLaughlin et al., 2017). Consequently, forest management plays a critical role for creating or maintaining supportive understory microclimates, because harvesting regimes and tree species selection do not only directly influence canopy shading levels, but also indirectly impact the water holding capacities of soils, run-off and infiltration, and thereby the cooling effect coming from evaporation. If understory buffering is reduced, more thermophilic species may become favoured (De Frenne et al., 2015; Govaert et al., 2021; Stevens et al., 2015). Hence, as soil moisture depletion can substantially change forest microclimate regimes, we can expect, in the long run, compositional changes in species communities not only directly in response to changes in temperature, but also as a result to changes in the local water balance caused by reduced water input and/or enhanced evapotranspiration. If the aim is to maintain a minimum level of understory buffering, climate adaptation of forest management could include supporting tree species with a high water-use efficiency (Cernusak et al., 2007) and/or high shade-casting ability (Verheyen et al., 2012) on sites that are threatened by increasing risks of soil drought. These management recommendations may apply also to urban environments, where green areas and trees can mitigate the exposure to heat waves (Bakhshoodeh et al., 2022; Wong et al., 2021) with important effects on human health. However, management actions aimed at increasing forest buffering via enhancing close canopies can go directly against nature conservation goals, as the historically open forests host the most diverse and endangered plant communities in central Europe (Kopecký et al., 2013).

## 5. Conclusions and outlook

Our study bridges the gap between the previously conducted small and large-scale assessments of soil moisture–temperature coupling in forest understories (Davis et al., 2019; Maclean and Klinges, 2021; Schwingshackl et al., 2017; Seneviratne et al., 2010; Von Arx et al., 2013) by investigating 4-year time series at a daily resolution from a large number of sites within the same landscape (and thus the same macroclimate and forest biome). Our results show the non-linear response of forest temperature buffering to soil moisture and refine knowledge about the topographical context and forest structure, in which soil moisture is a driving factor of forest microclimate. The clear role of soil moisture on forest microclimate calls for improved predictions of future forest understory temperatures, explicitly including variable and changing soil water availability. Our study also questions the recently suggested approach to model microclimate based on the concept of a stable linear slope between macroclimate and microclimate temperatures at any given site (Gril et al., 2022). An important next step towards reliable large-scale projections of forest microclimate under future climate and land use scenarios is therefore to develop models that can be parametrized with the increasingly available time series of soil moisture and near-ground temperature from other biomes and other forest types (Dorigo et al., 2011; Lembrechts et al., 2020). Such models could leverage statistical relationships, as presented and discussed here, thus providing an alternative to detailed mechanistic models that account for all components of the site's energy and mass balances (Luan and Vico, 2021; Maclean and Klinges, 2021; Nalevanková et al., 2020).

Forests create their own microclimate, which supports understory biodiversity and ecosystem functioning. We demonstrated how vulnerable this temperature buffering function is to soil drought and how forest microclimate refugia may depend on stable soil water levels, which are at risk under hotter and drier future climates. We also found an accelerated weakening of understory buffering when the soils dry out. As a consequence, abrupt and non-linear responses of forest ecosystems to climate change caused by moisture-temperature feedbacks can be expected in the future.

## CRediT authorship contribution statement

**Caroline Greiser:** Conceptualization, Formal analysis, Funding acquisition, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Lucia Hederová:** Data curation, Writing – review & editing. **Giulia Vico:** Conceptualization, Funding acquisition, Methodology, Writing – review & editing. **Jan Wild:** Data curation, Funding acquisition, Resources, Writing – review & editing. **Martin Macek:** Data curation, Formal analysis, Software, Writing – review & editing. **Martin Kopecký:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Visualization, Writing – review & editing.

## Declaration of Competing Interest

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

## Data availability

The data and code that support the findings of this study are openly available in the Figshare repository at 10.17045/sthlmuni.24247090.

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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2023.109828.

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