



RESEARCH ARTICLE

# Maximum air temperature controlled by landscape topography affects plant species composition in temperate forests

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## Abstract

**Context** Forest microclimates differ from regional macroclimates because forest canopies affect energy fluxes near the ground. However, little is known about the environmental drivers of understorey temperature heterogeneity and its effects on species assemblages, especially at landscape scales.

**Objectives** We aimed to identify which temperature variables best explain the landscape-scale distribution of forest vegetation and to disentangle the effects of elevation, terrain attributes and canopy cover on understorey temperatures.

**Methods** We measured growing season air temperature, canopy cover and plant community composition

within 46 plots established across a 400-km<sup>2</sup> area in Czech Republic. We linked growing season maximum, mean and minimum temperatures with elevation, canopy cover and topographic proxies for heat load, topographic position, soil moisture and cold air drainage, and created fine-scale topoclimatic maps of the region. We compared the biological relevance of in situ measured temperatures and temperatures derived from fine-scaled topoclimatic maps and global WorldClim 2 maps.

**Results** Maximum temperature was the best predictor of understorey plant species composition. Landscape-scale variation in maximum temperature was jointly driven by elevation and terrain topography ( $R^2_{\text{adj.}} = 0.79$ ) but not by canopy cover. Modelled maximum temperature derived from our topoclimatic maps explained significantly more variation in plant community composition than WorldClim 2 grids.

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**Conclusions** Terrain topography creates landscape-scale variation in maximum temperature, which in turn controls plant species assembly within the forest understorey. Maximum temperature is therefore an important but neglected microclimatic driver of species distribution across landscapes.

**Keywords** Canopy cover · iButton · Maximum temperature · Microclimate · Species composition · Temperate forest · Terrain attributes · Topoclimate · WorldClim 2

## Introduction

The relationship between the climate and the distribution of species is at the core of ecology and biogeography. However, this relationship is usually studied using coarse-grained climatic data which do not capture the actual microclimates experienced by organisms (Franklin et al. 2013). Moreover, the selection of climate variables used in species distribution modelling is seldom based on their physiological relevance. Instead, readily available data are preferentially used, with mean annual temperature being the most overused climate variable in ecological modelling (Gardner et al. 2019). The resulting mismatch between coarse-grained climatic data and the real drivers of species distribution acting on fine scales can substantially bias both species distribution models and predictions of species' vulnerability to climate change (Ashcroft et al. 2012; Potter et al. 2013; Slavich et al. 2014). Microclimatic data are therefore essential in assessing climatic effects on the biota (Lembrechts et al. 2018).

Temperature variability across landscapes is driven not only by decreasing temperatures with elevation caused by adiabatic cooling, but also by topographic processes such as anisotropic surface heating, cold air drainage and evaporative cooling (Geiger et al. 2009). Whereas physical processes affecting local temperature variability are well understood, their complexity makes modelling long-term temperature across landscapes challenging. The recent development of miniaturized low-cost data loggers has allowed continuous microclimatic measurements at many sites across entire landscapes (Lookingbill and Urban 2003; Ashcroft et al. 2008; Vanwallegem and Meentemeyer 2009;

Fridley 2009; Wild et al. 2019). Empirical spatial predictions from these measurements suggest that topography-driven temperature variability can be high enough to create local microclimatic refugia able to buffer the effects of climate change on organisms (Ashcroft et al. 2009; Kulonen et al. 2018).

Forest understorey microclimates differ from the macroclimate because tree canopies limit air mixing, absorb incident radiation and force evapotranspiration rates (Geiger et al. 2009; Von Arx et al. 2012). Although the tree canopy has a weak effect on mean temperatures, it can substantially decrease maximum temperatures and increase minimum temperatures near the ground; in other words, forest canopies behave like thermal insulating layers (Vanwallegem and Meentemeyer 2009; Suggitt et al. 2011; Davis et al. 2019). Therefore, understorey temperatures fluctuate less than those in tree-less habitats (Häntzschel et al. 2005). Because of this decoupling of forest microclimates from conditions above the canopy, topography is possibly a less influential driver of microclimates in forests than in tree-less habitats (Running et al. 1987; Treml and Banaš 2008; Vanwallegem and Meentemeyer 2009). However, the effect of the forest canopy on understorey temperatures depends on the meteorological situation and on structural attributes and phenological phase of the canopy, making it difficult to generalize the effects of the canopy, especially at landscape-scales or in the long term (Renaud and Rebetez 2009; Von Arx et al. 2012).

In temperate forests, the diversity of vascular plants is concentrated in the understorey (Gilliam 2007) and understorey plant species are sensitive to fine-scale microclimatic variation (Ashcroft et al. 2008; Tinya et al. 2019). Microclimatic conditions in the understorey are also relevant for tree seedling establishment and growth (Von Arx et al. 2013), causing possible feedbacks in the long-term.

It has been postulated that the effects of climate change in forests can be attenuated by increased canopy cover (De Frenne et al. 2013; Frey et al. 2016). However, the exact mechanism by which this can happen remains unclear because temperatures under forest canopy are not constantly offset from open-area temperatures, but positive offset in minimum and negative offset in maximum temperatures is the usual situation. In addition, the relative importance of different aspects of thermal variability for the forest

biota is largely unknown because of a lack of relevant studies and potential interactions with light and moisture microclimatic conditions (Chen et al. 1999; Von Arx et al. 2013). Direct microclimatic measurements are necessary for addressing links between spatial and temporal variation in microclimate and macroclimate, topography, forest structural attributes and plant communities because evidence based on bioindication or standard weather station data may provide misleading results (Harwood et al. 2014).

In the present study, we measured forest understorey temperatures, canopy cover and recorded plant species composition across a broad topographic gradient to: (1) explore how elevation, local topography and canopy cover variation affect understorey temperatures; (2) identify which temperature variable (maximum, mean, or minimum) is the most influential driver of understorey plant communities; and (3) test whether fine-scale empirical topoclimatic model based on forest microclimate measurements can explain gradients in plant species composition better than analogous climatic grids with coarser resolution based on interpolated weather station data, such as WorldClim 2 dataset (Fick and Hijmans 2017).

## Methods

### Study area

To explore links between local climates, terrain attributes and plant communities at a landscape scale, we set up a network of vegetation plots with in situ recorded temperatures in the České Středohoří region, Czech Republic ( $50^{\circ}29'–50^{\circ}37' \text{ N}$ ;  $13^{\circ}52'–14^{\circ}12' \text{ E}$ ; Fig. 1). The area is formed by a chain of extinct volcanic hills rising above a sedimentary plateau. Elevations range from 122 m a.s.l. in the Elbe river basin to 837 m a.s.l. at the top of Milešovka hill. The climate is temperate with mean annual temperatures ranging from 5 to 9 °C, mean annual precipitation of 450–600 mm and prevailing westerly winds (Tolasz et al. 2007).

Mostly semi-natural forests cover ca 28% of the region (Fig. S1 in Electronic Supplementary Material 1). Thermophilous woodlands with sessile oak (*Quercus petraea* agg.) and European hornbeam (*Carpinus betulus*) occur at low elevations and on south-facing slopes, European beech (*Fagus sylvatica*) forests

dominate on hilltops and northern slopes, and species-rich forests with limes (*Tilia cordata*, *T. platyphyllos*), maples (*Acer pseudoplatanus*, *A. platanoides*) and wych elm (*Ulmus glabra*) cover steep slopes and screes.

### Data collection

We established 53 plots ( $10 \times 10 \text{ m}$ ) in forests distributed across the  $400 \text{ km}^2$  region according to a stratified random sampling design with strata reflecting main topographic gradients (elevation, slope exposure and topographic wetness; Fig. 1, Fig S7). We excluded recently disturbed stands and coniferous plantations from the selection. We recorded the geographic positions of the plots using differential GPS (GeoExplorer 2008 GeoXH, Trimble Inc., USA) with data post-processing.

### Temperature

At each plot, we measured air temperature with DS1922L iButton Thermochron loggers (Maxim Integrated Inc., San Jose, CA) with a resolution of 0.0625 °C placed at a height of 2 m on the north side of a tree trunk and shaded by a passively ventilated plastic shield. The height of 2 m corresponds to the height at which standard meteorological data underlying the reference WorldClim 2 dataset are acquired. The temperature was recorded every three hours over the course of the growing season (1 May to 30 September) in the years 2015 to 2018. We used temperatures collected during the growing season because they are more important drivers of forest plant species distribution than yearly temperatures (Lenoir et al. 2013). As a result of datalogger malfunction or vandalism, we acquired continuous temperature measurements from 46 plots out of 53 in 2015 but obtained a complete record for all four seasons for only 27 plots. Therefore, to maximize the number of plots without missing values, we used for further analyses only data from the 2015 season used the data from the following seasons only to document the consistency of the observed patterns between years (Fig S2).

To identify the temperature variable most relevant for vegetation composition, we compared three variables capturing different aspects of the thermal climate (Ashcroft et al. 2014; Körner and Hiltbrunner 2018): (i) maximum temperature expressed by the 95th

percentile of daily maximum temperatures (Tmax95), (ii) mean temperature (Tmean) and (iii) minimum temperature expressed by the 5th percentile of daily minimum temperatures (Tmin5).

#### Plant community composition

At each 100-m<sup>2</sup> plot, we identified all vascular plant species growing in the understorey (herbs and woody species < 1.3-m height) and estimated their cover according to the Braun-Blanquet scale (Westhoff and Van Der Maarel 1978) transformed to percentage cover.

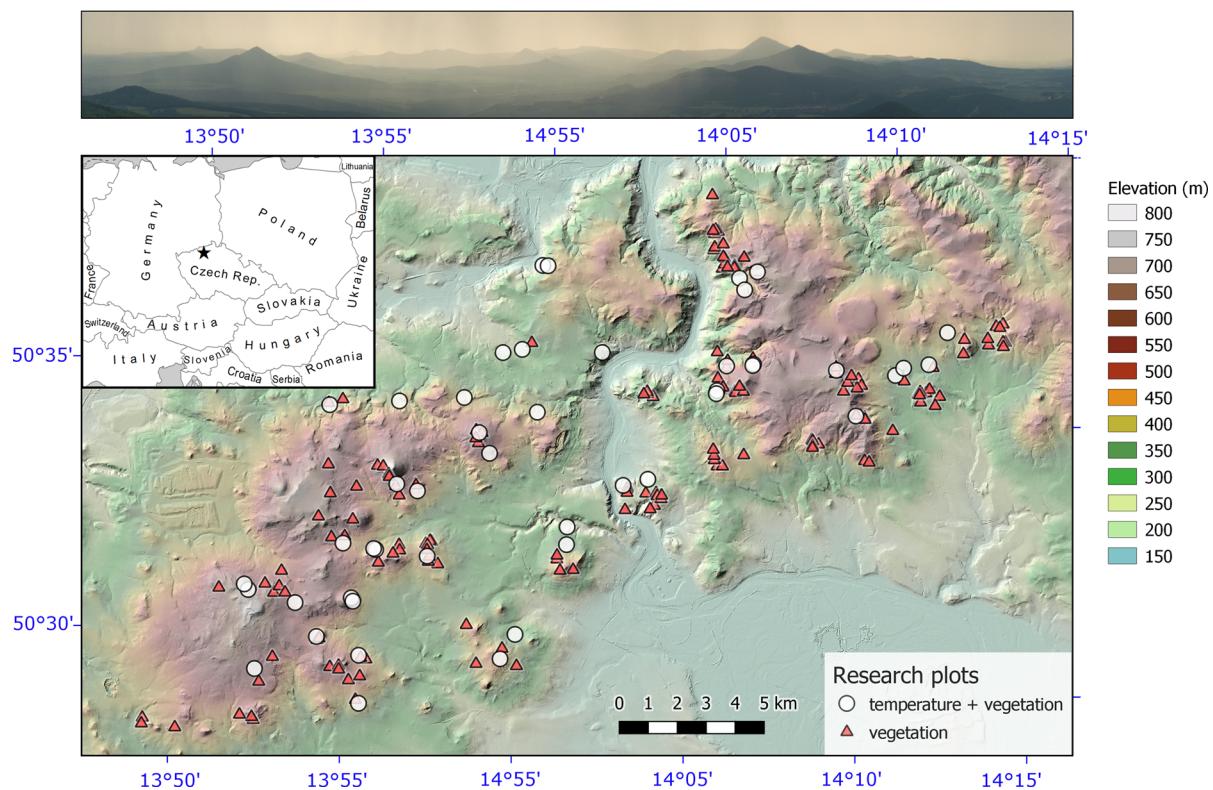
#### Canopy cover

To measure canopy cover at each plot, we took five hemispherical photographs within each plot—one in

the plot centre and four on the diagonals 5 m from the plot centre, using a Canon 40D camera with a Sigma 8 mm f/3.5 EX fish-eye lens levelled at the height of 1.3 m. We used WinScanopy ver. 2014a (Regent Instruments, Canada) to calculate percent canopy cover over a 50° zenith angle from each photograph and averaged these five canopy cover values into plot mean canopy cover (Canopy).

#### Topographic variables

To explore links among temperature, topography and vegetation, we extracted the elevation of each plot from a LiDAR-based digital terrain model with a horizontal resolution of 5 m ('DMR 4G', Czech Office for Surveying, Mapping and Cadastre) and calculated three climatically relevant topographic variables: the topographic position index (TPI), potential heat load



**Fig. 1** Map of the study area showing the locations of sampled forest vegetation plots. White dots indicate the 46 plots where we simultaneously ascertained air temperature, canopy cover and plant species composition. Red triangles indicate the independent dataset of 160 vegetation plots used to evaluate topoclimatic maps. Elevation is represented by a colour scale;

the terrain is visualized using a hillshade effect. The photograph at the top shows a view of the central part of the study area. The inset map shows the position of the study area (asterisk) within Central Europe. The geographic projection is S-JTSK Křovák, baseline data by © ČÚZK (DMR 4G digital elevation model with 5 m resolution)

(HL) and the SAGA wetness index (SWI), all calculated in SAGA GIS ver. 3.0.0 (Conrad et al. 2015).

The topographic position index (TPI) expresses the difference between the elevation of a plot and the mean elevation in its surroundings (Guisan et al. 1999) and captures the topographic exposure of the site, with positive values for ridge or hilltop positions, null on flats or midslopes and negative values on valley bottoms (Fig. S6). The TPI has been successfully used in many studies exploring temperature variation across landscapes (Strachan and Daly 2017; Jucker et al. 2018). With respect to the scale of topographic variability within our study region, we calculated the TPI using a 250-m radius.

Potential heat load (HL) defined as  $HL = \cos(202.5^\circ - \text{aspect}) \times \tan(\text{slope})$  was calculated using the function ‘anisotropic diurnal heat’ in Saga GIS (Böhner and Antonić 2009). Flat surfaces have zero HL values whereas northerly slopes have negative and southerly slopes positive HL values, with a maximum on SSW-facing slopes (Fig. S7). HL thus reflects maximum temperature patterns across a landscape with respect to diurnal variation in heat fluxes driven by surface exposure to solar radiation (Geiger et al. 2009). Because warm air is not static, local variation in slope and aspect produces unrealistic small-scale variation. We therefore smoothed HL values using a Gaussian filter with a 50-m range.

The topographic wetness index has been successfully used to model cold air pooling (Ashcroft et al. 2008; Kilibarda et al. 2014; Leempoel et al. 2015). We therefore calculated the SAGA wetness index (SWI), a variant of the topographic wetness index (Kopecký and Čížková 2010) with iteratively adjusted catchment area (Böhner and Selige 2006) (Fig. S8). Adjusted catchment area produces smoother patterns of the wetness index, especially in flat areas such as valley bottoms, and therefore better reflects the redistribution of cold air than the classical TWI (Böhner and Antonić 2009).

## Data analyses

### *Understorey temperature variability*

To explore the effects of topography and canopy cover on the spatial variability of understorey temperature, we constructed empirical models for each temperature variable using bidirectional elimination of model

variables in multiple linear regression based on the Bayesian information criterion (BIC). As predictors we used plot elevation, topographic variables (TPI, HL and SWI) and canopy cover. Prior to the analyses we standardized elevation and the SWI to zero means, leaving naturally centred variables (HL, TPI) untransformed. Variables entering the model were checked for co-linearity using variance inflation factors (VIF) from the ‘car’ package (Fox and Weisberg 2011) in R 3.2.5 (R Core Team 2016). All VIF values were below 1.6, indicating low co-linearity of the predictors (Fig. S9). We checked for spatial autocorrelation in observed temperature variables and in model residuals using Moran’s I calculated with the ‘ncf’ R package (Bjornstad 2018). Because the spatial autocorrelation of model residuals was low, we concluded that the model assumptions of independence of residuals were met and that it was not necessary to further correct for spatial dependence.

To calculate the relative importance of predictors used in the final models, we used the sequential  $R^2$  contribution averaged over all possible orderings of the regressors, implemented in the ‘relimpo’ R package as ‘LMG’metrics (after Lindeman, Merenda and Gold (1980) in Grömping 2006). To express absolute effect size in degrees Celsius, we subtracted the lowest from the highest predicted values at sampling points where either topographic variables (for elevational effects) or elevation (for topographic effects) were fixed to zero (Ashcroft and Gollan 2013). We evaluated the prediction accuracy of the final topoclimatic models using mean absolute error (MAE) and root-mean-square error (RMSE) statistics based on leave-one-out cross-validation. Because the various temperature variables had different absolute ranges, we also calculated normalized RMSE as absolute RMSE divided by the range of observed values.

Finally, we used these empirically derived models to create high-resolution ( $5 \times 5$  m pixel size) topoclimatic maps of Tmax95, Tmean and Tmin5 for the whole study area (Fig. 3). As a supplement to these topoclimatic maps, we provide spatially explicit information about topographic gradients covered by our sampling design (interpolated climate) and those not covered (extrapolated climate) in the supplementary material (Fig. S11).

### *Effects of in situ measured temperature on understorey plant communities*

To explore the effects of different temperature variables on understorey plant species composition, we performed two complementary multivariate analyses (Økland 1996). First, we explored main gradients in plant species composition and their relationship to environmental variables through indirect ordination and then we used direct ordination to calculate the variation in species composition explained by each in situ measured temperature variable (Legendre and Legendre 2012). We expressed dissimilarity in plant species composition as the percentage (aka Bray–Curtis) index (Legendre and Legendre 2012) calculated from species percentage cover estimates transformed using a base-2 logarithm to decrease the influence of the most abundant species (Anderson et al. 2006).

To explore the main gradients in plant species composition, we used global non-metric multidimensional scaling with primary ('weak') treatment of ties (NMDS) calculated in two dimensions with the 'metaMDS' function from the 'vegan' R package version 2.4-6 (Oksanen et al. 2018). To visualize relationships among the main compositional gradients and environmental variables, we projected all environmental variables onto the NMDS compositional space using the 'envfit' function from the 'vegan' R package.

To calculate the variation in species composition explained by the temperature variables, we used distance-based redundancy analysis (dbRDA, McArdle and Anderson 2001) performed using the 'dbRDA' function from the 'vegan' R package. We tested the statistical significance of temperature variables using 9999 permutations.

The proportion of variability explained by environmental gradients in direct multivariate analyses (such as dbRDA) tends to be low because explained variability depends on the compositional heterogeneity of the dataset (Økland 1999). It is therefore useful to express the relative importance (RI) of predictors calculated here as the variability explained by the predictor relative to the maximum variability that can be potentially explained by a single predictor. To calculate RI, we divided the variability in species composition explained by each temperature variable by the variability explained by the sample scores from

the first ordination axis of the Principal Coordinates Analysis (PCoA) supplied as a single explanatory variable to dbRDA. To provide uncertainty estimates for these RI values, we further calculated the 95% confidence interval of RI for each temperature variable by bootstrapping with 9999 replicates calculated using the adjusted bootstrap percentile (BCa) method from the 'boot' R package (Canty and Ripley 2017).

### *Topoclimatic and macroclimatic maps in ecological applications*

To assess the biological relevance of the newly created fine-scale topoclimatic maps, we used an independent dataset of 160 georeferenced forest vegetation plots without in situ temperature measurement, sampled across the same region by the authors (see Fig. 1 for the spatial distribution of the plots, Suppl. Fig. S10 for coverage of topographic gradients and Kopecký and Macek (2015) for a description of the sampling design).

We compared variation in plant species composition explained by temperature variables extracted from our high-resolution topoclimatic maps ( $5 \times 5$  m pixel size) to the widely used WorldClim 2 climate grids with 30 arc-second (ca  $930 \times 590$  m pixel size at this latitude) spatial resolution (Fick and Hijmans 2017). First, for each sample location we extracted Tmean, Tmax95 and Tmin5 from our topoclimate maps and analogous indices calculated using growing season (May to September) monthly data from WorldClim 2: maximum temperature of the warmest month (WC2 Tmax; Fig. S12), mean of average monthly temperature (WC2 Tmean; Fig. S13) and minimum temperature of the coldest month (WC2 Tmin; Fig. S14).

We used dbRDA with the same settings as we used to test the effects of in situ measured temperatures to assess the variation in understorey species composition explained by temperatures derived from fine-scale topoclimate maps and from WorldClim 2 climate grids. To test if the fine-scale topoclimate predicts vegetation composition better than analogous WorldClim 2 variables, we compared bootstrapped explained variances ( $R^2$ ) between pairs of models using topoclimatic and analogous WorldClim 2 predictor variables (e.g. Tmax95 vs WC2 Tmax) using one-sided empirical p-values corrected for finite sampling:

$$p = \left( 1 + \sum (R^2 \text{ topo} \leq R^2 \text{ WorldClim2}) \right) / (n + 1) \quad (1)$$

## Results

### Understorey temperature variability

Mean temperatures measured in the growing season 2015 (Tmean) varied by 2.55 °C, ranging from 15.02 to 17.57 °C across the landscape. Minimum and maximum temperatures were substantially more variable: Tmax95 differed between sites by as much as 6.86 °C (Table 1). Similar patterns in Tmax95 and Tmean were found for the next three years on a subset of 27 locations with continuous record (Pearson's correlation coefficient between different years was between 0.9 and 0.97 for Tmax95 and between 0.97 and 0.98 for Tmean). Higher interannual variability was found only for Tmin (Pearson's correlation coefficient between 0.32 and 0.93), Figs. S2–S4.

The final model for Tmax95 with four explanatory variables explained most of the variability in measured temperatures ( $R^2_{\text{adj.}} = 0.79$ ); it had RMSE = 0.76 °C and no spatial autocorrelation in residuals (Table 2; Fig. 3c). Elevation had a strong negative effect (lapse rate –11.4 °C km<sup>-1</sup>) with a relative importance of 62.9%. The topographic variables selected in the regression model were the TPI (positive effect, 15.4% RI), HL (positive effect, 15.3% RI) and SWI (negative effect, 6.2% RI). For detailed information on the

stepwise model selection see Supplementary Table S15.

The best topoclimatic model for Tmean explained most of the variability ( $R^2_{\text{adj.}} = 0.80$ ) and had good prediction accuracy (RMSE = 0.31 °C) and no autocorrelation in model residuals up to the distance of 10 km (Fig. 3f). The model included three variables—elevation, TPI and SWI (Table 2). Tmean decreased with elevation (lapse rate – 5.16 °C km<sup>-1</sup>), which was the most important variable in the model (73% RI). Tmean increased with increasing TPI (14.5% RI) and decreased with increasing SWI (12.4% RI).

Variation in Tmin5 showed low spatial autocorrelation (Fig. 3h) and was difficult to predict ( $R^2_{\text{adj.}} = 0.30$ ); the only predictor of Tmin5 selected in the stepwise-selection was SWI (Table 2). The negative relation between Tmin5 and SWI suggests cold air pooling at valley bottoms as the dominant process driving spatial patterns in Tmin5.

### Effects of in situ measured temperature on understorey plant communities

In total, we recorded 196 plant species (median 25.5, min. 4, max. 48 per plot). The main gradient in vegetation composition, as seen on NMDS ordination diagram, can be interpreted as the transition from thermophilous oak woodlands to mesic beech-dominated communities (Fig. 2). The second ordination axis in NMDS followed mainly nutrient status, from communities of acidic soils with *Vaccinium myrtillus* and *Avenella flexuosa* to the calcicole and nutrient

**Table 1** Environmental variables and their descriptive statistics across the 46 sites with temperature measurements

| Variable                                      | Abbrev. | Units | Min    | Mean   | Max   | SD    | Range |
|---|---------|-------|--------|--------|-------|-------|-------|
| Elevation                                     | Elev    | m     | 220    | 427.7  | 644   | 109.3 | 424   |
| Canopy cover                                  | Canopy  | %     | 79     | 91.8   | 97    | 3.37  | 18    |
| SAGA Wetness Index                            | SWI     | –     | 5.19   | 8.77   | 16.84 | 2.75  | 11.65 |
| Heat load                                     | HL      | –     | – 0.55 | – 0.04 | 0.43  | 0.21  | 0.98  |
| Topographic position index                    | TPI     | m     | – 39   | – 0.54 | 36    | 16.83 | 75    |
| 95th percentile of daily maximum temperatures | Tmax95  | °C    | 27.29  | 29.97  | 34.15 | 1.57  | 6.86  |
| Mean temperature                              | Tmean   | °C    | 15.02  | 16.13  | 17.57 | 0.69  | 2.55  |
| 5th percentile of daily minimum temperatures  | Tmin5   | °C    | 4.34   | 6.88   | 8.02  | 0.84  | 3.68  |

Topographic variables were derived from a high-resolution digital elevation model and canopy cover was calculated from hemispherical photographs. Temperature variables were measured using iButton Thermochron data loggers in the growing season of 2015 (1 May–30 September). Mean temperature is calculated as the average from all measurements recorded every 3 h

**Table 2** Microclimate regression model parameters for minimum, mean and maximum temperatures. The effect size for elevation (Elev. e.s.) was calculated as the range of predicted values for observed plot elevations with all other variables held constant. Topographic effect size (Topo. e.s.) is the range of predicted values for constant elevation and original values of topographic variables

| Variable | Intercept | Elev       | SWI       | TPI       | HL       | Canopy | R <sup>2</sup> <sub>adj.</sub> | Elev.<br>e.s. | Topo.<br>e.s. | MAE | RMSE | nRMSE |       |
|----------|-----------|------------|-----------|-----------|----------|--------|--------------------------------|---------------|---------------|-----|------|-------|-------|
| Tmax95   | 29.52***  | -0.0114*** | -0.709**  | 0.0362*** | 2.281*** | n.s.   | 0.79                           | 4.74          | 4.27          | *** | 0.62 | 0.76  | 0.112 |
| Tmean    | 15.80***  | -0.0057*** | -0.446*** | 0.0141*** | n.s.     | n.s.   | 0.80                           | 2.36          | 1.72          | *** | 0.24 | 0.31  | 0.123 |
| Tmin5    | 6.34***   | n.s.       | -0.781*** | n.s.      | n.s.     | n.s.   | 0.30                           | —             | 1.87          | **  | 0.57 | 0.72  | 0.195 |

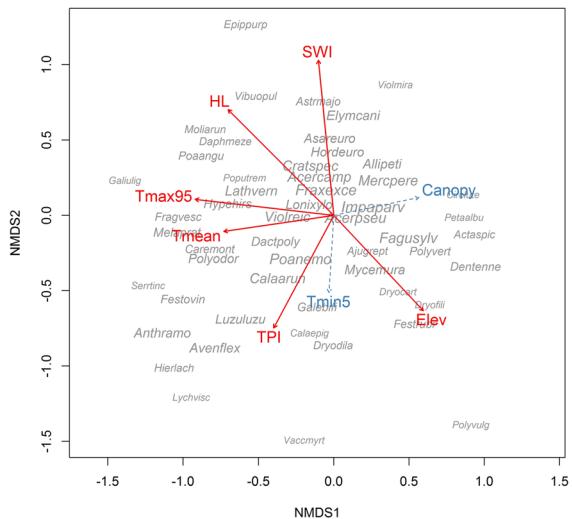
MAE mean absolute error, RMSE root-mean-square-error, nRMSE normalized root-mean-square-error (RMSE divided by the observed range of values)  
Significance codes: n.s. not significant; \*p < 0.05; \*\*p < 0.01; \*\*\*p < 0.001

demanding species like *Astrantia major* or *Viola mirabilis*. Whereas Tmax95 and Tmean were both closely related to the first axis of the NMDS ordination, Tmin5 had only weak correlation with the second ordination axis (Fig. 2).

Direct gradient analysis (dbRDA) revealed that species composition was most strongly controlled by Tmax95, less by Tmean and only weakly by Tmin5 (Table 3).

#### Topoclimatic and macroclimatic maps in ecological applications

In the independent dataset, microclimatic variables extracted from fine-scale topoclimatic maps (Fig. 3) explained less variability in plant community composition than was explained by in situ measured temperatures in the original dataset, but the ranking of individual variables was the same as for in situ measured temperatures (Table 3). The best predictor of plant community composition was again Tmax95, which was a significantly better predictor of



**Fig. 2** Ordination diagram from non-metric multidimensional scaling showing main vegetation gradients with passively projected climatic and topographic variables. Environmental variables with statistically significant ( $p < 0.05$ ) correlations with sample scores in the ordination space are depicted by solid red lines; insignificant variables are indicated by dashed blue lines (see Table 1 for variable abbreviations and descriptions). Contractions of species names are composed of the first four letters of the generic name and the first four letters of the specific epithet; font size is proportional to the species' frequencies in the dataset (see Table S16 for full names). In cases of overlapping labels, only the more frequent species is plotted

**Table 3** Variation in species composition explained by in situ measured temperatures in the training dataset, fine-scale topoclimatic spatial predictions of these variables for the independent dataset, and variation explained by analogous

variables extracted from monthly temperatures (May to September) from WorldClim 2 climate grids for the independent dataset

| Explanatory variable                   | F model | R <sup>2</sup> | p       | RI      | RI 95% conf. int. |
|--|---------|----------------|---------|---------|-------------------|
| In situ measured temperatures (n = 46) |         |                |         |         |                   |
| Tmax95                                 | 4.184   | 0.087          | < 0.001 | 0.513*  | (0.325; 0.663)    |
| Tmean                                  | 3.488   | 0.073          | < 0.001 | 0.434*  | (0.238; 0.594)    |
| Tmin5                                  | 1.788   | 0.039          | 0.025   | 0.230*  | (0.112; 0.327)    |
| Topoclimatic grids (n = 160)           |         |                |         |         |                   |
| Tmax95                                 | 9.516   | 0.057          | < 0.001 | 0.393** | (0.264; 0.514)    |
| Tmean                                  | 6.897   | 0.042          | < 0.001 | 0.290** | (0.178; 0.385)    |
| Tmin5                                  | 4.900   | 0.030          | < 0.001 | 0.208** | (0.123; 0.265)    |
| WorldClim 2 grids (n = 160)            |         |                |         |         |                   |
| Tmax5,9                                | 6.166   | 0.038          | < 0.001 | 0.260** | (0.16; 0.344)     |
| Tmean5,9                               | 6.890   | 0.042          | < 0.001 | 0.289** | (0.19; 0.377)     |
| Tmin5,9                                | 6.606   | 0.040          | < 0.001 | 0.278** | (0.181; 0.363)    |

R<sup>2</sup> is the variability explained in the dbRDA model using a single explanatory variable; p-values are based on 9999 permutations. RI is the relative importance of the variable ( $R^2$  of the model with the selected explanatory variable divided by the  $R^2$  of the model using scores of the first PCoA axis as the explanatory variable). RI for the original dataset and its 95% bootstrapped confidence intervals are shown (RI; RI 95% conf. int.)

\*The value of R<sup>2</sup> for scores from the first PCoA ordination axis (i.e. the maximum variability explainable by one predictor in dbRDA) used to calculate RI was 0.169 in this dataset

\*\*The value of R<sup>2</sup> for scores from the first PCoA ordination axis was 0.145 in this dataset

vegetation composition than maximum temperature extracted from WorldClim 2 ( $p = 0.005$ ). However, the explanatory power of Tmean and Tmin5 from topoclimatic maps was not better than that of Tmean ( $p = 0.52$ ) and Tmin ( $p = 0.87$ ) from WorldClim 2.

maps of maximum temperatures can explain forest understorey composition substantially better than the WorldClim 2 gridded climate data, which lack sufficient resolution and do not account for topographic effects other than elevation.

## Discussion

Different sets of topographic variables explained spatial variability in minimum, mean and maximum temperatures, while spatial variability of understorey temperatures driven by differences in canopy openness was insignificant. Maximum temperatures were the most variable in space, with variability controlled jointly by elevation, heat load, topographic position and topographic wetness. Understorey plant community composition was best explained by a gradient of in situ measured maximum temperatures. Using an independent dataset of vegetation samples, we showed that the had the strongest relation to understorey plant community composition. Fine-scaled topoclimatic

## Drivers of understorey temperature variability

It has been suggested that topographic effects on near-surface temperatures are reduced under dense forest canopies (Wilson and Gallant 2000; Körner and Paulsen 2004). However, our results clearly show that topography has a strong effect even in closed-canopy forests. Although we found a significant effect of heat load on maximum temperatures, heat load did not affect mean temperatures significantly, probably because the contrast in temperatures on south-facing slopes is pronounced only around noon on sunny days, which contribute little to seasonal means. By contrast, the SWI, which is a topographic proxy for soil moisture and cold air pooling (Olaya and Conrad 2009; Kilibarda et al. 2014), correlated significantly

with all temperature variables. The effect of cold air drainage affecting maximum temperatures during daytime in the growing season seems rather odd. However, beneath the forest canopy, topographically driven downslope flow of the cold air can persist all day, in contrast to conditions above the canopy, where the air flow is reversed during the daytime (Pypker et al. 2007).

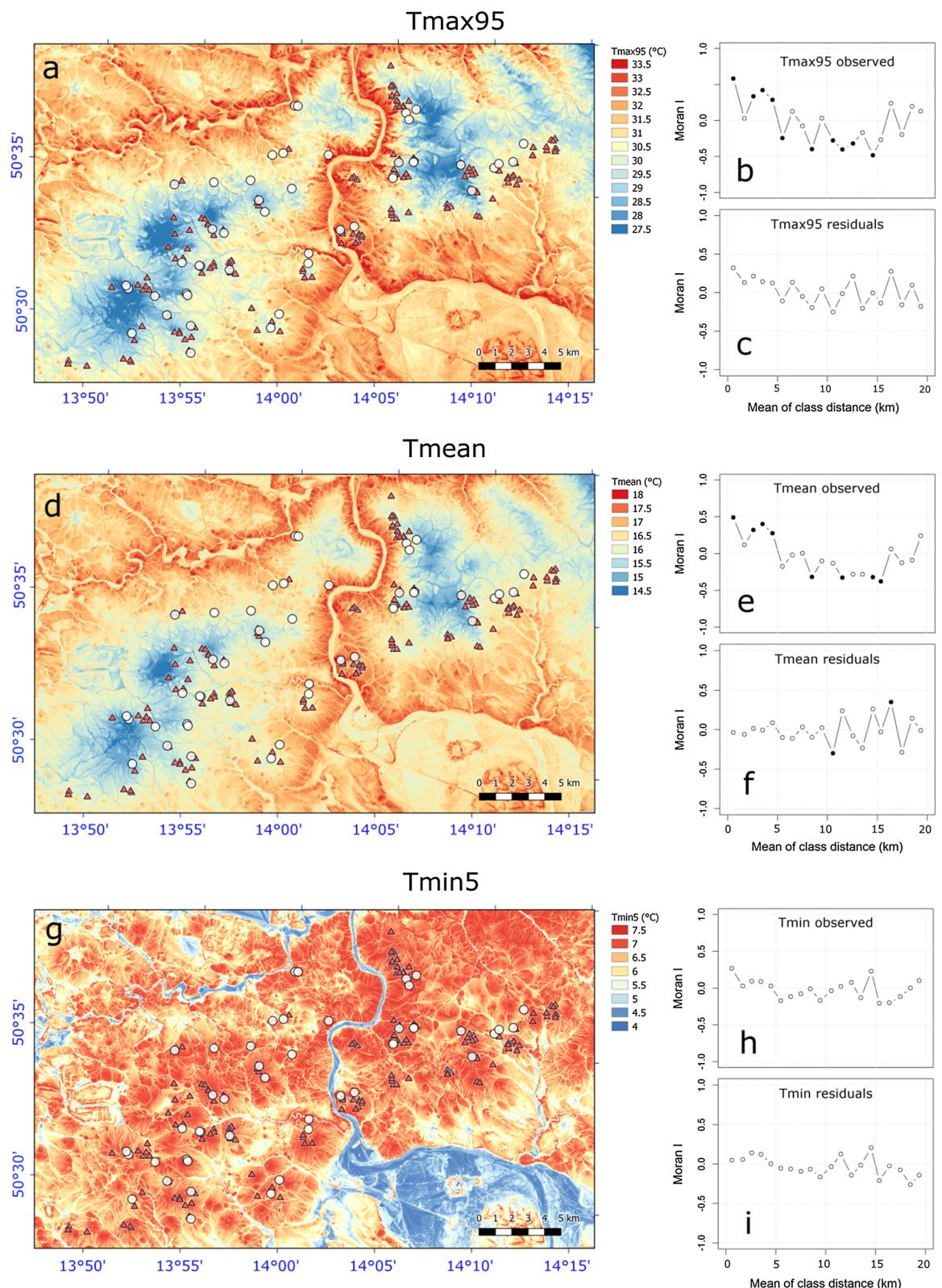
Within our study region, the temperature variability driven by topography was comparable to the temperature variability driven by elevation. Terrain topography thus creates contrasting fine-scale microclimatic patterns across the landscape (Fig. 3). Interestingly, the magnitude of topographically driven variability in maximum temperatures observed in our study is in line with values reported from Australia (Ashcroft and Gollan 2012) and France (Joly and Gillet 2017). Similar topographic effects on effective temperatures in the forest understorey have been also demonstrated in Germany, where bioindicated temperature was better predicted by models including the topographic heat load index along with conventional interpolated temperature grids (Reger et al. 2011). Together, these results suggest that topographically driven temperature variability should be considered in ecological studies (Vanwallegem and Meentemeyer 2009; Ashcroft et al. 2012).

Surprisingly, we did not find any significant correlation between variation in canopy cover and understorey temperature. The average buffering effect of the forest canopy compared to open habitats on maximum air temperatures has been quantified to be ca 2 °C in broadleaved forests (Von Arx et al. 2012; Zellweger et al. 2019) and ca 1.4 °C in coniferous ones (Davis et al. 2019). The estimated effect of canopy cover, albeit insignificant, in our full model was roughly comparable to these values, tending towards 2.6 °C, but with a high standard error of 2.4 °C. In contrast to studies reporting significant effects of canopy cover (e.g. Ashcroft and Gollan 2012; Von Arx et al. 2013; Greiser et al. 2018), we did not measure temperature in non-forest habitats. It can therefore be argued that we did not find any effects of canopy cover because we sampled only a limited gradient of canopy cover. However, we selected our plot locations according to a stratified random design with strata defined only by topographic variables; canopy cover in our plots thus reflects typical variation within the region. While most plots were established within

**Fig. 3** Predicted topoclimatic maps and respective Moran's I ► statistics showing the spatial autocorrelation of observed temperatures and model residuals. Spatial variability of Tmax95 was efficiently fitted by a topoclimatic model (**a**) which accounted for the observed spatial autocorrelation (**b**), showing weak, statistically not significant autocorrelation of residuals at all spatial scales (**c**). Tmean (**d**) followed generally the same pattern but was less influenced by terrain properties with spatial autocorrelation (**e**) sufficiently accounted for by the model (**f**). Cold air pooling affected the distribution of Tmin5 (**g**), creating a contrasting picture to Tmax95 and Tmean but with low spatial autocorrelation of both observed temperatures (**h**) and model residuals (**i**). Statistically significant ( $p < 0.05$ ) values of Moran's I are plotted as full circles

close-canopy forests dominating the region, we measured temperatures also in tree-fall gaps and open forests on steep slopes with shallow soils and the range of canopy cover values observed in our study is fully comparable to values reported from other temperate forests, even in studies that also considered canopy gaps (Canham et al. 1990; Valverde and Silvertown 1997; Tinya et al. 2009; Hofmeister et al. 2009). Nevertheless, we acknowledge that part of the unexplained temperature variability can be potentially attributed to variation in other forest structural attributes like canopy height or stem density (Frey et al. 2016; Kovács et al. 2017).

Recently, it has been shown that forest canopy ability to buffer understorey temperatures in temperate deciduous forests does not increase linearly with increasing canopy cover, but is constant beyond a threshold of ca 75% canopy cover (Zellweger et al. 2019). As all sites in our study have canopy cover above 75% (Table 1), lack of effect of canopy cover on measured temperatures is fully in line with Zellweger et al. results. Likewise, Gray et al. (2002) have compared temperatures under closed canopy and canopy gaps of different size, reporting that minimum and mean temperatures were not affected by gaps, but only the maximum air temperatures measured in the largest gaps were significantly affected. Together, these results suggest that there is some threshold value of canopy cover above which the effect of canopy on air temperature is saturated. The temperature variability potentially driven by variation in canopy cover within forest stands is therefore relatively small compared to topography-driven variability (over 4 °C in our region).



## Effects of in situ measured temperature on understorey plant communities

We found that maximum temperatures have a stronger effect on understorey plant communities than mean or minimum temperatures. Tmax95 explained 51% of the variability explainable by a single predictor variable in the multivariate analysis, which indicates a high importance of maximum temperatures. Our results thus support previous studies arguing that not average climatic conditions but rather climatic extremes are the determinants of species distribution and community assembly (Suggitt et al. 2011; Ashcroft and Gollan 2012). The range and spatial heterogeneity observed for maximum temperatures was also broader than that of mean or minimum temperatures (Fig. 3) and which may also contribute to the greater explanatory power of maximum temperatures.

In our opinion, maximum temperature acts on forest plant species as a permanent stress factor rather than an episodic disturbance agent because spatial pattern of maximum temperature was consistent between years (Fig. S2). Plants growing at sites regularly exposed to high maximum temperatures are not only affected by physiological stress caused directly by high temperatures, but they are also exposed to high vapour pressure deficit, which is physically linked to temperature, resulting in high evapotranspiration rates (Kovács et al. 2017; Davis et al. 2019). The effects of high temperature stress on plant communities thus may be accentuated as a result of trade-offs with shade adaptations of forest plants, which make them more sensitive to water deficit under high-temperature conditions (Valladares and Niinemets 2008). Indeed, sites with lower maximum temperatures host typical forest species such as *Actaea spicata* or ferns *Dryopteris carthusiana* and *D. filix-mas* whereas sites on the ‘hot’ end of the gradient host many plant species that can be found also in forest edges, shrublands or in non-forest habitats, for example *Serratula tinctoria*, *Fragaria vesca* or graminoids such as *Festuca ovina*, *Carex montana* and *Poa angustifolia* (Fig. 2).

The species composition of temperate forest understories changed substantially less than had been expected from the observed changes in mean temperature in the past decades (Bertrand et al. 2011; De Frenne et al. 2013). One explanation for this discrepancy, proposed by De Frenne et al. (2013), is the

microclimatic buffering of understorey temperatures caused by increasing canopy cover. However, our results suggest that the potential buffering effect of canopy cover on temperature variability within forests in this region is relatively weak: Even if the relation between canopy cover and maximum temperatures was linear and canopy cover in all our plots was to increase to 100%, the potential difference in buffering effect on maximum temperatures in the forest understorey compared to current situation would not exceed 0.25 °C according to the effect reported by Von Arx et al. (2012), but no additional buffering effect with increasing canopy cover can be expected if there is a threshold value in canopy cover above which the temperatures do not further respond to increasing canopy cover, as was reported by Zellweger et al. (2019). Even when the buffering effect is expressed directly as thermophilization of plant communities, using the most extreme estimate of effect sizes from De Frenne et al. (2013) and simulated increase in canopy cover to 100% on all plots, the expected mean buffering effect mitigating plant community thermophilization would be as low as 0.003 °C. Such values are far below the expected rise in temperatures during the 21st century, but also below the observed rise of temperatures in the past decades (IPCC 2014). Our data thus challenge the potential of forests to buffer climate warming by increasing canopy closure at the landscape-scale (De Frenne et al. 2013; Frey et al. 2016). However, significant effects of altered temperature regime on understorey vegetation can be expected locally in response to moderate to severe canopy disturbance or stand development following such disturbance (Stevens et al. 2015; Brice et al. 2019), but such dynamics is accompanied also by dramatic changes in light, water and nutrient availability, affecting understorey vegetation in a complex way (Canham et al. 1990; Gray et al. 2002; Gálhidy et al. 2005). This makes disentangling the effects of the temperature from other driving forces challenging.

Interestingly, maximum daily temperatures, which proved to be the most determining factor for understorey species composition, have risen globally at a lower rate compared to mean or minimum temperatures (Easterling et al. 1997). The slower increase in maximum temperature and its greater spatial heterogeneity can theoretically be at least partly responsible for the lower rate of change in forest understorey vegetation observed across temperate forests.

However, only long-term microclimatic data measured along gradients of canopy cover can disentangle links between the changing climate, forest canopies, topographic complexity and directional change in forest understorey vegetation, so far deduced mostly from indirect evidence based on space-for-time substitutions (Frey et al. 2016; De Frenne et al. 2019) or bioindication (De Frenne et al. 2013).

#### Topoclimatic and macroclimatic maps in ecological applications

Our findings stress that fine-scale information about maximum temperatures in the growing season is essential for a proper assessment of the effect of climate change and is also vital for species distribution modelling (see also Parmesan et al. 2000; Ashcroft and Gollan 2012; Gardner et al. 2019). The common limitations of currently available global climatic datasets, including WorldClim 2, are their insufficient spatial resolution, possible bias in temperature interpolations and, finally, the fact that weather-station data behind these datasets do not reflect specific forest microclimates and topographic complexity (Bedia et al. 2013; Nadeau et al. 2017; Bramer et al. 2018). Elevation is still the only topographic attribute used in interpolations of WorldClim 2 climate grids (Fick and Hijmans 2017), but we found that other aspects of topographic complexity, including anisotropic heating and cold air pooling can be similarly important at landscape scales. This is the likely reason why maximum temperature from WorldClim 2 explained substantially less variation in species composition than both in situ measured maximum temperatures and maximum temperatures from our interpolated topoclimatic grids. However, the explanatory power of mean temperature was comparable between topoclimatic grids and WorldClim 2. This is probably caused by the lower spatial variability in mean temperatures and greater relative importance of elevation compared to other topographic attributes, which makes mean temperature predictions in WorldClim 2 more realistic compared to maximum temperature predictions based on the same dataset.

Together, our results show that it is possible to improve bioclimatic maps using topographic variables and thus substantially enhance the ecological relevance of these maps. Therefore, despite substantial improvements in the precision and spatial resolution

of global climate grids (Fick and Hijmans 2017), there is still a need to incorporate local topography into these grids (Slavich et al. 2014; Aalto et al. 2017). We show that such topoclimatic maps capture more biologically relevant information and can therefore increase the predictive accuracy of ecological models.

#### Conclusion

Elevational gradients together with terrain topography create complex microclimatic mosaics across forested landscapes. Plant species growing in forest understoreys are sensitive to these microclimatic mosaics and most strongly respond to maximum temperature. At landscape scales, maximum temperatures can be successfully modelled using topographic variables derived from high-resolution DEMs, suggesting promising avenues for the refinement of species distribution models and the modelling of species' vulnerability to climate change.

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