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TECHNICAL ADVANCE

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ForestTemp – Sub-canopy microclimate temperatures of European forests

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Abstract

Ecological research heavily relies on coarse-gridded climate data based on standardized temperature measurements recorded at 2 m height in open landscapes. However, many organisms experience environmental conditions that differ substantially from those captured by these macroclimatic (i.e. free air) temperature grids. In forests, the tree canopy functions as a thermal insulator and buffers sub-canopy microclimatic conditions, thereby affecting biological and ecological processes. To improve the assessment of climatic conditions and climate-change-related impacts on forest-floor biodiversity and functioning, high-resolution temperature grids reflecting forest microclimates are thus urgently needed. Combining more than 1200 time series of in situ near-surface forest temperature with topographical, biological and macroclimatic variables in a machine learning model, we predicted the mean monthly offset between sub-canopy temperature at 15 cm above the surface and free-air temperature over the period 2000–2020 at a spatial resolution of 25 m across Europe. This offset was used to evaluate the difference between microclimate and macroclimate across space and seasons and finally enabled us to calculate mean annual and monthly temperatures for European forest understories. We found that sub-canopy air temperatures differ substantially from free-air temperatures, being on average 2.1°C (standard deviation ± 1.6°C) lower in summer and 2.0°C higher (±0.7°C) in winter across Europe. Additionally, our high-resolution maps expose considerable microclimatic variation within landscapes, not captured by the gridded macroclimatic products. The provided forest sub-canopy temperature maps will enable future research to model below-canopy biological processes and patterns, as well as species distributions more accurately.

KEYWORDS
biodiversity, boosted regression trees, climate change, ecosystem processes, forest microclimate, SoilTemp, species distributions, thermal buffering

1 | INTRODUCTION

Climate change is having profound impacts on Earth's biodiversity and ecosystem functioning (Lenoir et al., 2020; Pecl et al., 2017; Scheffers et al., 2016). Ecological research assessing the consequences of climate change is, however, largely based on coarse-gridded climate data of approximately 1 km^2 or more (Lenoir et al., 2013; Willis & Bhagwat, 2009), such as WorldClim (1 km^2; Fick & Hijmans, 2017), CHELSA (1 km^2; Karger et al., 2017) and TerraClimate (16 km^2; Abatzoglou et al., 2018). For the terrestrial parts of the globe, these climatic grids are derived from standardized meteorological stations recording weather conditions at approximately 2 m height in open and windy habitats to remove microclimatic effects (Jarraud, 2008). Consequently, these grids are representative for long-term free-air temperatures (the 'macroclimate') in open ecosystems. However, many organisms experience temperatures that substantially deviate from those captured by macroclimatic grids (Bramer et al., 2018; De Frenne et al., 2019). These so-called microclimatic temperatures play a crucial role in dictating biological and ecological processes close to the ground surface such as vegetation, carbon and nutrient dynamics and species distributions (Lembrechts et al., 2018; Nilsson & Wardle, 2005; Perry, 1994).

The available coarse-grained macroclimate data have been shown to fall short in its ability to capture small-scale biological and physical processes close to the ground surface (Lembrechts et al., 2019; Lenoir et al., 2017). For example, small herbaceous plants are responding to microclimatic temperatures near the ground surface rather than free-air temperatures at 2 m height, and it has been shown that the currently available macroclimate data inaccurately reflect the distribution of these species (Lembrechts et al., 2019). This may lead to erroneous predictions of species range dynamics (Lembrechts et al., 2018). The core of this problem is twofold. First, macroclimatic grids do not consider many climate-forcing factors operating near the ground surface. The ground and canopy surfaces absorb solar radiation and low wind speeds reduce thermal mixing of the air, leading to significant fine-scale vertical and horizontal variation in air temperature (Geiger, 1950; Monin & Obukhov, 1954; Richardson, 1922). Second, data readily available from global macroclimatic grids consider the Earth to be a homogeneous surface of short vegetation with shading consistent with that of a weather station. However, microclimates are arguably nowhere more evident than in forests, where the amount of sunlight reaching the ground surfaces and absorbed by leaves varies substantially owing to the structural complexity of forest canopies and significant variation in evapotranspirative cooling (Bramer et al., 2018; De Frenne et al., 2019; Lenoir et al., 2017). Furthermore, landscapes characterized by considerable topographic variation (e.g. slope, aspect, elevation) have shown to harbour ample microclimatic variation (Lenoir et al., 2013; Macek et al., 2019) due to the effect of topography on processes such as cold air drainage, incident solar radiation and hydrology.

Although not a new discipline, microclimate ecology has gained renewed interest over the past years (Bramer et al., 2018; De Frenne et al., 2021), providing the scientific community with many insights on the processes underlying microclimate variability, especially related to the implications of climate change. For example, several mechanistic models are available to derive microclimatic temperatures (Kearney & Porter, 2017; Kearney et al., 2014; Maclean, 2019). Other studies make use of an empirical design, in which a network of microclimate temperature loggers is installed within a certain region to cover large environmental gradients (Frey et al., 2016; George et al., 2015; Govaert et al., 2020; Greiser et al., 2018; Macek et al., 2019; Meeussen et al., 2021). Nonetheless, when moving to a continental extent, these methods often reach their limits. Although mechanistic models are capable of making accurate predictions at high spatiotemporal resolution across restricted spatial extents, they struggle to do this over large spatial extents, as the processes must be modelled in hourly timesteps and are thus more computationally intensive than their statistical counterparts (Maclean et al., 2019). Moreover, the unpredictable nature of wind gusts underneath heterogeneous forest canopies and the effects of these on temperature gradients make it challenging to develop mechanistic models of below-canopy microclimates (Landuyt et al., 2018). On the other hand, empirical data from regional logger networks had not yet been combined within one database until very recently (Lembrechts et al., 2020). To better model ecosystem functioning and predict the effects of climate change on organisms living close to the Earth's surface, gridded microclimate data with a broad geographical extent are thus urgently needed (Körner & Hiltbrunner, 2018; Lembrechts & Lenoir, 2020; Zellweger et al., 2019). Yet, the spatiotemporal resolution used to define microclimate is organism specific (Potter et al., 2013) and fractal by nature. This means that the fractal dimension, in terms of spatiotemporal resolution, of microclimate as experienced by understorey plants, for instance, might be orders of magnitude larger than the fractal dimension of microclimate as experienced by smaller organisms, like insects living in tree holes or dead wood (Pincebourde & Woods, 2020).

To help fill this critical knowledge gap, the SoilTemp global database of soil and near-surface temperature time series has recently been launched (Lembrechts et al., 2020), collecting in situ temperature logger data from regional microclimate logger networks in various habitats across the globe. The currently available time series from 1248 aboveground temperature sensors across European forests provide a unique opportunity to accurately predict sub-canopy forest temperature at a continental scale and at a spatial resolution that matters for organisms living in the forest understorey. Here, given our focus on the forest floor, we decided to work with a spatial resolution of 25 m. Not only for practical reasons (i.e. the resolution at which predictor variables are available at a continental extent), but also for ecological reasons as this is the scale at which both foresters (i.e. forest inventories usually use plots ranging between 625 and 1000 m^2) and botanists (i.e. forest vegetation surveys usually use 100–500 m^2 plots) work to describe the forest understorey in the field. For this, we calculated the mean monthly temperature offset between microclimate temperature, based on in situ temperature measurements from the SoilTemp database (Lembrechts et al., 2020), and macroclimate temperature, based on ERA5-Land reanalysis data (Muñoz-Sabater et al., 2021). This offset was then related to different variables (i.e. topographical, biological and macroclimatic) to quantify the difference between microclimate and macroclimate across space and seasons and to derive gridded microclimate products that are meaningful for studying biodiversity on the forest floor. Moreover, the offset enables us to (i) model average sub-canopy temperatures over a 20-year period and (ii) quantify the buffering capacities of forests across Europe, where buffering is defined as a dampening of the macroclimate, such that temporal fluctuations related to the macroclimate still exist, yet much less pronounced than outside of the forest (De Frenne et al., 2021).

2 | METHODS

2.1 | Data acquisition

In situ microclimatic temperature measurements were compiled in SoilTemp, a global database of soil and near-surface air temperature measurements combining both published and unpublished data sources (Lembrechts et al., 2020). First, we only included measurement locations within European mainland forest habitats, defined as all tree elements detectable from multispectral high-resolution (20 m) satellite (Sentinel-2, Landsat 8) imagery (European Union, 2020) in all 27 EU countries, plus Albania, Bosnia and Herzegovina, Kosovo, Liechtenstein, Montenegro, North Macedonia, Norway, Serbia, the United Kingdom and Switzerland. Second, we selected near-surface air temperature measurements at a height between 0 and 100 cm above ground from time series spanning at least 1 month and a temporal resolution of less than 4 hours. Measurements taken at the same location, but at different heights, were included as separate data points while keeping track of logger ID to account for potential pseudo-replication issues (i.e. keeping data with the same logger ID either in the training data or in the testing data for cross-validation purposes). This resulted in 1248 time series at 1092 locations, extending over the period from 2000 to 2020 and geographically spanning a latitudinal gradient over Europe from Portugal (38.54N 8.00W) to Sweden (64.11N 19.45E) and a longitudinal gradient from Portugal (38.64N 8.60W) to Finland (62.33N 30.37E; Figure S1a). Note that different sensor and shielding combinations were used within the input data and that they might contribute to errors in the model (Table S1). However, experimental research has shown that such errors are relatively small in shaded environments such as forests (Maclean et al., 2021), an order of magnitude smaller than the measured offsets.

Next, we aggregated the time series, usually available at hourly or sub-daily (e.g. every 2 or 4 h) native resolutions, to mean monthly temperatures, after visually checking each time series for outliers and erroneous data. We further only selected months with at least 28 days of data, resulting in a cumulative 24,291 months of near-surface air temperature (Table S2).

2.2 | Offset calculation

We derived a monthly temperature offset value between microclimate (i.e. sub-canopy) and macroclimate (i.e. free-air) temperature measurements (ΔT = sub-canopy T°C – free-air T°C) in order to relate this ΔT to different explanatory variables and quantify the difference between microclimate and macroclimate across space and seasons. Positive offset values thus indicate, on average, warmer forest microclimate conditions, whereas negative values point to a colder forest microclimate. The offset (ΔT) was calculated as the difference between the monthly mean microclimate temperature, as measured by the loggers, and the corresponding monthly mean air temperature value at 2 m height for exactly the same month, year and grid cell from ERA5-Land reanalysis data with a spatial resolution of 0.1 × 0.1 degrees (Muñoz-Sabater et al., 2021).

2.3 | Acquisition of covariate layers

Covariates were selected based on their known relevance for forest microclimatic temperatures according to literature (Greiser et al., 2018; Zellweger et al., 2019), spatial resolution and availability at the continental scale. In total, 20 covariate layers were selected to create a covariate layer stack, including topographical, biological and macroclimatic variables.

Topographic layers were derived from a digital elevation model (EU-DEM v1.1) at 25 m resolution (European Union, 2020). Both northness and eastness were derived as the cosine and sine of the aspect (°), respectively. Additionally, we incorporated slope (°), elevation (m a.s.l.) and latitude to account for the variation in incoming solar radiation (Lenoir & Svenning, 2013; Meineri & Hylander, 2017). Relative elevation (m) represents the elevational difference between each pixel and the lowest pixel within a 500 m buffer. This is often used as a proxy for cold air drainage, as cold air moves downslope (Ashcroft & Gollan, 2013). Distance to the coast was included because the heat capacity of the ocean has an important effect on (microclimatic) temperatures (Vercauteren et al., 2013; Zellweger et al., 2019). Furthermore, the effect of increased water vapour content in the atmosphere near the coast affects cloud patterns which, in turn, influence incoming solar radiation (Zellweger et al., 2019). Finally, the topographic wetness index (TWI) was used as a proxy for soil moisture (Meineri et al., 2015). This index quantifies the effect of topographic variation on hydrological processes by taking into account both slope and specific catchment area (Beven & Kirkby, 1979). We calculated TWI by using the *Freeman FD8* flow algorithm with a flow dispersion of 1.0, a flow width equal to the raster cell size (i.e. 25 m) and a local slope gradient (Kopecký et al., 2021).

The 2015 high-resolution (20 m) Copernicus maps of tree cover density (%), referring to the percentage of tree cover per raster cell, and forest type (broadleaf vs. coniferous) were included. To quantitatively capture the phenological differences between broadleaved and coniferous forests, we calculated two NDVI values, representative for winter (December–February) and summer months (June–August). NDVI variables were derived from Landsat 4, 5, 7 and 8 satellite images over a period from 2000 to 2020 provided in Google Earth Engine (Gorelick et al., 2017). Each image underwent pre-processing by converting low-quality data (e.g. due to the presence of clouds, snow or shadows) into missing values based on the masks provided with the downloaded images.

Furthermore, long-term average macroclimatic conditions were considered by including four WorldClim bioclimatic variables covering the period between 1970 and 2000 (Fick & Hijmans, 2017): BIO1 (Mean Annual Temperature); BIO5 (Maximum Temperature of the Warmest Month); BIO6 (Minimum Temperature of the Coldest Month); and BIO12 (Annual Precipitation). These were chosen due to the specific interaction of these variables with some of the topographical and biological variables. For instance, Greiser et al. (2018) found that forest density was an important driver for minimum and maximum microclimate temperatures in summer, whereas topography had a stronger influence on extreme temperatures in autumn and winter. Furthermore, mean annual cloud cover (%) over 2000–2014 derived from MODIS products was included to account for the effect of cloud cover on incoming solar radiation (Wilson & Jetz, 2016). Annual snow cover probability (%) was derived as the average of monthly snow probability based on a pixel-wise frequency of snow occurrence (snow cover >10%) in MODIS daily snow cover products (MOD10A1 & MYD10A1; Hall et al., 2002) over 2001–2019. Finally, we also included the sensor height above the ground surface as a covariate in our models, as this significantly impacts the magnitude of the temperature offset (De Frenne et al., 2019; Geiger, 1950).

When necessary, covariate map layers were reprojected and resampled to an equal area projection in EPSG:3035 (ETRS89-extended/LAEA Europe) at 25 m resolution using bilinear interpolation for quantitative data and the nearest neighbour method for categorical data. We present variable importance quantitatively and the relationship between each covariate and the response visually in partial dependence plots (Figure S2). Furthermore, we show the strongest two- and three-way interactions among covariates (Figure S3).

2.4 | Geospatial modelling

Machine learning techniques often outperform other statistical techniques such as generalized linear models (GLMs) or generalized additive models (GAMs) in terms of predictive power (Appelhans et al., 2015). As we aim to maximize predictive power within the environmental space covered by our data rather than explanatory power, we used boosted regression trees (BRTs), also referred to as gradient boosting machine, to model the relationship between the selected covariates and ΔT (Appelhans et al., 2015; Elith et al., 2008). Especially for regression, BRTs are particularly valuable due to their capacity to uncover nonlinear relationships as well as their automatic detection of complex interactions among covariates (Figure S3). Furthermore, this algorithm is capable to handle multicollinearity among covariates (Figure S4), outliers and missing data. On the other hand, BRTs are prone to (i) overfitting due to sequential fitting of trees (Elith et al., 2008) and (ii) errors when extrapolating outside the boundaries of the training data. To deal with these issues, we (i) implemented model regularization by means of low learning rate values (0.1–0.001) and cross-validation (Elith et al., 2008) and by (ii) providing a map indicating where the model is extrapolating beyond the values of the training data.

BRTs were built using the *gbm* R package (Greenwell et al., 2020). We searched for the optimal hyperparameter values with the *caret* package (Kuhn, 2012) by means of a grid search over the possible values of the four hyperparameters: interaction depth (2–6); total number of trees (100–10,000); learning rate (0.1–0.001); and the minimal observations in each terminal node (8–12; Elith et al., 2008). In total, 14,925 models were evaluated by 10-fold cross-validation (CV) while (i) taking into account logger ID to avoid pseudo-replication between folds and (ii) stratifying by the biogeographical regions of Europe (Cervellini et al., 2020), meaning that each fold contained 10% of the loggers in each biogeographical region. Finally, optimal hyperparameter values were selected by maximizing R^2_{CV}.

Once the optimal hyperparameter values were determined, we applied a stratified bootstrap approach to fit 30 different models (van den Hoogen et al., 2019). The bootstrapping procedure randomly sampled the data each time with replacement to fit the model. The biogeographical regions of Europe (Cervellini et al., 2020) were used as stratum for the random sampling to ensure that every biogeographical region was proportionally represented according to data availability in each region. Each of the bootstrapped models made separate predictions for each month – that is 3,141,115,825 European forest pixels classified 360 times (12 months × 30 bootstraps). Model precision was then quantified by calculating, per pixel, a 95% confidence interval (mean ± 1.96 SE) for each month. We predicted temperature at 15 cm height as this is the most common height within the input data (Table S2). Furthermore, most understorey forest plant species (e.g. herbs, grasses, sedges and ferns) fit, on average, to this height.

Machine learning techniques, like BRTs, are known to be less capable in extrapolating beyond the boundaries set by the environmental variables in the original training data. To assess where our model is extrapolating – and thus possibly providing less reliable predictions – we calculated for each pixel the percentage of quantitative covariate layers for which the pixel value lies outside the range of data covered by the dataset. Finally, we used a spatial leave-one-out cross-validation analysis to test the effect of spatial autocorrelation in the dataset (Figure S5; Roberts et al., 2017; van den Hoogen et al., 2021). This approach each time validates a model on data from one distinct location and trains a model on the remaining data. This is repeatedly done for each of our 1092 locations. Because of potential spatial autocorrelation close to the validation location, this process is repeated with an increasing buffer around the validation location, each time excluding data points that fall within the defined buffer zone from the training data. This method allows assessing the influence of spatial autocorrelation on the R^2.

2.5 | Offset and forest microclimate temperature maps at 25 m resolution

Here, we make the European monthly temperature offset grids available as open data. These can, in turn, be used to convert gridded macroclimate products into gridded microclimate products. We opted to illustrate the calculation of the mean annual forest microclimatic temperature (further referred to as 'forestBIO1'), but this calculation can be carried out for all other temperature-related bioclimatic variables from BIO1 to BIO11 (Fick & Hijmans, 2017; Karger et al., 2017). First, we calculated (i) the mean annual temperature offset as the average of the monthly offset maps and (ii) the mean annual temperature over 2000–2019 from monthly TerraClimate data (Abatzoglou et al., 2018). Second, we calculated forestBIO1 by adding anomalies of the predicted mean annual offset to the corresponding TerraClimate mean annual temperature map (Abatzoglou et al., 2018).

All calculations were performed in R version 4.0.2 (R Core Team, 2020). The *Tier-2 Genius* cluster from the high-performance computing facilities of Flanders was used to perform the calculations.

3 | RESULTS AND DISCUSSION

3.1 | ForestTemp – Microclimatic temperature maps of European forests

Our bootstrapped models for the monthly temperature offset performed well with a coefficient of determination (R^2) of 0.79 (95% CI: 0.78–0.80), a root mean square error of 1.19°C (1.17–1.21°C) and a mean absolute error of 0.87°C (0.85–0.89°C). The spatial leave-one-out cross-validation also showed reasonably good predictive performance with R^2 stabilizing around 0.55 when increasing the buffer size above 100 km (Figure S5). Mean monthly temperature offsets at 15 cm above ground over 30 bootstrap iterations ranged between −2.5 and 10.8°C in January and from −5.8 to 3.2°C in July (Table S3). Model predictions described expected patterns in ΔT, with forest microclimates overall being warmer than the macroclimate during winter and colder during summer (Figure 1). This corresponds to earlier findings for temperate systems, where forests act as a thermal insulator: on average cooling the understorey by 2.1°C in summer and warming it by 2.0°C in winter compared to monthly free-air temperature (De Frenne et al., 2019; Geiger, 1950). Our model was also able to capture the phenological difference between broadleaved and coniferous forests. We found bimodal peaks in winter, particularly pronounced in January (Figure 2), with temperature offsets in coniferous forests, on average, 1.0°C warmer (Figure S6). This likely relates to the differences in tree cover density between these two forest types during that time of year. The observed pattern can further be caused by the fact that coniferous forests are, at the continental scale, more abundant in places with snow, which is known to act as an additional thermal insulator (Aalto et al., 2018). Mean annual temperature offsets ranged between −5.7 and 7.8°C, which translate into a mean annual forest microclimate temperature (forestBIO1) between −2.0 and 22.1°C across Europe (Figure 3), compared to mean annual macroclimate temperature ranging between −3.5 and 20.4°C.

The bootstrapped models turned out robust, as standard errors were generally small compared to the modelled temperature offsets: standard errors of the mean of monthly temperature offsets stayed below 0.6°C in most months and across most parts of Europe (Figure 4; Table S3). Higher standard errors are noticed when predicting the offset at very high (above mid-Sweden) and very low latitudes (southern Spain) as well as in high-elevational regions, which are expected to be caused by extrapolation outside the environmental gradient covered by the availability of temperature loggers installed in forest ecosystems (Figure 5a; Figure S1b). The overall precision of each prediction is represented by the width of the 95% confidence interval for each pixel (Figure 5b), which maximally reaches 2.5°C in winter (January) and 1.2°C in summer (July, Table S3).

As for any other machine learning technique, we caution against the use of data from regions where the model is extrapolating (mainly in southern Spain, high-elevational areas of the Alps and Scandinavia, Figure 5a). As with any spatial model, our model is calibrated on certain environmental conditions and predictions outside these conditions might induce errors. This problem partly stems from undersampled regions in the database (e.g. southern Spain, the United Kingdom, large parts of eastern Europe and high-elevation forested areas), which should be a scope of future research. The extrapolation (Figure 5a) and precision (Figure 5b) maps could therefore be used as spatial masks to remove or downweight the pixels for which predictions are beyond the range of values covered by the models or unprecise.

3.2 | Drivers of microclimate

As expected, seasonality (i.e. month of the year) plays a crucial role in defining the direction of the monthly temperature offset, overall being positive in autumn and winter and negative during spring and summer (Figure S2). Bioclimatic variables seem to be important covariates, with the exception of mean annual temperature due to its high collinearity with other climatic variables (Figure S4). However, we notice an overall negative relationship between the offset and mean annual temperature (Figure S2), which might be related to the predicted decoupling of forest microclimate warming from warming of the free air (De Frenne et al., 2019; Lenoir et al., 2017). However, global warming-related disturbances such as extreme droughts, pest outbreaks (e.g. pathogens, bark beetles) and increased fire incidence could nullify the insulation capacity of the forest canopy under changing conditions, disrupting this low coupling. Furthermore, the high importance of distance to the coast and mean annual precipitation suggest an important role for water (McLaughlin et al., 2017). On the one hand, temperature buffering is a function of local soil moisture, which, in turn, can be driven by distance to water bodies and precipitation (Davis et al., 2019). For instance, it is the effect of increased water vapour content in the atmosphere near the coast which affects cloudiness, which, in turn, is an important variable as it affects shading and incoming solar radiation. On the other hand, moisture can have an impact in different ways, for example, by increasing the vegetation or snow cover. Besides, snow also seems to be important in driving the temperature offset (Aalto et al., 2018). The interaction between snow cover and sensor height (Figure S3c) clearly hints towards an insulating effect of snow on the sensor which is, contrary to standardized meteorological stations, not kept free of snow or ice. We thus expect that large positive wintertime offsets

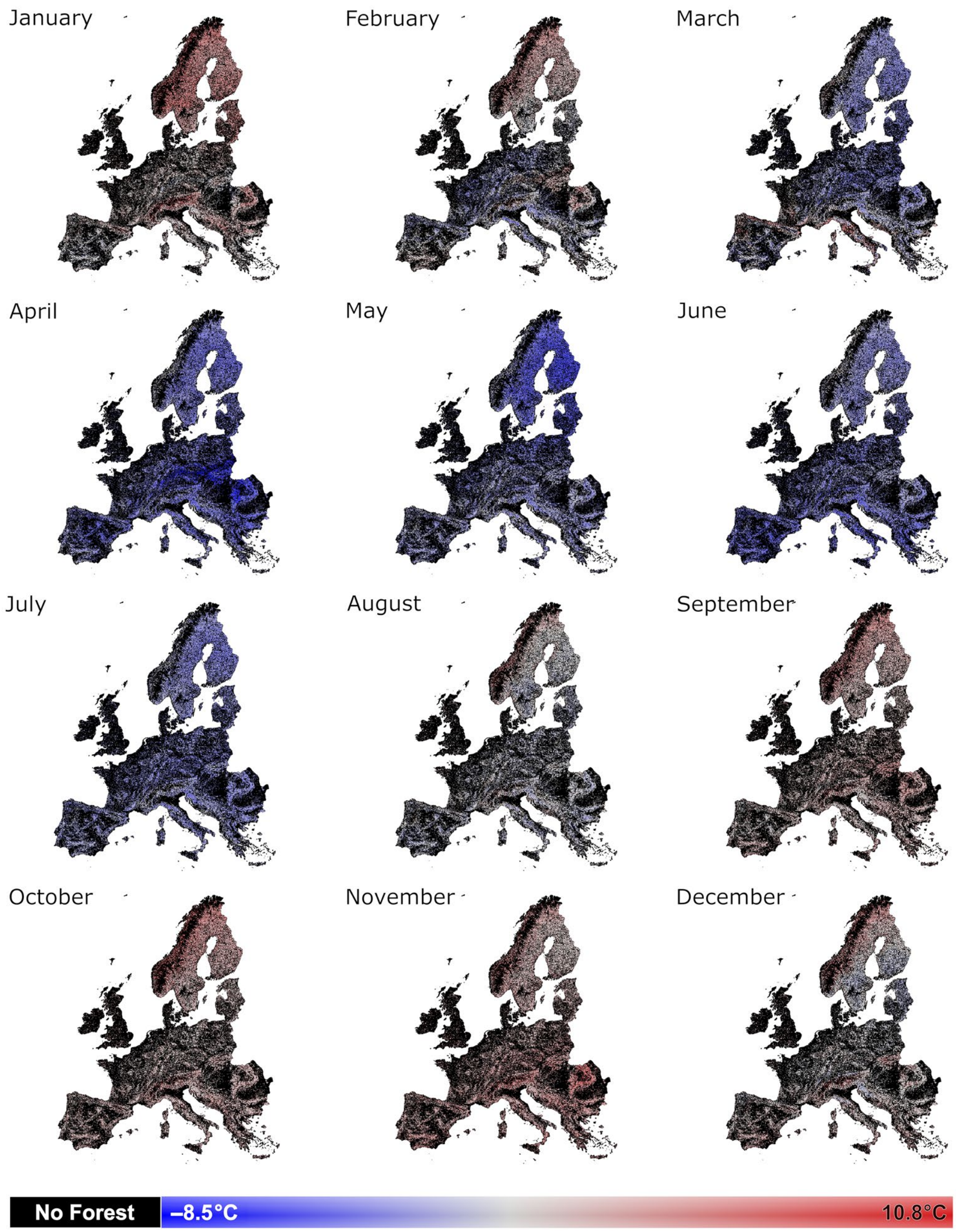

FIGURE 1 Predicted mean monthly air temperature offset across European forests. Mean monthly temperature offset at 15 cm above ground between in situ forest microclimate and free-air temperatures (sub-canopy T°C minus free-air T°C) (in °C)

in regions with high snow cover probability (i.e. high-latitudinal and high-elevational regions) are mainly caused by this snow insulation effect. Of moderate importance are topographic variables such as slope and elevation, which show a positive and negative relationship with ΔT, respectively. Moreover, sensor height, with a clear positive effect on ΔT, and the NDVI play an intermediate role. Surprisingly, biotic variables such as tree cover density or forest type seem to be less good predictors for the offset at the continental scale. However, the spatial resolution of 25 m used here is probably still too coarse to fully capture these effects (Kašpar et al., 2021). Importantly, the availability of accurate stand-level data at 25 m resolution (e.g. basal area, stem density, leaf area density or tree height) is still limited. Spaceborne, airborne or terrestrial LiDAR-derived variables could be a valuable source of data to solve such issues in the future (Frey et al., 2016; George et al., 2015; Kašpar et al., 2021). However, just as with mean annual temperature, these effects might already be partially captured by or confounded with the combination of seasonality and NDVI.

Note that we do not intend to unravel the physical mechanisms driving the offset between forest microclimate temperatures and free-air temperature. We are aware that most of our explanatory variables (e.g. tree cover density, northness or slope) are indirect drivers and rather affect the physical mechanisms driving the offset (e.g. incoming solar radiation, wind speed) than sub-canopy

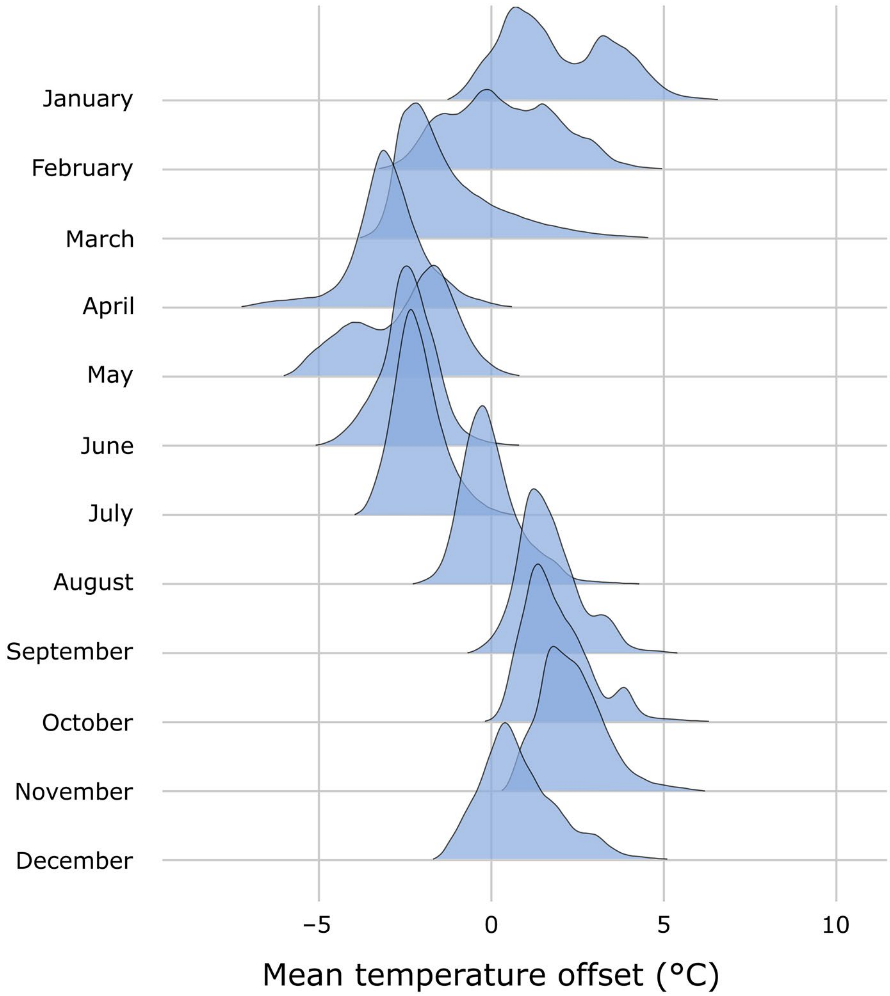

FIGURE 2 Histograms of mean monthly temperature offsets. Density ridgeplots for the monthly temperature offset at 15 cm above ground between in situ forest microclimate and free-air temperatures (sub-canopy T°C minus free-air T°C) (in °C) indicating, per month, the distribution of 1,000,000 randomly sampled raster pixel values across European forests

temperatures directly (Bennie et al., 2008). However, as we aim to create continental high-resolution sub-canopy temperature maps for understorey vegetation in European forests, a few strong correlative relationships could be better than complex, physical models that are computationally difficult to run at the continental extent and at high spatial resolution. Additionally, some potentially important variables are not incorporated within our models, either due to the limited availability or coarse spatial resolution of those variables. One of the possible limitations of our study is the assumption that forests, and their characteristics, are static over time. However, large parts of European forests are managed (Senf & Seidl, 2021), which makes it virtually impossible to incorporate up-to-date vegetation variables such as forest height, basal area or age. Furthermore, although we incorporated snow cover probability in the model, which shows an important interaction with sensor height, we do need the exact snow height and duration at high spatiotemporal resolution to quantify the insulation effect of snow on the logger sensors at different heights (Gisnås et al., 2016). Unfortunately, data on snow water equivalent, needed to calculate snow height and duration, are only available at a coarse spatial resolution of 5 km^2. Incorporating this into the model would not improve the model as there is still high, fine-scale spatial variability within each pixel. In addition, given the strong correlation of fine-scale snow dynamics with topography, inclusion of the latter is likely to partially capture this effect (Aalto et al., 2018; Niittynen & Luoto, 2018).

Finally, the 25 m spatial resolution is a significant step forward compared to existing microclimate products across large spatial extents. Nonetheless, we have to acknowledge the remaining within-pixel variability both in spatial and temporal terms. Moreover, we know that some organisms, depending on their body size, utilize microclimatic variation at orders of magnitude less than the spatio-temporal resolution used in this study. For instance, small insects can use sunflecks and microhabitats (tree holes and dead wood) available within a 25 m × 25 m grid cell to seek microvariation in temperature throughout the course of the day. Hence, recent research argues in favour of incorporating especially higher temporal resolutions in ecological analyses (Bütikofer et al., 2020). However, given current-day data availability and computational power as well as our focus on the forest floor, this study mapped microclimates at a continental scale according to the state-of-the-art.

3.3 | Applications and future perspectives

The outcomes of this study allow researchers to use accurate forest microclimate temperature data in large-scale analyses. This is

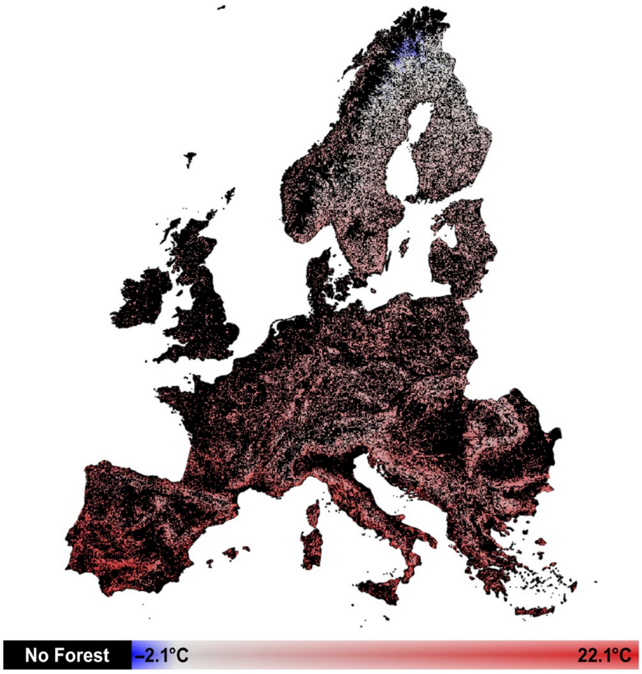

FIGURE 3 forestBIO1. Mean annual temperature at 15 cm above ground in European forests (in °C) with a spatial resolution of 25 m, representative of the 2000–2020 period, calculated using the maps of monthly mean air temperature offsets at 25 m resolution (Figure 2) added to the mean annual air temperature from TerraClimate at 4 km resolution

an important step forward as the mismatch between macroclimate and microclimate forest temperatures is substantial and can seriously bias the outcome of ecological and global change studies. For example, microclimate-informed species distribution models (SDM; Lenoir et al., 2017) could reveal more accurate insights into the various processes underlying species vulnerability to climate change on different aspects, including climate change exposure, sensitivity, adaptability and dispersal (Pacifici et al., 2015). Climate change exposure can be buffered by microclimate, whereas climate sensitivity impacts a species' ability to cope with microclimatic warming. Furthermore, microclimatic variation affects the spatial distribution of adaptive genetic variation and thus the ability of a population to survive climate change (De Kort et al., 2020; Graae et al., 2018). Finally, microclimate drives the spatial distribution of dispersal pathways throughout the landscape and thus directly impacts dispersal ability and populations in fragmented landscapes. Understanding how these processes interact with microclimate to shape species responses and their vulnerability to climate change is fundamental to predicting range dynamics.

We trust the predicted thermal offsets for forest ecosystems and their possibility to derive gridded microclimate products will enable future research to more accurately model ecological processes and patterns in the forest understorey, as well as forest-dwelling species distributions affected by climate change. These maps are available as GeoTIFFs for download through figshare (https://doi.org/10.6084/

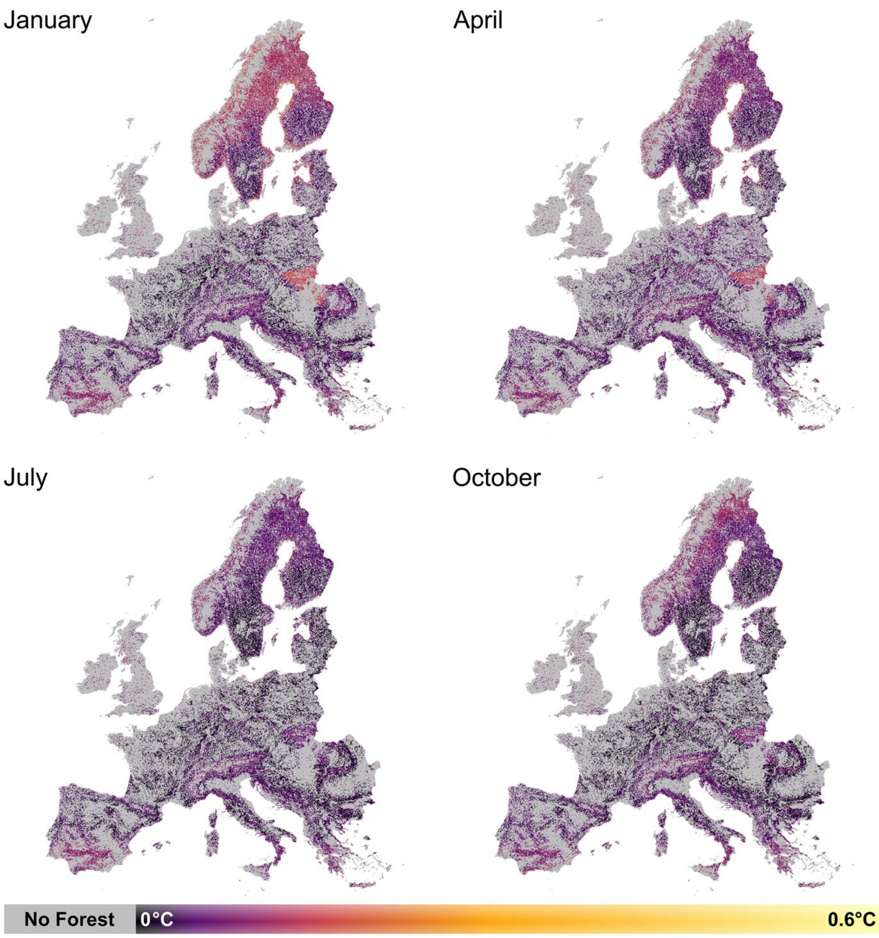

FIGURE 4 Robustness of the temperature offset model at 15 cm above ground across European forests. Standard errors of the mean from predicted mean monthly temperature offsets (sub-canopy T°C minus free-air T°C) at 15 cm above ground derived from 30 bootstrapped models (in °C). For additional months, see Figure S7. See Table S3 for detailed quantitative data

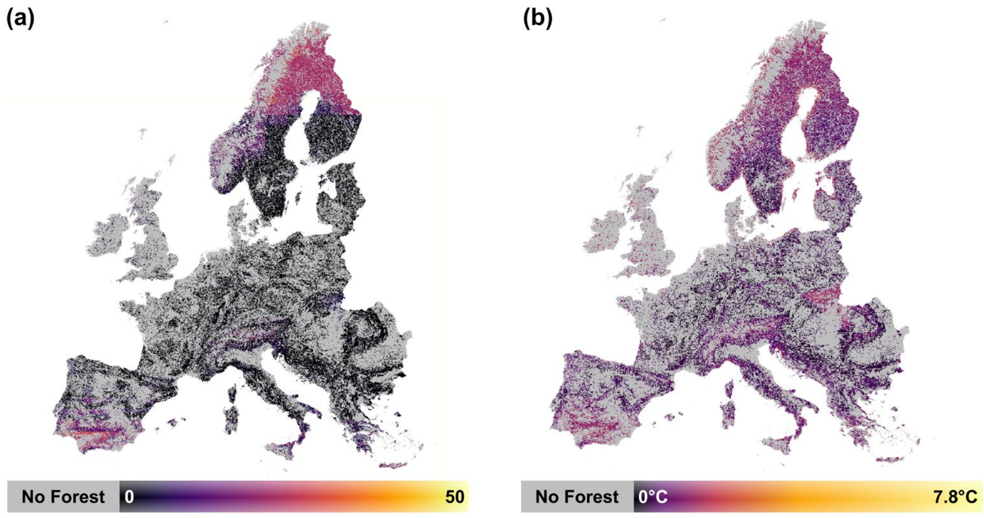

FIGURE 5 Extrapolation and precision maps. (a) The percentage of quantitative variables for which the pixel lies outside the range of data covered by the training data. Pixels with high values indicate that the model has to extrapolate for many of the covariates for that specific pixel (i.e. due to missing in situ measurements). (b) Precision of predictions for each pixel, calculated as the width of the bootstrapped 95% confidence interval for each pixel

m9.figshare.14618235) and will be updated as more or better data become available.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The processed input data (i.e. monthly temperature offset values) that support the findings of this study as well as all raster layers (GeoTIFFs) produced in this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.14618235 while the raw temperature time series necessary to process monthly temperature offset values are available from SoilTemp, a global database of soil and near-surface air temperature measurements data. Restrictions apply to the availability of raw SoilTemp data, which were used under license for this study. The raw temperature time-series data are available from Jonas Lembrechts/Stef Haesen with the permission of SoilTemp data contributors of this study.

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