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Running title – Incorporating microclimate into SDMs

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SH, JL, PDF, JJL, and KVM designed the research. SH performed the data analyses, with contributions from JL, EG, PDF, JJL, MK, MM, MM, JW and KVM. SH wrote the manuscript, with contributions from JL, EG, PDF, JJL, MK, MM, MM, JW and KVM. All authors contributed substantially to revisions.

Data accessibility statement

Code and data are available at https://figshare.com/s/c25cdebad1474201b733. The raw biodiversity data is available at https://doi.org/10.15468/dl.kf533a. ForestClim is freely-available at https://doi.org/10.6084/m9.figshare.22059125.

ABSTRACT

Species distributions are conventionally modelled using coarse-grained macroclimate data measured in open areas, potentially leading to biased predictions since most terrestrial species on Earth reside in the shade of trees. Here, we compared conventional macroclimate-based species distribution models (SDMs) with models corrected for forest microclimate buffering, at both coarse and high spatial resolution, for forest plant species across Europe. We show that microclimate-based SDMs at high spatial resolution outperformed models using macroclimate and microclimate data at coarser resolution. Additionally, macroclimate-based models introduced a systematic bias in modelled species response curves, which could result in erroneous range shift predictions under climate change. Critically important for conservation science, these models were unable to identify warm and cold refugia at the range edges of species distributions. Our study emphasizes the crucial role of microclimate data when SDMs are used to gain insights into biodiversity conservation in the face of climate change, particularly given the growing policy and management focus on the conservation of refugia worldwide.

INTRODUCTION

Over the last decades, species distribution models (SDMs, also known as habitat suitability models or ecological niche models), have emerged as a central method to project the effects of changing environmental conditions on species' distributions in space and time (Booth et al., 2014; Elith & Leathwick, 2009; Guisan & Zimmermann, 2000; Zimmermann et al., 2010). Most SDMs are correlative models that infer relationships between species occurrences and the environment using statistical or machine learning methods (Elith & Leathwick, 2009). Conventional SDM practices involve the incorporation of a standard set of bioclimatic variables with a typical spatial resolution of 30 arc seconds such as in the WorldClim (Fick & Hijmans, 2017) or CHELSA (Karger et al., 2017) datasets. However, these climatological data are derived from standardized meteorological stations at approximately 2 meters height above short grass, exposed to wind, and well away from trees to minimize any noise generated by microclimatic effects (Jarraud, 2008). Gridded macroclimatic data interpolate such weather stations' data and thus represent the free-air temperature conditions in open ecosystems. Although these data are sufficient to adequately capture changes in free-air temperatures, SDMs based on coarse-scale climate data should be expected to introduce a bias, which stems from the simplified assumptions these models make about the causal relationship between spatially-averaged climatic predictors and the fitness of individual organisms or likelihood of persistent populations (Fourcade et al., 2018; Lozier et al., 2009). This might be especially problematic when using these data to model the response curves of species that live close to the ground, in topographically heterogenous terrain, or under trees and shrubs.

Variation in microclimates results from physical processes such as airflow and incoming solar radiation that interact with topographic factors such as slope, aspect and surface roughness (Geiger, 1950). Additionally, vegetation cover is known to affect local microclimate temperature (De Frenne et al., 2019; Lenoir et al., 2017). Indeed, it is currently well acknowledged that forests harbour distinct microclimatic conditions owing to the structural complexity of the canopy, resulting in shading and evapotranspirative cooling (Geiger, 1950). Forest canopies are characterized by their buffering capacities of extreme temperatures in comparison to weather station data, with cooler sub-canopy maximum temperatures and warmer sub-canopy minimum temperatures (De Frenne et al., 2019). In European forests, this difference can add up to 9°C for mean monthly temperatures (Haesen et al., 2021). There is an urgent need for greater use of fine-scale microclimatic data in ecology as ignoring the mismatch between conventionally-used macroclimatic data and the microclimatic conditions might lead to erroneous predictions, wrong ecological interpretations and, ultimately, questionable conservation decisions (Körner & Hiltbrunner, 2018).

This study aims to evaluate the influence of large-scale, gridded microclimate data on the accuracy of SDMs and associated environmental niches and projected geographic ranges of European plant species constrained to forest habitats. Challenging conventional SDMs, we separately tested the effects of using microclimate instead of macroclimate data, as well as of the spatial resolution of these data. To achieve this, we employed three types of SDMs using (1) a macroclimatic dataset at a spatial resolution of 1 × 1 km²; (2) an aggregated microclimatic dataset that matched the resolution of the macroclimatic dataset but using sub-canopy microclimate temperatures; and (3) a microclimatic dataset with a spatial resolution of 25 × 25 m², matching the species compositional patterns in the forest understory vegetation and using the microclimate temperatures as perceived below the canopy (Figure 1; Haesen et al., 2023).

Forests are recognized for their capacity to moderate temperature, and as such, plant species adapted to forest ecosystems are likely to respond to warmer minimum temperatures and cooler maximum temperatures than those estimated by free-air temperature data collected from weather stations. Therefore, we hypothesized that (1) the actual thermal response curves of forest specialist species are more narrow than the thermal response curve as modelled from gridded macroclimate data. We also expect that (2) ranges projected from macroclimate-based models are overestimated, because the presence of a species at locations with distinct microclimates compared to their surroundings, may be erroneously attributed to the species' ability to survive in the entire area with that macroclimate. Finally, assuming that species are constrained by the maximum temperature at the southern limit of their latitudinal range and by the minimum temperature at their northern limit, we hypothesized that (3) populations of forest specialist species may survive in local microrefugia, which are cooler than the surrounding landscape at the southern latitudinal limit but warmer than the surrounding area at the northern latitudinal limit.

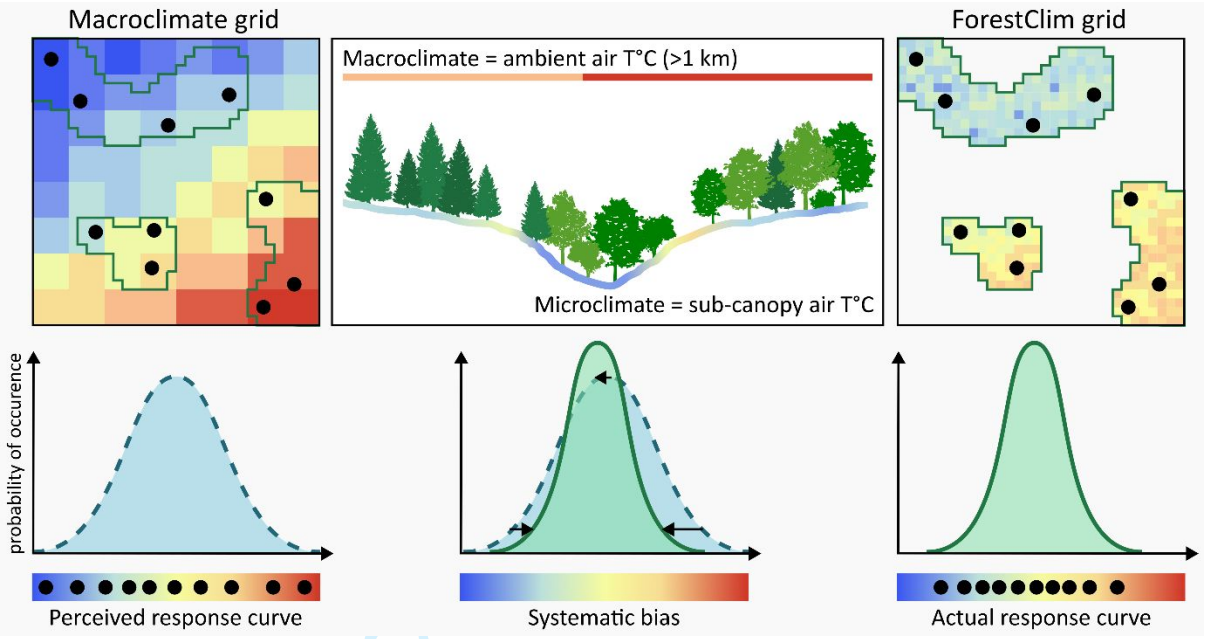

Figure 1: Design of this comparative study, where we compared species distribution models with different set-ups of climatic data. As forests are known to buffer sub-canopy temperatures, forest specialist plant species respond to warmer minimum temperatures and colder maximum temperatures as perceived by the free-air (i.e. macroclimate) temperature data. Therefore, we hypothesize that the actual thermal response curves of forest specialist species, as modelled with the high-resolution ForestClim dataset, would be narrower than the thermal response curve modelled by macroclimate-based SDMs. Note that ForestClim is only available for forest areas, which are delineated by green lines within the simulated grids. Black points indicate species occurrences of a virtual forest plant species (adapted from Lenoir et al., 2017).

METHODS

Study area & species selection

Our study area encompasses all 27 EU countries, plus Albania, Andorra, Bosnia and Herzegovina, Kosovo, Liechtenstein, Montenegro, North Macedonia, Norway, San Marino, Serbia, Switzerland and the United Kingdom. The Canary Islands and Azores, as well as Europe's overseas territories were excluded from the analysis.

Forest specialist species were selected based on the European forest vascular plant species list (Heinken et al., 2022), which is based on vegetation databases, literature and expert knowledge. From this list, we first selected shrub and herb species, which – unlike tree species – usually complete their entire life cycle within the forest understory layer, thus experiencing forest microclimate dynamics (Caron et al., 2021). Subsequently, we selected the species categorized as forest specialists (i.e., categories 1.1 and 1.2) throughout their entire range, meaning that these species occur only in closed-canopy forests, forest edges or forest openings.

Environmental predictors

Three different sets of bioclimatic temperature-related variables (i.e., macroclimatic data at 1 × 1 km², microclimatic data aggregated at the spatial resolution matching the gridded macroclimate data at 1 × 1 km² and microclimatic data at the native spatial resolution of 25 × 25 m²) were used to construct our SDMs, starting from the conventional set of eleven bioclimatic temperature variables. However, we excluded mean temperature of the wettest quarter (BIO8) and mean temperature of the driest quarter (BIO9) as these were recently criticized for their use within species distribution models (Booth, 2022). As the available CHELSA and WorldClim data are not fully covering our study period (2000-2020), we used TerraClimate to construct the 'macroclimatic dataset' at the typical spatial resolution of 1 × 1 km² as used in conventional SDMs. However, TerraClimate bioclimatic variables covering the 2000-2020 period are available at a spatial resolution of 4 × 4 km² and thus were spatially downscaled to a spatial resolution of 1 × 1 km². To do this, we first calculated, for each 1 × 1 km² grid cell, the difference between the bioclimatic variables of TerraClimate (1970-2000 period) and WorldClim (1970-2000 period) and then added these offset values or anomalies to the TerraClimate bioclimatic variables for the 2000-2020 period to obtain a final macroclimate layer of 1 × 1 km² resolution. This method assumes that the offset values from the long-term average period of 1970-2000 are still valid for the period 2000-2020.

The 'microclimatic dataset' consists of the original bioclimatic variables provided within ForestClim, a new high-resolution dataset of forest understory temperature for all European forests

at a spatial resolution of 25 × 25 m² derived from the ForestTemp model (Haesen et al., 2021, 2023). Briefly, ForestTemp was created by combining more than 1,200 time series of *in situ* near-surface forest temperatures from across Europe with topographical, biological and macroclimatic predictors in a machine learning model. The 'aggregated dataset' was generated by averaging the ForestClim bioclimatic variables to a 1 × 1 km² resolution. Note that we did not opt to include a high-resolution macroclimatic dataset (i.e., 25 × 25 m²; topographically downscaled) within this comparative study as this would be representative for topoclimatic conditions, which are proximal as well. However, topoclimate would not capture the influence of the canopy cover on below-canopy temperatures, which would turn it into an intermediate 'mesoclimate' product, adding extra layers of complexity to the comparative analyses. Besides, the benefit of using topoclimate over macroclimate in SDMs is fairly well covered in the scientific literature (Dobrowski, 2011; Man et al., 2022).

Each set of bioclimatic temperature variables was complemented with six bioclimatic precipitation variables. From the conventional set of eight bioclimatic precipitation variables, we omitted precipitation of the warmest quarter (BIO18) and precipitation of the coldest quarter (BIO19) for similar reasons discussed by (Booth, 2022). The six bioclimatic precipitation variables were calculated from TerraClimate precipitation data for the 2000-2020 period and disaggregated to match the spatial resolution of each bioclimatic set. Finally, edaphic variables were added, since soil data often increase model performance (Hageer et al., 2017). Based on their effects on plant demography, we selected four soil variables: bulk density (bdod; cg/cm³), which reflects the soil porosity; soil clay content (clay; g/kg), which reflects the soil texture; pH H_2O (pH; unitless); and cation exchange capacity (cec; $mmol_c$/kg; (Hageer et al., 2017)). The soil raster layers were downloaded from the SoilGrids 2.0 database (Poggio et al., 2021) at a resolution of 250 m for three different depths: 0-5 cm; 5-15 cm; and 15-30 cm. These three layers were averaged into one single layer representing the depth from 0 cm to 30 cm, with the exception of soil pH (i.e., a logarithmic scale), which was aggregated using the median value over the three layers.

To reduce overfitting of SDMs, multicollinearity between the predictors was assessed using a pairwise Spearman correlation test (Figure S1). Highly correlated variables (Spearman correlation coefficients > 0.7) were removed from the analysis in order to reach the most parsimonious model (Dormann et al., 2013). When excluding one of the correlated covariate pair, we preferentially retained variables which are known to be more important for plant species distributions (Macek et al., 2019). The final selection of covariates encompassed two temperature variables (maximum temperature of the warmest month (BIO5) and minimum temperature of the coldest month (BIO6)), two precipitation variables (mean annual precipitation, (BIO12) and precipitation seasonality (BIO15))

and two edaphic variables (cation exchange capacity and soil clay content). All covariate layers were projected in an equal-area projection (epsg:3035; ETRS89/LAEA).

Species occurrence data

Georeferenced occurrence data were downloaded from the Global Biodiversity Information Facility on the 13th of September 2022 (https://doi.org/10.15468/dl.kf533a). To improve data quality for each species, the occurrence data were filtered in the following sequential steps: (1) only records of 'human observations' were selected; (2) records with an unknown coordinate uncertainty or coordinate uncertainty larger than 25 m (i.e., the pixel size) were excluded; (3) records located at country or capital centroids and biodiversity institutions (e.g., botanical gardens) were omitted (Cheng et al., 2021); (4) duplicate records were removed; (5) records outside our study area were deleted; (6) only records observed during our climatic reference period (2000-2020) were selected; (7) records were spatially thinned to one random observation per 25 × 25 m² grid cell; and (8) species with less than 50 cleaned occurrence records were omitted, which has been postulated as a minimum standard to build robust SDMs (van Proosdij et al., 2016).

Filtering of species occurrence data resulted in a final dataset of 140 species, which are further used for the analyses (Table S1). Note that the same occurrence datasets are needed over the different climatic set-ups to have comparable model outputs. Here, we decided to work with occurrence datasets that underwent a cleaning protocol based upon the characteristics of the microclimatic dataset (i.e., maximum coordinate uncertainty of 25 m, and spatial thinning to a 25 × 25 m² grid cell).

Species distribution modelling

We used MaxEnt, a presence-background algorithm that combines species presence-only data with environmental predictors for the current climate to predict the environmental suitability of each study species across our study area (Phillips et al., 2017). We did that for each of the three sets of bioclimatic variables (i.e., the macroclimatic set, the aggregated microclimatic set and the microclimatic set at the native resolution), thus generating three sets of habitat suitability maps for each study species. Background data were generated by sampling an equal amount of background points as occurrence points (i.e., so that species prevalence equals 50%) based on a 2D kernel-density estimate of the occurrence point (Venables & Ripley, 2002), meaning that the spatial density of the background points is proportional to the spatial density of occurrence points for a given species, thereby accounting for spatial bias in the occurrence points (Lake et al., 2020).

Although widely-used in scientific research, MaxEnt could suffer from issues like spatial bias and bad model performance due to overfitting (Radosavljevic & Anderson, 2014). To deal with the

problem of spatial bias, we conducted spatially independent evaluations in ENMeval2.0 (Kass et al., 2021; Muscarella et al., 2014) using block cross-validation and allocating 80% of our occurrence points to this cross-validation procedure (20% is kept for independent evaluation). Furthermore, model performance was improved by tuning the model settings in ENMeval2.0 rather than working with the default settings of MaxEnt. This was implemented by means of a grid search over the possible values of the two hyperparameters: feature classes (Linear, Quadratic, Product) and regularization multipliers (0.5, 1, 2, 3, 4 and 5). Linear, quadratic and product features were selected to allow for linear and quadratic relationships as well as interactions among predictors (Merow et al., 2013). Regularization multipliers, on the other hand, control model complexity and overfitting. The larger these regularization multipliers, the smoother the model predictions. Here, we ensured that feature classes and regularization multipliers were tuned to limit overfitting and increase model performance by using an independent subset of the data (i.e., 20%) not involved in the block cross-validation procedure.

Model performance & sensitivity

In order to customize the settings for the feature classes and the regularization multipliers, a total of 24 different models were run for every single species. The Akaike Information Criterion (AIC) for small sample sizes (20 % of occurrence points) was used to select the best candidate models (Burnham & Anderson, 2004). Next, model performance was assessed using the Continuous Boyce Index (CBI), instead of the commonly-used area under the receiver-operating characteristic curve (AUC). The latter has recently been shown to be biased in presence-only models and should therefore be avoided (Jiménez & Soberón, 2020). The CBI is a threshold-independent metric that represents the relationship between predicted habitat suitability and the distribution of occurrence records (Hirzel et al., 2006). Additionally, we calculated the sensitivity enabling us to quantify how good our model is able at distinguishing true positives from false negatives. Both were calculated based on the independent 20% subset of the data.

Finally, we used Bayesian regression models (BRMs) in order to assess differences in model performance and sensitivity between SDMs constructed using the three different sources of climate data. We opted for BRMs as they are able to account for data dependencies (i.e., values clustered within species), unequal variances among groups and skewed distributions. The final model structures are added in Table S2. Both sensitivity and CBI were modelled with a beta distribution. The CBI metric was rescaled between 0 and 1 before analysis. Bayesian regression models were run using the *brms* package (Bürkner, 2021). All models were first run using standard priors and with 2 chains, 10,000 iterations and a warm-up of 1000 runs. When models did not converge, the flat priors were replaced

by weakly informative priors (Table S2) and the models were run again with 4 chains. The final models converged with $\hat{R}$ values close to 1 (Gelman and Rubin's diagnostic) and all bulk and tail effective sample sizes of the means were greater than 2500. When the highest posterior density intervals (α = 0.05) of the contrasts, calculated using the *emmeans* package (Lenth, 2021), did not overlap with zero, contrasts are considered 'significant'.

Model predictions

Habitat suitability was predicted for each species and for each of the three sets of bioclimatic temperature variables (macroclimatic, aggregated microclimatic and microclimatic) for the 2000-2020 period. Furthermore, we transformed the logistic maps (i.e., probability values for habitat suitability) to binary (presence-absence) maps using the 10% training presence as a threshold, meaning that the suitable area contains 90% of the original occurrence records (Benito et al., 2013).

To compare between model predictions from SDMs constructed with different climate sources and resolutions, we calculated both the potential suitable area and the potential latitudinal range of each species. To make a valid comparison between the three climate types, we disaggregated the binary maps derived from macroclimatic and aggregated data (1 × 1 km²) to the finer resolution (25 × 25 m²), and subsequently masked out all non-forest pixels. First, the potential suitable area (km²), for each modelled species, was calculated as the sum of all forest pixels classified as potentially suitable under the binary maps. Second, the northern and southern latitudinal limit of the predicted distributional ranges were defined as the 95% and 5% quantile in latitudinal position, respectively, of all pixels classified as potentially suitable. Next, we quantified species thermal response curves for mean annual temperature (BIO1), maximum temperature of the warmest month (BIO5) and minimum temperature of the coldest month (BIO6) by extracting the climatic conditions over the entire potentially suitable area. To optimize computation power, we randomly sampled 1,000,000 pixels over the potentially suitable area for microclimate-based maps. For each variable, we derived the cold limit (Q05), the optimum (mode), the warm limit (Q95), and the niche width (Q95 – Q05). Analogous to the model performance calculations, we used BRMs with the same settings to assess differences in model predictions between the SDMs based on the three types of climate data (Table S2). Values of bioclimatic variables were standardized before the analysis to aid model convergence.

Finally, we analyzed whether species are constrained to specific (relative) temperature conditions (i.e., here defined as microrefugia) at their northern and southern latitudinal limits, as this is important for biodiversity conservation. For the northern and southern latitudinal limit, we extracted the 5% most southern and northern occurrence records, respectively. Using paired two-sided t-tests (α = 0.05), we compared the local temperature conditions of these occurrence points to

the mean surrounding microclimatic conditions over a range of circular buffers (i.e., 100 m, 500 m, 1000 m, 2500 m, 5000 m; Figure S2) around each occurrence record. A significant t-test implied a significant difference in local temperatures at the presence locations as compared with the surrounding area, suggesting that occurrences were restricted to microrefugia.

All calculations were performed in R version 4.1.1 (R Core Team, 2021). The Tier-2 Genius cluster from the high-performance computing facilities of Flanders was used to make the predictions. In order to improve reproducibility, we followed the ODMAP (Overview, Data, Model, Assessment and Prediction; Zurell et al., 2020) protocol to report on the SDMs in this study (Table S3).

RESULTS

Model performance & sensitivity

We found significant differences (α = 0.05) in model performance between models constructed with: (i) macroclimatic (mean CBI = 0.09; se = 0.04) and microclimatic (mean CBI = 0.67; se = 0.02) data; (ii) macroclimatic and microclimatic data but aggregated at a spatial resolution matching macroclimate data (mean CBI = 0.28; se = 0.04); and (iii) aggregated microclimatic and microclimatic data at the native resolution (Figure 2a). For 92% of the species, fine-grained microclimate data systematically improved model performance (Figure 2b). Here, 39% of macroclimate-based SDMs are characterized by CBI values smaller than zero, meaning that these models perform worse than random. On the other hand, CBI values are positive for almost all (96%) microclimate-based SDMs. Furthermore, there were no significant differences between any of the groups regarding the sensitivity of the models.

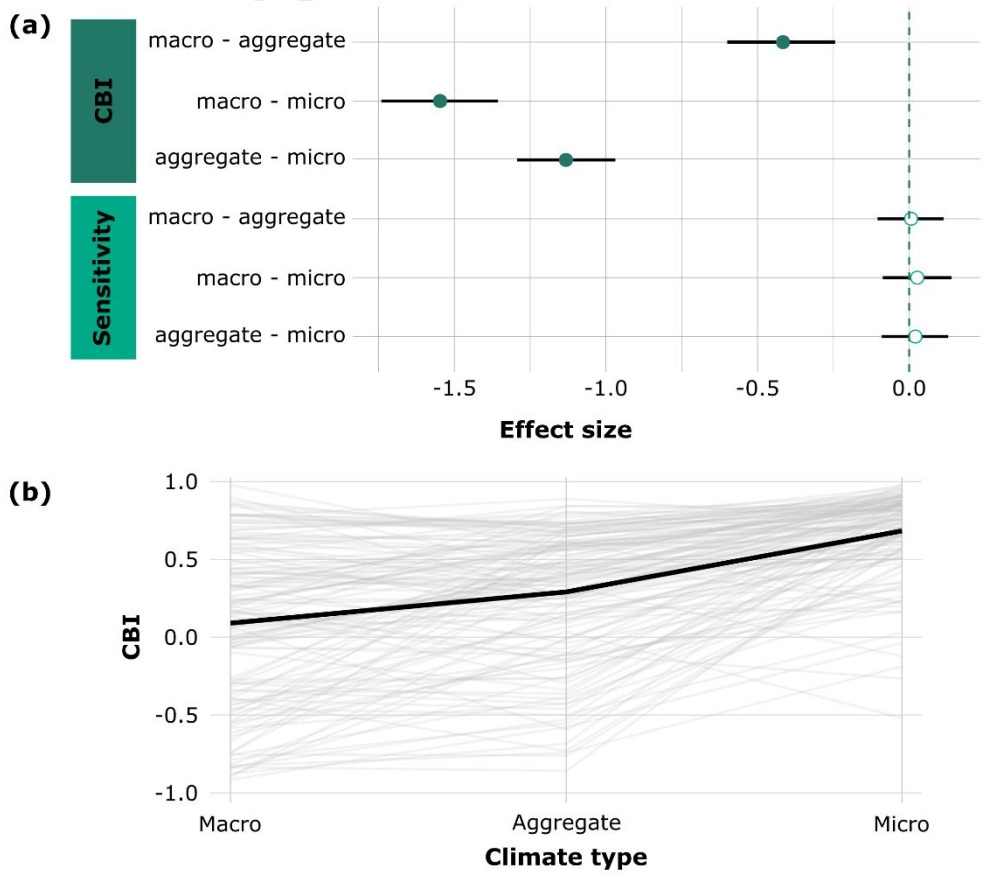

Figure 2: (a) Pairwise comparison of model performance (quantified as the Continuous Boyce Index, CBI) and sensitivity between SDMs built with macroclimatic, aggregated microclimatic and microclimatic data. A positive effect size of the comparison reflects a higher model performance and sensitivity in SDMs built with the first group of climate data compared to the second group of climate data. Negative effect sizes reflect the opposite result. Points and associated black error bars correspond to posterior means and 95% highest posterior density intervals of the differences (of the scaled CBI and sensitivity). Significant differences are indicated by solid dots whereas non-significant differences are indicated by transparent dots; (b) The performance of each SDM per species (grey lines) over the three types of climate data (i.e., macroclimatic data, aggregated microclimatic data and microclimatic data). The thick black line shows the average CBI value over each of the three climate types.

Potential suitable area & latitudinal range

The binary distribution maps showed clear differences in the potential suitable area and the potential latitudinal range covered by each species between models calibrated with macroclimatic data and models calibrated with microclimatic data at the native spatial resolution of 25 × 25 m² (e.g., *Paris quadrifolia*; Figure S3). Bayesian regression models confirm these visual interpretations for all modelled species (Figure 3). Relative to microclimate-based SDMs at the native spatial resolution, both the northern and southern limit of the species' latitudinal ranges are significantly overestimated when using either macroclimate-based SDMs or the aggregated version of microclimate-based SDMs. Consequently, species' potential latitudinal ranges are significantly narrower when using SDMs calibrated with microclimatic data (mean = 2,261 km; se = 42 km) in comparison with SDMs calibrated with aggregated microclimatic data (mean = 2,580 km; se = 43 km) or macroclimatic data (mean = 2,620 km; se = 49 km). Analogous, a species' potential suitable area is significantly smaller when using SDMs calibrated with microclimatic data (mean = 911,845 km²; se = 30,383 km²) in comparison with SDMs calibrated with aggregated microclimatic data (mean = 1,148,763 km²; se = 33,527 km²) or macroclimatic data (mean = 1,268,189 km²; se = 38,274 km²).

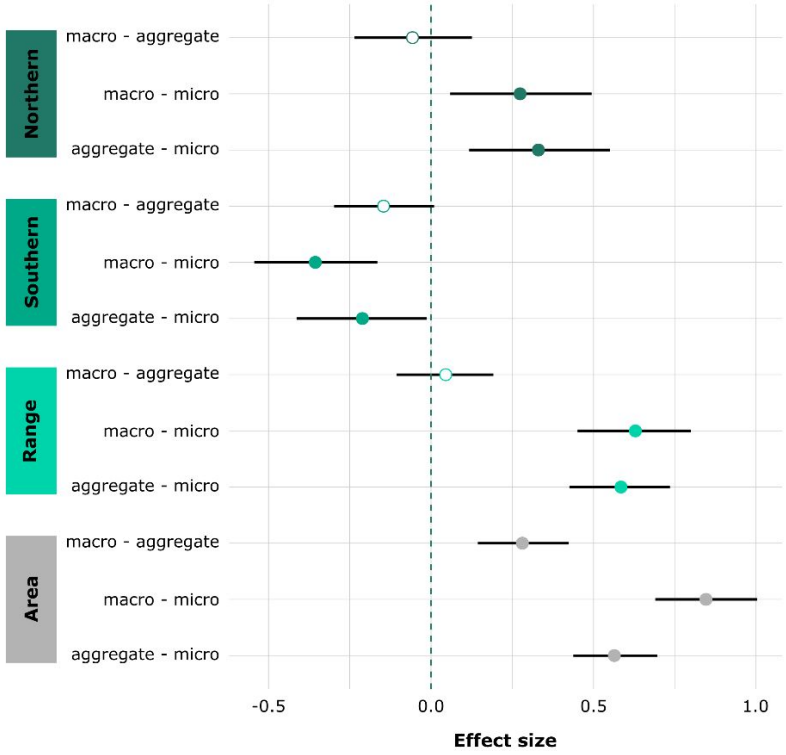

Figure 3: Pairwise comparison of the northern edge, southern edge, latitudinal range and potential suitable area, respectively between SDMs build with macroclimatic, aggregated microclimatic and microclimatic data. A positive effect size of the comparison reflects more northern latitudinal limits (at the northern and/or southern edge), higher latitudinal ranges and more potentially suitable area in SDMs built with the first group of climate data compared to the second group of climate data. Negative effect sizes reflect the opposite result. Points and associated black error bars correspond to posterior means and 95% highest posterior density intervals of the differences (of the standardized variables). Significant differences are indicated by solid dots whereas non-significant differences are indicated by transparent dots.

Species response curves

A first visual assessment of the response curves showed that microclimate-based response curves of minimum temperature of the coldest month, mean annual temperature and maximum temperature of the warmest month have different optima, and narrower niches compared to macroclimate-based response curves (e.g., *Paris quadrifolia*; Figure 4).

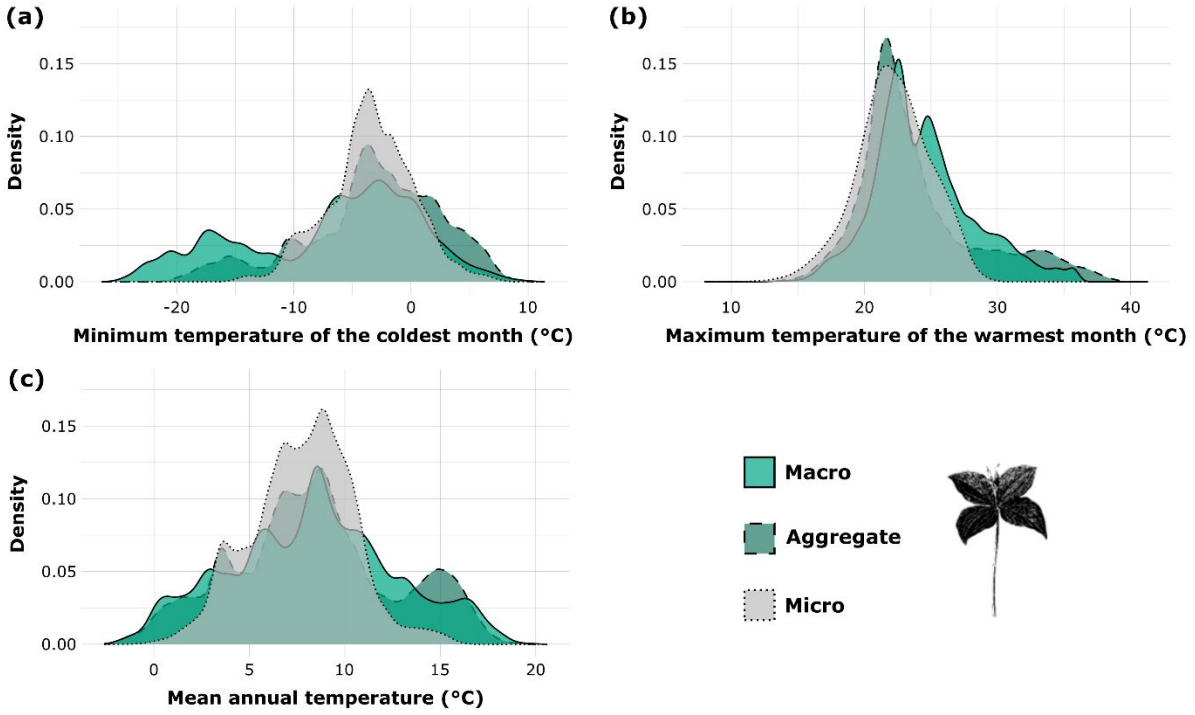

Figure 4: Species response curves for (a) minimum temperature of the coldest month, (b) maximum temperature of the warmest month and (c) mean annual temperature for Paris quadrifolia, illustrating the buffering effect that forest could exert on the thermal niche of species. Here, minimum temperatures are buffered at the cold edge of the response curve, whereas maximum temperatures are buffered at the warm edge of the response curve.

Bayesian regression models showed that, for all modelled species, optima significantly differed between SDMs run with microclimate and macroclimate data for minimum and maximum temperatures, with warmer optima in minimum temperature and cooler optima in maximum temperature for microclimate-based SDMs relative to macroclimate based SDMs (Figure 5). However, for mean temperature there were no significant differences in optima between the different climate types. Furthermore, the niche width was narrower in minimum and mean temperatures for microclimate-based SDMs relative to macroclimate based SDMs. Surprisingly, the niche width was significantly wider in maximum temperatures for microclimate-based SDMs relative to macroclimate based SDMs.

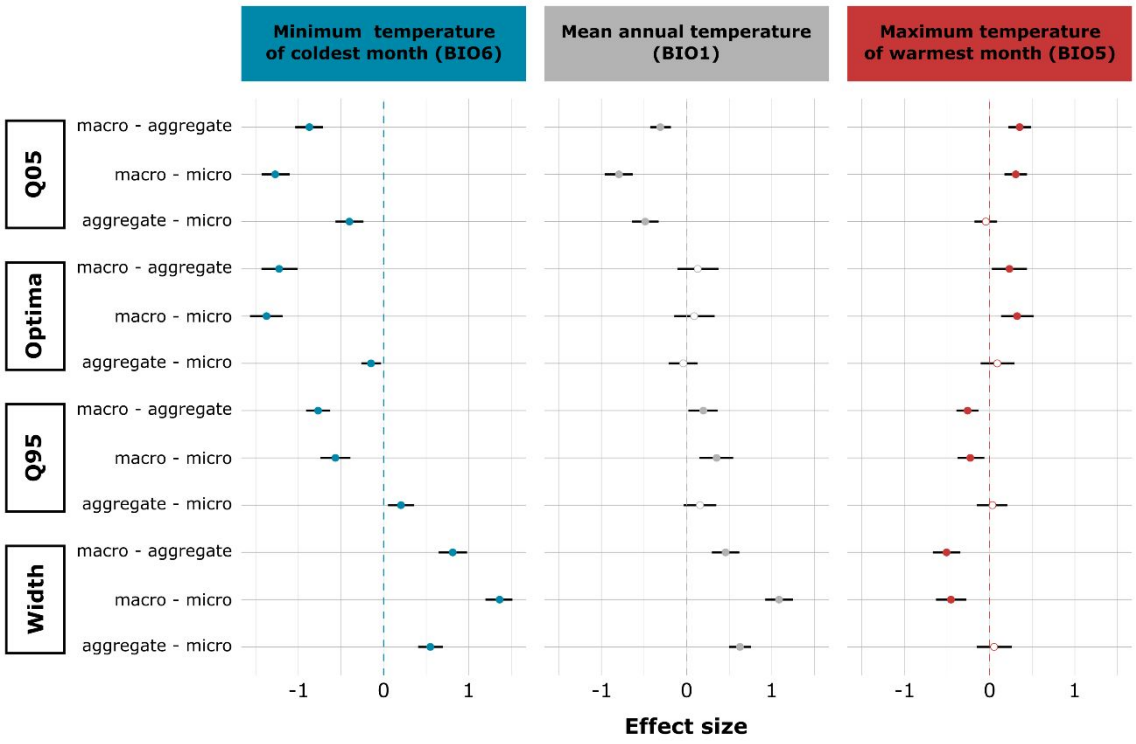

Figure 5: Pairwise comparison of the cold edge (Q05), optimum, warm edge (Q95) and niche width, respectively between SDMs build with macroclimatic, aggregated microclimatic and microclimatic data. Each of the comparisons is made for minimum temperature of the coldest month (BIO6), mean annual temperature (BIO1), and maximum temperature of the warmest month (BIO5), respectively. A positive effect size reflects warmer values for the cold edge, optima and warm edge as well as wider niche widths, respectively, in SDMs built with the first group of climate data compared to the second group of climate data. Negative effect sizes reflect the opposite result. Points and associated black error bars correspond to posterior means and 95% highest posterior density intervals of the differences (of the standardized variables). Significant differences are indicated by solid dots whereas non-significant differences are indicated by transparent dots.

Microrefugia

We found that 66% of all studied species are constrained to local microrefugia at their range limits. More specifically, 41% of the species occur in warm refugia relative to the surrounding landscape, at the northern limit of their latitudinal while 49% of the modelled species occur as remnant populations in cool refugia relative to the surrounding landscape, at the southern limit of their latitudinal range (e.g., *Paris quadrifolia*; Figure 6).

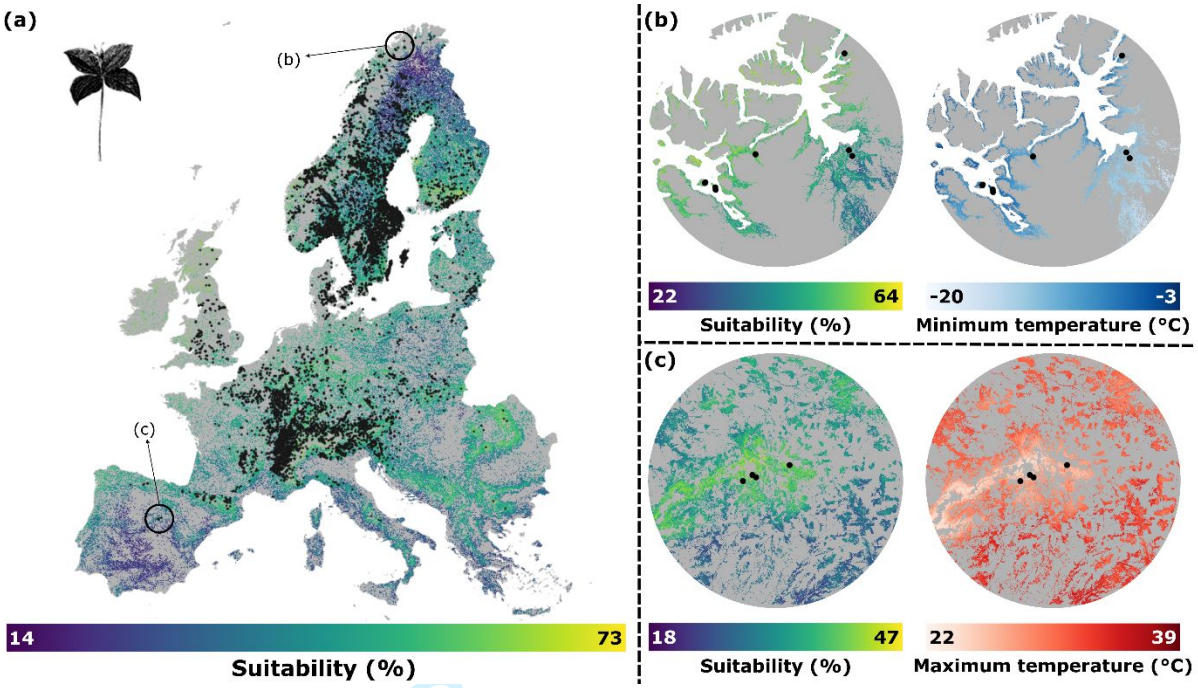

Figure 6: (a) Suitability map for Paris quadrifolia resulting from an SDM built with microclimatic data at 25 × 25 m² resolution. The black dots represent the occurrence points extracted from GBIF and used as an input to the SDMs. We see that the species can occur in (b) warm refugia (i.e., higher minimum temperature values in the coldest month of the year) at its northern latitudinal limit and in (c) cool refugia (i.e., lower maximum temperature values in the warmest month of the year) at its southern latitudinal limit. The grey background shows non-forest areas.

DISCUSSION

Over the last years, microclimate research focused on improving our understanding of the drivers behind the differences between microclimate and macroclimate temperatures (Zellweger et al., 2019) and predicting and mapping microclimate temperatures across space and time (Greiser et al., 2018; Kearney et al., 2020). Although the drivers behind forest microclimates are relatively well understood, testing how microclimate layers perform within ecological applications such as SDMs has been limited, especially so across large (e.g., continental) spatial extents. However, with the recent advent of sub-canopy microclimate layers for European forests at 25 × 25 m² resolution, a new avenue of species distribution modelling can be explored (Haesen et al., 2023). We found substantial differences in the model performance (based on the Continuous Boyce Index), indicating that microclimate-based SDMs significantly outperformed their conventional (i.e., macroclimate) counterparts and that aggregating microclimate data at coarser spatial resolutions leads to significant loss in model performance. Importantly, the use of aggregated microclimate data was still a significant improvement over the use of conventional macroclimate data in SDMs, which is especially interesting when computational capacity is limited. Our results thus agree with previous research reporting an increased performance of microclimate-based SDMs on regional scales (Ashcroft et al., 2008; Slavich et al., 2014; Stark & Fridley, 2022). However, this study additionally shows significant alterations of the species response curves to temperatures fitted with microclimatic data at a finer spatial resolution, matching the scale of the studied organisms (i.e., understory plants) more closely. This particular finding represents a major scientific advance with important implications in terms of SDMs' abilities to capture physiological processes that better reflect individual fitness.

We found significant differences in the shape of the species response curves obtained from the model predictions using different temperature sources. These outcomes underscore the importance of integrating microclimate data into SDMs, as previously proposed by Lembrechts et al. (2019). The recent increased availability of microclimatic data products at fine spatial resolution that cover large spatial extents has enabled us to uncover the true realized thermal niches and reveal the environmental conditions that actually matter for species living close to the ground surface (such as tree seedlings and herbaceous plants growing in the shade of trees). We demonstrate that species response curves derived from conventional macroclimate-based SDMs are much wider than one would expect given the buffering effect of forests (De Frenne et al., 2019; Harwood et al., 2014). Conventional SDMs might thus capture spurious correlations and fail to encompass the genuine factors constraining species distributions. The optima of the species response curves to maximum and minimum temperatures systematically shifted towards colder and warmer conditions, respectively, when using microclimate-based SDMs at fine spatial resolution, suggesting significant improvements

in SDMs' abilities to capture plant individual fitness in the forest understory. The same argument applies to the species' thermal tolerance limits as we found systematic shifts towards warmer conditions for the cold and warm tolerance limits of forest understory plants when using microclimate-based SDMs at fine spatial resolution. The ability of microclimate-informed SDMs to more accurately capture thermal tolerance limits holds important implications for exploring broader macrophysiological thermal response patterns and organismal processes (Lancaster & Humphreys, 2020; Sentinella et al., 2020; Sunday et al., 2012). This capability could further advance the research domain, aiding in the enhanced comprehension of plants' thermal safety margins in the face of climate change, which are intricately tied to their survival, productivity, and reproductive capacities (Lancaster & Humphreys, 2020).

Wider niches estimated by macroclimate-based SDMs also resulted in an overestimation of the predicted range sizes, thereby confirming our second hypothesis. Indeed, the occurrence of a species' individual within a specific macroclimatic pixel does not guarantee that the species will occur in all other macroclimatic pixels with the same temperature because of considerable variations in microclimate heterogeneity. This is especially important at range edges, where species will be found in macroclimate pixels with above-average microclimate heterogeneity. Indeed, the populations of 66% of the studied species at the northern and southern limits of their latitudinal range are confined to warm or cold spots in the landscape, respectively (Figure 6; Figure S2). Microclimate-based SDMs thus allow for better identification of local microrefugia. Current macroclimate-based SDM practices are unable to identify these microrefugia correctly as conventional macroclimate data represent the overarching free-air temperatures rather than the local temperatures as perceived by organisms living inside these microrefugia (Lenoir et al., 2017). Given the importance of microrefugia regarding the accumulation and conservation of biodiversity (Finocchiaro et al., 2023; Nadeau et al., 2022), forest management practices should be optimized to protect local microclimates and increase the capacity of species and communities to resist to climate change (Hylander et al., 2022).

There are various reasons for the increased performance of microclimate-based SDMs, which mainly relate to characteristics of the two primary input sources of each SDM: the occurrence points and predictor variables. First, each occurrence point is subjected to a certain amount of positional error (Wüest et al., 2020). In this study, we exclusively used records with a reported coordinate uncertainty below 25 m. Nevertheless, applying a threshold on the positional error like this may induce a loss of model performance by decreasing the number of occurrence points (Guisan et al., 2007). Thus, it is conventionally recommended to decrease the spatial resolution of the analysis to account for any positional errors in the occurrence points, rather than excluding the less precise records. However, SDMs are sensitive to changes in the spatial resolution (Chauvier et al., 2022; Manzoor et

al., 2018). Decreasing spatial resolution inherently induces a loss of information as the data is smoothed (i.e., aggregated), which comes at the cost of model performance as shown by the CBI values from the models built with aggregated microclimatic data. Therefore, recent research strongly recommends to fit SDMs as close as possible to the spatial grain that matches the biology of the focal species (Gábor et al., 2022), meaning that it is recommended to calibrate SDMs with environmental data consistent with the biological scale of the system or organism under study (Randin et al., 2009). For instance, when modelling sessile species (i.e., species with limited mobility) or organisms in ecosystems with high environmental heterogeneity, higher-resolution predictors are essential to more precisely capture the intricacies of their niches (Norberg et al., 2019). For example, sessile species are more prone to microclimate limitations due to their inability to actively relocate, rendering them highly sensitive to variability in local environmental conditions and more likely to be spatially limited to habitats with a particular microclimate. As a result, we anticipate that the findings of this study may not be readily transferable when studying mobile species (such as birds or mammals) or uniform environments.

Although promising, microclimate-based SDMs inherently face challenges beyond just microclimate considerations. Analogous to other correlative climate-based SDMs, they are likely to fail for many reasons unrelated to the accuracy and resolution of the climate data. For example, SDMs often do not consider demographic processes and biotic interactions that mediate population responses (Sanczuk et al., 2023). However, the SDM toolbox has been extended to accommodate these shortcomings. For instance, range dynamic models explicitly consider demographic processes such as dispersal and population dynamics (Zurell et al., 2016) and joint SDMs infer species interactions from co-occurrence data (Ovaskainen & Abrego, 2020). Genomics-informed SDMs aiming at including adaptability and demographic processes also offer interesting research avenues (Hudson et al., 2021). Additionally, many SDMs do not include the fine-grained spatial heterogeneity of soil conditions that may occur across few meters and which matter for species distributions (Beauregard & de Blois, 2014; Buri et al., 2017; Roe et al., 2022). Disregarding the edaphic dimension in SDMs may lead to overestimating the species' potential distribution as well as underestimating its spatial fragmentation with important implications under anthropogenic climate change (Bertrand et al., 2012).

Gridded microclimatic data at a resolution of 25 × 25 m^2 are currently restricted to European forests, which limits this study to 140 forest specialist plant species that exclusively live in forests throughout their range. Herbaceous plant species living in open habitats, such as grasslands or heathlands, are not included, as gridded microclimate data with the necessary spatial resolution is not currently available for these environments at continental scale. The main reason for this is that

temperature sensors in open ecosystems are highly exposed to direct solar radiation, leading to significant errors in the measurements recorded by the microclimate loggers (Maclean et al., 2021). Consequently, the development of accurate microclimatic grids for these habitats is hindered. Alternatively, mechanistic models that provided fine-grained gridded data products over large spatial extents could also be used, but they are still missing because of computational challenges (Maclean, 2020). Nevertheless, accurate microclimate data over large spatial extents in open systems are urgently needed to assess the transferability of the results from this study to a wider range of species. Finally, while current microclimate products allow improved predictions of current species distributions, microclimatic data predicted under future shared socioeconomic pathways (SSPs) are needed to assess the impact of microclimate change on species ranges or the composition of species communities (Lembrechts, 2023). However, forests are dynamic systems and their structural characteristics that influence the forest microclimate cannot be assumed to remain constant over time, making the development of such products challenging (De Lombaerde et al., 2022; Lenoir et al., 2017). In a warming world, disturbances affecting forest canopies (e.g., drought, pests, storms) will become more frequent and pronounced, drastically affecting the sub-canopy microclimate drastically (Carlson et al., 2021; Kopáček et al., 2020; Thom et al., 2020) . Given that many forest specialist species have slow dispersal rates, often only several meters per year (Hermy et al., 1999; Svenning et al., 2008), accurately evaluating their distribution ranges becomes crucial. It is very unlikely that these species will be able to keep pace with contemporary macroclimate warming, wherein climate zones are shifting several kilometres each year along the latitudinal gradient (Burrows et al., 2011). In this regard, microclimate-based SDMs may allow us to accurately assess the velocity of microclimate warming experienced by organisms in their immediate habitats and identify the locations where species may become impacted due to climate change. While not explored in this study, this approach could potentially reveal that microclimate heterogeneity mitigates the impact of climate change (Maclean & Early, 2023), and therefore presents opportunities and obvious priorities for area-based conservation.

CONCLUSIONS

To summarize, our study highlights the significant benefits of including microclimatic data in species distribution models for forest plant species. By using microclimate-based SDMs, we were able to uncover the hidden niche of forest plants, providing insights into their tolerance limits in response to climate warming. This is in contrast to macroclimatic data, which estimated broader niches and could not identify warm and cold refugia at the range edges of species distributions. Microclimate-based SDMs are therefore essential for biodiversity conservation in the face of climate change, by providing insights to optimize management actions and prioritize conservation efforts, particularly given the growing policy and management focus on conservation of refugia worldwide.

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