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DATA ARTICLE

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ClimPlant: Realized climatic niches of vascular plants in European forest understoreys

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Abstract

Motivation: Detailed knowledge on the climatic tolerances of species is crucial to understand, quantify and predict the impact of climate change on biodiversity and ecosystem functions. However, quantitative data are limited; often, only expert-based qualitative estimates are available. With the ClimPlant database, we capitalize on the link between species distribution ranges and macroclimate to infer the realized climatic niches of 968 European forest plant species.

Main types of variables contained: The ClimPlant database contains information on the distribution of monthly, growing-season and annual mean, minimum and maximum temperature and total precipitation within the distribution range of 968 European forest plants.

Spatial location and grain: Europe in 10 arc-min grid cells; the study area has been cropped rectangularly at 15° W (Atlantic Ocean), 60° E (Ural Mountains), 25° N (Sahara) and 75° N (Arctic Ocean).

Time period and grain: The distribution ranges of forest plant species are based on two renowned distribution atlases. The monthly mean, minimum and maximum temperature and precipitation between 1970 and 2000 were extracted from WorldClim v.2.

Major taxa and level of measurement: Nine hundred and sixty-eight vascular plant species of European forests, with taxonomy following the Euro+Med PlantBase nomenclature .

Software format: Data in 56 CSV files, with 1,000 values for monthly, growing season and annual observations of mean, minimum and maximum temperature and precipitation in the distribution range for every species. One summary CSV file with summary statistics (mean, median, fifth and 95th percentile), for every species, of each climatic variable, together with seven key geographical descriptors: area of the distribution range, latitude and longitude of the centroid, and northern, eastern, western and southern range limits within the study area.

KEYWORDS

climate change, distribution range, European temperate forests, forest plants, realized climatic niche, thermal tolerance

1 | INTRODUCTION

The climate of the Earth is warming rapidly, pushing plant species to shift their distribution ranges (Chen et al., 2011; Lenoir & Svenning, 2015). These distribution shifts are changing the composition of plant communities, with potential impacts on ecosystem functioning and services (Pecl et al., 2017). Determining which organisms are most vulnerable to climate change and understanding the impact of recent climate change on biodiversity and ecosystem functioning are important and timely topics of global ecology and biogeography (Broennimann et al., 2006; Urban, 2015).

Temperate forests persist in one of the most populated parts of the globe and are important for biodiversity conservation (Gilliam, 2016). In temperate forests, *c*. 80% of the plant diversity can be found at the forest floor (Gilliam, 2007). Nevertheless, our knowledge on the climatic tolerances of vascular plant species, even in intensively studied European temperate forests, remains very limited. The ecological indicator values developed by H. Ellenberg for the Central European flora contain a so-called temperature (*T*) value associated with species thermal tolerance (Ellenberg & Leuschner, 2010). This indicator was developed based on a combination of the distribution data range and from local distribution and habitat heat load and is, as such, a hybrid between an ecological site indicator and a biogeographical indicator value (Berg et al., 2017). However, this indicator has important drawbacks: It is a single number per species, with no associated uncertainty and range, which limits its application in statistical models (Bartelheimer & Poschlod, 2016; Diekmann, 2003). The Ellenberg value also corresponds, in part, to floristic zones and is biased by environmental preferences of listed species in Central Europe and their elevational distributions (see Berg et al., 2017). In addition, it is missing for many European species.

The climatic tolerance of a species is best characterized by its fundamental climatic niche, that is, the theoretical climatic niche space where a species can survive and reproduce (Pearman et al., 2008; Soberón & Arroyo-Peña, 2017). However, to determine the fundamental climatic niche emperically in field or laboratory conditions would require detailed ecophysiological measurements, experiments and long-term studies and is impractical for a large number of species and climatic dimensions (Peterson et al., 2011). An alternative way to estimate the climatic tolerance of many species is via their distribution range. Indeed, the suite of environments where a species occurs can be used to infer their realized climatic niche, that is, the climatic niche space that is genuinely occupied by a species (Peterson et al., 2011). The realized climatic niche is usually narrower than the fundamental niche because the distribution range is limited not only by climate, but also by habitat preference, biotic interactions, dispersal limitation or other limiting biotic or abiotic factors (Pellissier et al., 2013; Silvertown, 2004). Although imperfect, realized climatic niches as inferred from species distribution ranges are often the only available estimation of the climatic tolerance of a species and have been used extensively in ecological niche modelling for decades (Peterson et al., 2011). The realized climatic niche concept is best applied at large spatio-temporal scales (Schweiger & Beierkuhnlein, 2016) and when uncertainty in estimated climatic tolerances is considered appropriately (De Frenne et al., 2013; Rodríguez-Sánchez et al., 2012).

Here, we aim to fill a knowledge gap regarding climatic tolerances of European forest plant species and contribute a new dataset to the toolbox of ecologists and biogeographers. We have digitized distribution maps of 968 vascular plant species, covering a large proportion of the vegetation in temperate European forests. By combining the distribution ranges with spatial data on temperature and precipitation, we provide quantitative profiles of the climatic conditions occupied by each species as estimates of their realized climatic niches. We hereby make these data open and available as the ClimPlant database. These data can aid ecologists to evaluate climate change impacts in European forests, to understand better the biotic responses at the species and community levels and to answer important fundamental ecological questions. The dataset has been used previously in several assessments of climate-driven changes in European forest plant communities (De Frenne et al., 2013, 2015; Staude et al., 2020; Zellweger et al., 2020).

2 | MATERIALS AND METHODS

We obtained the distribution maps from two renowned atlases of Hultén and Fries (1986) (584 species) and Meusel et al. (1965, 1978) and Meusel and Jäger (1992) (384 species). The expert maps of the natural distributions in these atlases are based on a synthesis of accumulated regional fieldwork data. We focused on species that occur in forestREplot (www.forestREplot.ugent.be), an extensive database of > 4,000 temperate forest resurvey plots spread across Europe, capturing a large part of the plant diversity of European temperate forests. For studies using the forestREplot database, see Baeten et al. (2014); Bernhardt-Römermann et al. (2015), Staude et al. (2020), Verheyen et al. (2012) and Zellweger et al. (2020). We included herbaceous and woody species of forest understoreys, but excluded bryophytes. In total, we digitized distribution maps of 968 species [following the Euro+Med PlantBase nomenclature (Euro+Med, 2006); Supporting Information Table S1], which represent 93.9% of the estimated vegetation cover in the plots of the database. The ClimPlant database thus holds information for the vast majority of understorey plants in the forestREplot database, which is an extensive sample of temperate European forests.

The scanned maps were georeferenced using Quantum GIS (QGIS Development Team, 2020) with a thin-plate transformation and a nearest-neighbour resampling method (Figure 1a) (De Frenne et al., 2013). The monthly mean, minimum and maximum temperature and precipitation data were based on the mean of the 1970–2000 period and were downloaded from WorldClim v.2 as a raster file with 10 arc-min resolution (Fick & Hijmans, 2017). Forest microclimates vary at extremely small scales across space and time, mostly driven by changes in canopy cover (De Frenne et al., 2019; Maclean, 2020; Zellweger et al., 2019). Hence, Worldclim spatial

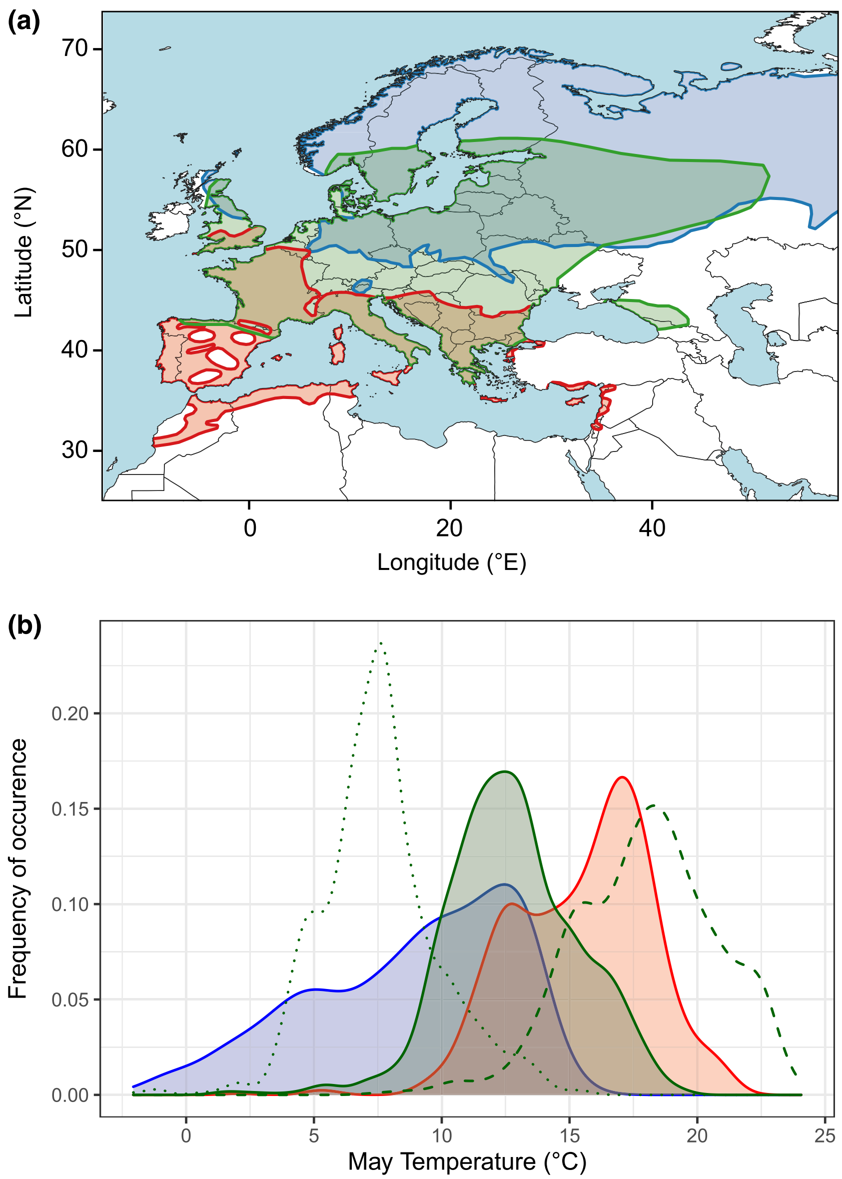

FIGURE 1 (a) Map of the study area, with digitized distribution ranges of three example species: *Trientalis europaea* (blue), *Polygonatum multiflorum* (green) and *Ruscus aculeatus* (red). The map was made with QGIS (QGIS Development Team, 2020). (b) Density plots of the mean 1970–2000 May temperature within the distribution range of the same three species. For *P. multiflorum*, we also plotted the minimum (dotted line) and maximum (dashed line) May temperature within the distribution range.

resolution is still coarse to represent the real climatic conditions experienced by these plants in the field, especially in forests. However, high-resolution European microclimate maps are not yet available. Moreover, using smaller grid cells for the climatic data is not useful, because the resolution of the scanned distribution maps itself is also a limiting spatial factor.

To estimate the realized climatic niche of each species, we set the study area extent to all land between 15° W (Atlantic Ocean) and 60° E (Ural Mountains) and between 25° N (Sahara) and 75° N (Arctic Ocean), comprising a total of 22,650 grid cells of 20 km × 20 km. We selected four climatic variables (mean, maximum and minimum temperature and precipitation) for 14 different time periods (for every month, for the whole year and for the growing season defined as April–September) to obtain 56 combinations. For each species, we sampled 1,000 grid cells randomly, with replacement, within the species distribution range for every climatic variable and time period (Figure 1b). For 66 species (6.82% of the total species pool), the distribution range was < 1,000 grid squares. To generate consistent data series for all species (1,000 values), we used random sampling with replacement instead of a random sample or all grid squares, thus obtaining 56 data files with 1,000 observations for each of the 968 species. From these, we also extracted a summary file with key statistics (mean, median, fifth and 95th percentiles) of growing-season and yearly climatic values for every species, complemented by seven geographical parameters: Area of the distribution range, latitude and longitude of the centroid, and northern, eastern, western and southern range limits within the study area. All analyses were performed in R v.3.6.3 (R Core Team, 2020).

3 | RESULTS

The data contained in the ClimPlant database allow ecologists and biogeographers easily to obtain detailed quantitative estimates of the realized climatic niche of 968 European temperate forest species. The database covers a wide phylogenetic range (98 families represented; 20 families with ≥ 15 species; Supporting Information Table S2). Importantly, ClimPlant provides the full distribution of climatic values for each species, hence enabling researchers to consider intraspecific variation and propagate uncertainty in the realized climatic niches (Rodríguez-Sánchez et al., 2012). Key summary statistics, such as mean annual temperature, annual precipitation and centroids of the distribution range within the study area, are also readily available for every species (Figure 2).

Of the 968 species contained in the ClimPlant database, fewer than half (46%) had Ellenberg *T*-values available; therefore, ClimPlant provides much-needed information on climatic tolerances for 523 new species. For the 445 species having Ellenberg *T*-values (Ellenberg & Leuschner, 2010), we found a clear relationship between these and the mean annual temperature within the distribution range, albeit with a large variation ($p < .01$, $R^2 = .22$; Supporting Information Figure S1). As mentioned earlier, the Ellenberg *T*-values lack the intraspecific variation and uncertainty estimates available in ClimPlant.

4 | DISCUSSION

The ClimPlant database fills an essential knowledge gap in the study of climate change impacts in temperate European forests. The database provides climatic niche estimates for nearly 1,000 plant species representing a large part of the temperate European forest flora. The realized climatic niche data from ClimPlant are correlated with existing categorical indicator values, such as the Ellenberg *T*-values, but are objective, transparent and data driven (BOX 1). They allow the incorporation of uncertainty in the climatic responses of species, increasing the robustness and opening up new possibilities for quantitative data analyses.

The realized climatic niches were inferred from atlas distribution maps with a limited spatial resolution. Hence, those distribution ranges reflect the extent of occurrence rather than the area of occupancy, which includes only areas where the species genuinely appears (Gaston & Fuller, 2009; Sheth et al., 2020). The distributions also include smaller unsuitable habitats, such as urban

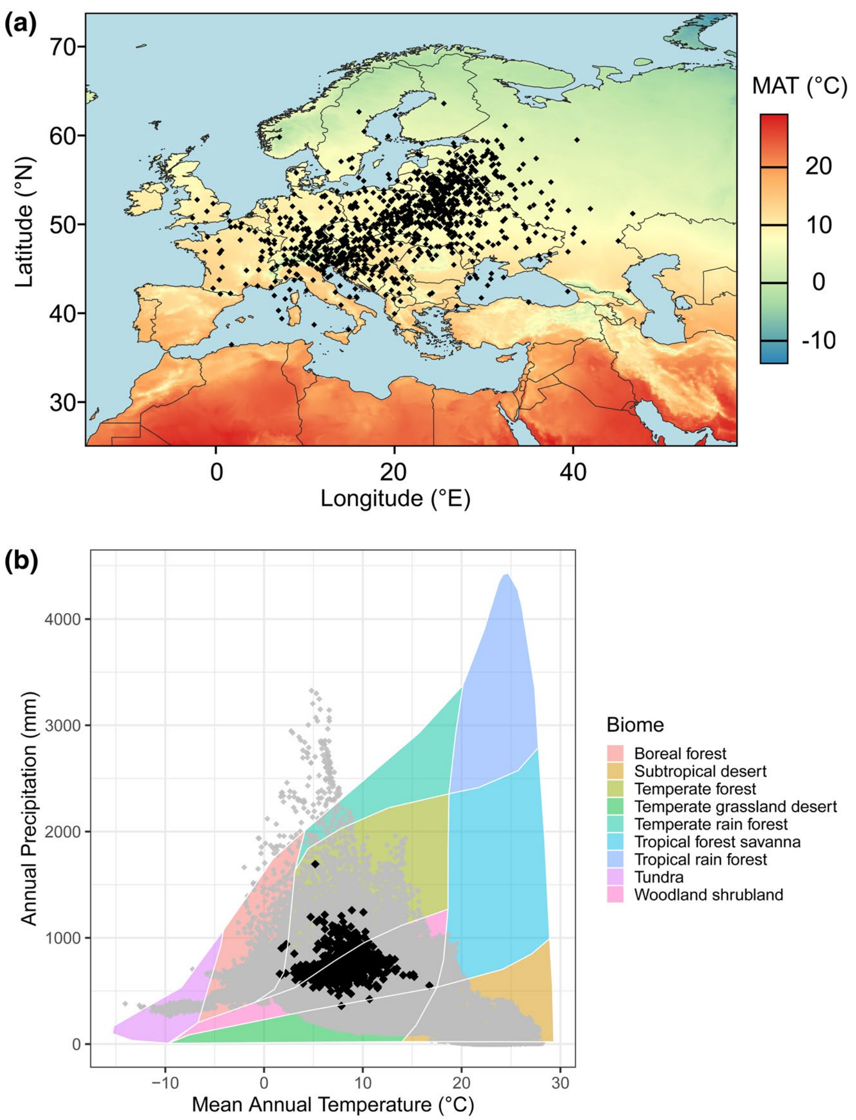

FIGURE 2 (a) Centroids of the distribution range within the study area of the 968 temperate forest species contained in the ClimPlant database, with the 1970–2000 mean annual temperature (MAT; in degrees Celsius) as background raster. The map was made with QGIS (QGIS Development Team, 2020). (b) The 1970–2000 mean annual temperature (in degrees Celsius) and annual precipitation (in millimetres) of every grid cell in the study area (grey) and the mean annual temperature (in degrees Celsius) and mean annual precipitation (in millimetres) across the distribution range of the 968 temperate forest species (black), plotted on Whittaker's biomes (Ricklefs, 2008; as obtained from Kunstler, 2014).

> **BOX 1** Strengths and limitations of the ClimPlant database
>
> **Major strengths**
>
> - Realized climatic niches are derived from expert-based, natural distribution ranges where plants have persisted within the studied time frame.
> - Estimated climatic niches are calculated through objective, transparent protocols and incorporate the full distribution of climatic profiles, thus increasing the robustness and opening new possibilities for quantitative data analyses.
> - Data are already available for 968 vascular plant species, capturing a large part of the diversity in European forests; they are perfectly suited to determine floristic temperatures of plant communities.
>
> **Major limitations**
>
> - ClimPlant provides estimates of species' climatic tolerances based on realized niches, which might differ from physiological tolerances, owing to factors such as dispersal limitation, competition, herbivory and disease.
> - Estimated niches are based on distribution and climate data with coarse spatial resolution, not reflecting microclimatic conditions.
> - Climatic niche estimates are uncertain and should be used with caution.

areas. Nonetheless, larger discontinuities in the distribution range, such as absence in mountain regions, are often mapped correctly (e.g., absence of *Ruscus aculeatus* in the Pyrenees; Figure 1a). If suitable data on the area of occupancy of plant species were available at the continental scale, this would be a great improvement for species distribution modelling, because it would be possible to link the presence of a species to local attributes, such as microclimate and co-occurrence with other species. However, we still lack such data for most European plants. The ongoing Atlas Florae Europaea covers *c*. 25% of the European flora from a few families so far, at a resolution of *c*. 50 km × 50 km (Lahti & Lampinen, 1999). Point-based observations (such as those provided by GBIF; GBIF.org, 2020) are another common source of distribution data. Nevertheless, these databases are still incomplete for many species, have issues with misidentifications and are often geographically biased (e.g., data-deficient regions, such as eastern Europe and northern Africa) (Boakes et al., 2010; Lozier et al., 2009; Meyer et al., 2016), which can lead to important biases in the inferred climatic tolerances. Moreover, point-based observational data also often include records in areas outside the natural distribution range; for instance, owing to anthropogenic introductions in artificial conditions where the species will not manage to persist without human assistance. Hence, in order to infer plant climatic niches at a continental scale at present, it seems more sensible to rely on robust atlas distribution maps, as was done to develop the ClimPlant database (De Frenne et al., 2014; Fourcade, 2016).

The ClimPlant database builds on the relationship between climatic tolerance and the current species distribution. Climate is an important driver of species distributions (Gaston, 2003; Woodward, 1987), particularly at large spatio-temporal scales (Pearson & Dawson, 2003; Peterson et al., 2011; Schweiger & Beierkuhnlein, 2016), but it is not the only one. Other non-climatic factors, such as land use (history), dispersal limitation or biotic interactions, can condition the assumed equilibrium of species distribution with climate (Silvertown, 2004; Peterson et al., 2011), potentially resulting in a difference between the realized climatic niche and the fundamental climatic niche. The ClimPlant database should, therefore, be used with care, acknowledging the uncertainties inherent to such distribution-based climatic tolerance estimates (Araújo & Peterson, 2012; Bahn & McGill, 2007; Fourcade et al., 2018; Journé et al., 2020). The uncertainty and risk of bias might be inversely related to range size (Bocsi et al., 2016); therefore, increased caution should be exercised regarding species with small distribution ranges (range size is included as a variable in ClimPlant and could be used to filter out species with small ranges). Attempts to extrapolate these climatic tolerances into new areas or time frames (e.g., with correlative species distribution models; Journé et al., 2020) are particularly risky and are likely to require more sophisticated approaches involving multivariable models (Briscoe et al., 2019). Nonetheless, there are many legitimate research questions for which we are lacking basic information on species tolerances or, simply put, the types of climate that species inhabit. By providing a statistical distribution of climatic values across species ranges, the ClimPlant database represents a step forwards in that regard, particularly in comparison to the use of simple indicator values with no associated uncertainty (Rodríguez-Sánchez et al., 2012).

ClimPlant can be instrumental in assessments of climate change impact and to advance our understanding of species ranges and community dynamics. These data can, for instance, be used to quantify species reshuffling, to assess the degree of "thermophilization" of plant communities driven by climate warming (De Frenne et al., 2013; Zellweger et al., 2020), or to investigate the relationship between distribution range and vulnerability to global change (Staude et al., 2020). The ClimPlant database is conceived as a dynamic database, because we plan to extend it with additional species and update it when more or better maps become available, including forest microclimate maps when available at the European scale (e.g., Lembrechts et al., 2020). As such, the ClimPlant database will be a significant step forwards for the modelling of vegetation in the face of global climate change.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

P.V. and P.D.F conceived and designed the study; all authors digitized distribution maps; P.V. performed the data analyses and wrote the manuscript with contributions from all authors.

DATA AVAILABILITY STATEMENT

The full dataset is accessible at: https://doi.org/10.6084/m9.figshare.12199628

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BIOSKETCH

We are a group of researchers focusing on the impact of global change on plant communities and ecosystem functioning in the understorey of temperate European forests at different spatio-temporal scales.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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