

RESEARCH ARTICLE

Using warming tolerances to predict understory plant responses to climate change

Liping Wei^{1,2}  | Pieter Sanczuk²  | Karen De Pauw²  | Maria Mercedes Caron^{3,4}  |
 Federico Selvi⁵  | Per-Ola Hedwall⁶  | Jörg Brunet⁶  | Sara A. O. Cousins⁷  |
 Jan Plue⁸  | Fabien Spicher⁹  | Cristina Gasperini⁵  | Giovanni Iacopetti⁵  |
 Anna Orczewska¹⁰  | Jaime Uria-Diez¹¹  | Jonathan Lenoir⁹  |
 Pieter Vangansbeke^{2,12}  | Pieter De Frenne² 

¹CAS Engineering Laboratory for Vegetation Ecosystem Restoration on Islands and Coastal Zones, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou, China

²Forest & Nature Lab, Department of Environment, Faculty of Bioscience Engineering, Ghent University, Melle-Gontrode, Belgium

³Consejo Nacional de Investigaciones Científicas y Técnicas, Instituto Multidisciplinario de Biología Vegetal (IMBIV), CONICET, Córdoba, Argentina

⁴European Forest Institute-Mediterranean Facility, Barcelona, Spain

⁵Department of Agriculture, Food, Environment and Forestry, University of Florence, Florence, Italy

⁶Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, Lomma, Sweden

⁷Landscapes, Environment and Geomatics, Department of Physical Geography, Stockholm University, Stockholm, Sweden

⁸Department of Urban and Rural Development, SLU Swedish Biodiversity Centre (CBM), Institutionen för stad och land, Uppsala, Sweden

⁹UMR CNRS 7058 Ecologie et Dynamique des Systèmes Anthropisés (EDYSAN), Université de Picardie Jules Verne, Amiens, France

¹⁰Institute of Biology, Biotechnology and Environmental Protection, Faculty of Natural Sciences, University of Silesia, Katowice, Poland

¹¹Department of Forest Sciences, NEIKER-Basque Institute for Agricultural Research and Development, Basque Research and Technology Alliance (BRTA), Derio, Spain

¹²Earth and Life Institute, Université Catholique de Louvain, Louvain-la-Neuve, Belgium

Correspondence

Liping Wei, Forest & Nature Lab,
 Department of Environment, Faculty of
 Bioscience Engineering, Ghent University,
 Geraardsbergsesteenweg 267, 9090
 Melle-Gontrode, Belgium.
 Email: liping.wei@ugent.be; liping.wei228@hotmail.com

Funding information

European Research Council, Grant/
 Award Number: FORMICA 757833;
 Fonds Wetenschappelijk Onderzoek,
 Grant/Award Number: ASP035-19;
 National Natural Science Foundation of
 China—Research Foundation Flanders,
 Grant/Award Number: NSFC-FWO,
 32211530482

Abstract

Climate change is pushing species towards and potentially beyond their critical thermal limits. The extent to which species can cope with temperatures exceeding their critical thermal limits is still uncertain. To better assess species' responses to warming, we compute the warming tolerance (ΔT_{niche}) as a thermal vulnerability index, using species' upper thermal limits (the temperature at the warm limit of their distribution range) minus the local habitat temperature actually experienced at a given location. This metric is useful to predict how much more warming species can tolerate before negative impacts are expected to occur. Here we set up a cross-continental transplant experiment involving five regions distributed along a latitudinal gradient across Europe (43°N–61°N). Transplant sites were located in dense and open forests stands, and at forest edges and in interiors. We estimated the warming tolerance for 12 understory plant species common in European temperate forests. During 3 years, we examined the effects of the warming tolerance of each species across all transplanted locations on local plant performance, in terms of survival, height, ground cover, flowering probabilities and flower number. We found that the warming tolerance (ΔT_{niche})

of the 12 studied understory species was significantly different across Europe and varied by up to 8°C. In general, ΔT_{niche} were smaller (less positive) towards the forest edge and in open stands. Plant performance (growth and reproduction) increased with increasing ΔT_{niche} across all 12 species. Our study demonstrated that ΔT_{niche} of understory plant species varied with macroclimatic differences among regions across Europe, as well as in response to forest microclimates, albeit to a lesser extent. Our findings support the hypothesis that plant performance across species decreases in terms of growth and reproduction as local temperature conditions reach or exceed the warm limit of the focal species.

KEYWORDS

climate change, cross-continental transplant experiment, forest ecosystems, microclimate, species traits, thermal niche, understory species, warming tolerance

1 | INTRODUCTION

Anthropogenic climate change increases the risks that temperatures go beyond the thermal limits of species (Feeley et al., 2020; Parmesan & Hanley, 2015). Yet, our scientific knowledge on whether or not and to what extent species can cope with temperatures that exceed the limits of their thermal niches is still scarce. Most current studies test the “abundance-centre hypothesis” based on the idea that the geographic distance to a species' range centroid determines species performance, albeit the results of these studies are often mixed (e.g., Chevalier et al., 2021; Dallas et al., 2017; Martínez-Meyer et al., 2013; Osorio-Olvera et al., 2020; Santini et al., 2019). Recent studies suggest that species performance should be evaluated within the niche space, rather than the geographical space (Martínez-Gutiérrez et al., 2018; Martínez-Meyer et al., 2013). Comprehending species' thermal niche characteristics by focusing on the warm limit and species' response to rising temperatures can provide a more direct insight into species performance under climate change.

The thermal niche of a plant species refers to the range of temperature conditions that a species can tolerate and thrive in. It is characterized by the species' thermal optimum, which is the temperature allowing maximal plant performance, as well as the thermal tolerance and its limits, which are the upper and lower critical temperature limit beyond which the species cannot survive or reproduce in the wild (Cuesta et al., 2019; Inouye, 2008). The upper critical temperature limit—or the warm limit—of a species, in particular, can reflect the vulnerability of a plant species to climate warming and extreme heat (Mellert et al., 2016; Stahl et al., 2014). As temperatures approach to or exceed the warm limit of a plant species' thermal niche, its ability to tolerate and thrive in its environment decreases, making it more vulnerable to negative impacts of climate change (Angert et al., 2011; Inouye, 2008; Morin & Chuine, 2006). For instance, during prolonged hot days or heatwaves, plants close their stomata to avoid lethal damages due to cavitation (McDowell & Allen, 2015). However, when temperatures

surpass a plant species' warm limit, the protective capacity of its stomatal closure may become inadequate (Marchin et al., 2022). Therefore, the “warming tolerance” of a given species (hereafter abbreviated as ΔT_{niche}), is here defined as the difference between the temperature limits that a species can tolerate according to its thermal niche and the actual temperature conditions that a plant individual experiences at a given location (Clusella-Trullas et al., 2021; Deutsch et al., 2008). This proxy may serve as a valuable predictor of the change in species performance or fitness in response to changing climate. The warming tolerance is usually computed relative to the upper limit of the thermal niche of the focal species, such that ΔT_{niche} is positive when the local temperature conditions remain cooler than the upper thermal limit of the focal species and negative otherwise (see Figure 1). If a given species at a given location has a low warming tolerance (i.e., less positive and close to zero) and experiences a warming exposure greater than the local warming tolerance, then this species is at risk and will likely exhibit a significant and rapid change in performance or fitness as the climate continues to warm in that location. Hence, the ΔT_{niche} as defined by Deutsch et al. (2008) and used here provides information on how close a species is to the warm limit of its thermal niche and how much additional warming it can tolerate before experiencing negative impacts (i.e., $\Delta T_{\text{niche}} \leq 0$) on its performance or fitness. For example, if a plant species is already close to its warm limit ($\Delta T_{\text{niche}} \sim 0$), even a small increase in temperature due to climate change could have significant negative impacts on its survival and growth. On the other hand, if a species has more space to tolerate warming, i.e., is farther away from its warming tolerance ($\Delta T_{\text{niche}} > > 0$), it may be able to adapt to changing conditions more easily. By using ΔT_{niche} to assess a species' vulnerability to climate change, researchers and conservationists can prioritize conservation efforts and develop management strategies for determining conservation priority of species and habitats, as well as for managing ecosystems in a changing climate. Yet, previous studies on ΔT_{niche} were chiefly focusing on ectotherms and insects (e.g., Deutsch et al., 2008; Diamond et al., 2012; Frazier et al., 2006; Kingsolver et al., 2013; Sunday et al., 2014), while few

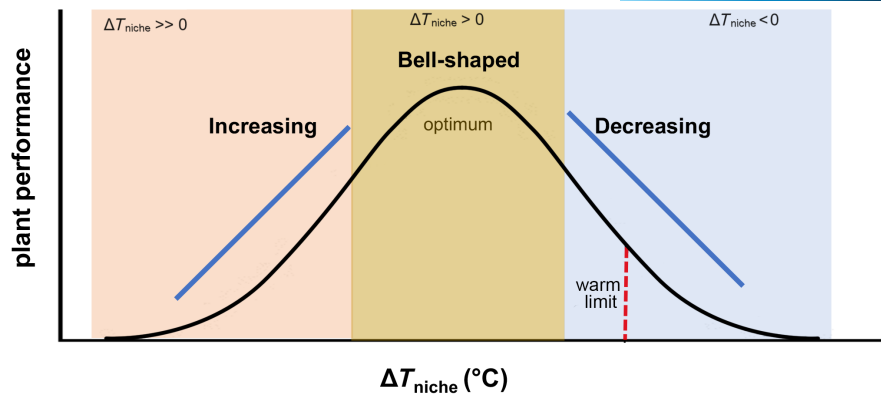


FIGURE 1 Conceptual diagram of our hypothesis on species' performance responses to ΔT_{niche} (thermal niche at 0.95 percentile – microclimate site temperature). The red dashed line represents the warm limit of a species thermal niche ($\Delta T_{\text{niche}} = 0$). In a warmer region or site, relatively to the thermal niche of the focal species, even a moderate change in temperatures over time is expected to rapidly exceed the warm limit of the focal species (i.e., $\Delta T_{\text{niche}} < 0$). In such situations (i.e., $\Delta T_{\text{niche}} < 0$), the more the temperatures exceed the warm limit of the species' thermal niche, the more negative the impact on the species' performance or fitness will be. Hence we expect a negative response in species performance to negative values of ΔT_{niche} (blue area on the right). In a colder region or site, relatively to the thermal niche of the focal species, when temperatures are well below the warm limit and even below the thermal niche optimum of the focal species (i.e., $\Delta T_{\text{niche}} >> 0$), we expect a positive response in species performance or fitness to increasing ΔT_{niche} (light brown on the left). At locations where temperatures are close to the thermal niche optimum of the focal species, we expect a Gaussian response curve in species performance to changes in ΔT_{niche} ($\Delta T_{\text{niche}} > 0$) (brown area in the centre of the graph). We therefore expect that species' responses to climate warming will depend on the relationship between the experienced temperature at a given site and the warm limit of each species' thermal niche.

studies to date have quantified the relationship between the ΔT_{niche} and plant species' survival, growth or reproduction (e.g., Marchin et al., 2022).

When considering the responses of plant species to ΔT_{niche} , the typical “bell-shaped” Gaussian response curves can be expected if local adaptation is not taken into account (Sexton et al., 2009) (Figure 1). That is, a plant species should perform best in habitats where the temperature is closer to its thermal niche optimum, with a decreasing performance when the temperature is increasing beyond its warm limit (that is, $\Delta T_{\text{niche}} \leq 0$) (Brown, 1984; Hengeveld, 1992; Mantley et al., 2015). Furthermore, this dependence of species performance to ΔT_{niche} also indicates that the magnitude and direction of plant species' responses to climate change not only depends on the exposure to climate change at a given location but it also depends on the baseline climatic conditions within the focal location (Pearman et al., 2008; Soberón & Arroyo-Peña, 2017) (Figure 1). Because the temperature experienced by a species is a crucial element of the ΔT_{niche} based approach, the necessity to work with local microclimate temperature instead of macroclimate temperature is evident.

Climate change projections are largely based on macroclimate temperature data as measured in open fields (Moritz & Agudo, 2013). However, most organisms experience temperature conditions that differ from the macroclimate (De Frenne et al., 2021; Potter et al., 2013). Forest canopies shelter the majority of forest plant species from external influences, by modifying the thermal conditions and buffering macroclimatic temperature extremes (De Frenne et al., 2019). Plant species that grow under dense tree canopies are subjected to reduced incoming solar radiation, lower

daytime temperatures and thus cooler daytime and more stable microclimatic conditions compared to open forests or forest edges (Meeussen et al., 2021; Zellweger et al., 2020). The magnitude of differences in temperature at small spatial scales (often <100 m) can be as high as that of broad latitudinal gradients, or as the projected thermal increase by the end of the century (De Frenne et al., 2019). Accordingly, when estimating ΔT_{niche} of a species, not macroclimatic temperatures, but microclimatic temperatures should be considered to accurately predict the species response to warming. This has also been increasingly emphasized and applied in studies regarding warming tolerance for ectotherms and insects (Clusella-Trullas et al., 2021; Kearney et al., 2021; Pincebourde & Casas, 2019; Sunday et al., 2014).

Here we first quantified ΔT_{niche} for 12 common understory plant species across large macroclimatic and microclimatic gradients in European temperate forests through a cross-continental transplant experiment (macroclimate differences), and with transplant locations in dense and open forest stands, and at forest edges and in interiors (microclimatic differences). Indeed, to take both macroclimate and microclimate into account, the experiment involved two climatic gradients operating at different spatial extents and resolutions: a macroclimate gradient from northern to southern Europe (region effect) and local microclimate gradients driven by forest structure (warmer open vs. cooler dense forests) and the distance to the forest edge (cool forest interior to warmer edge). Then, we investigated the effect of local species-by-site-specific values of ΔT_{niche} on the local plant performance in terms of survival, height, cover, flowering probability and flower number. In total, the experiment consisted of 2880 plant individuals, individually monitored

for three consecutive years, covering 12 species across five regions in Europe. Our research questions were: (1) Is ΔT_{niche} mainly driven by microclimate (distance to forest edge and forest structure) or by macroclimate (region)? (2) What are the effects of ΔT_{niche} on species performance (survival, growth and reproduction) for understory plants? (3) How is the performance of understory plants impacted by distance to forest edge, forest structure and their interaction with macroclimate?

2 | MATERIALS AND METHODS

2.1 | Study area

This study was carried out in five regions along a latitudinal gradient of Europe, from central Sweden to Italy (between 10°W–20°E and 43°N–61°N, Figure 2). The latitudinal gradient spans most of the temperate forest biome and represents a significant gradient in macroclimate. We focused on deciduous forests dominated by oaks (*Quercus* sp.) and beech (*Fagus sylvatica*), as they cover a large part of temperate forests in Europe (Barbati et al., 2014) and support a high number of associated species and rich woodland diversity (Eaton et al., 2016; Mölder et al., 2019).

2.2 | Study species

Twelve common understory plant species of temperate European forests were studied: *Alliaria petiolata*; *Allium ursinum*; *Anemone nemorosa*; *Carex sylvatica*; *Deschampsia cespitosa*; *Geranium robertianum*; *Geranium sylvaticum*; *Geum urbanum*; *Oxalis acetosella*; *Poa nemoralis*; *Urtica dioica*; and *Vinca minor*. These species were carefully selected based on their realized thermal niche and colonization capacity. To determine the realized thermal niche of the species, species' thermal niche optima were calculated as the mean annual temperature across species' distribution range (De Pauw et al., 2022). These values were obtained from the ClimPlant database (Vangansbeke et al., 2021). The selected species represent a gradient of temperature preference, ranging from cold-adapted to warm-adapted species. The Colonization Capacity Index (CCI) (De Frenne, Baeten, et al., 2011; Verheyen et al., 2003) was used to ensure that variation in life-history syndromes and the degree of forest specialization were crossed with the variation in temperature preference. The CCI is an index that quantifies species' preferential occurrence in ancient versus recent forests and is linked to species' specialization for forest habitat and life-history syndrome. It offers a continuous gradient ranging from -100 (strong association with recent forest) to +100 (strong association with ancient forest) (De

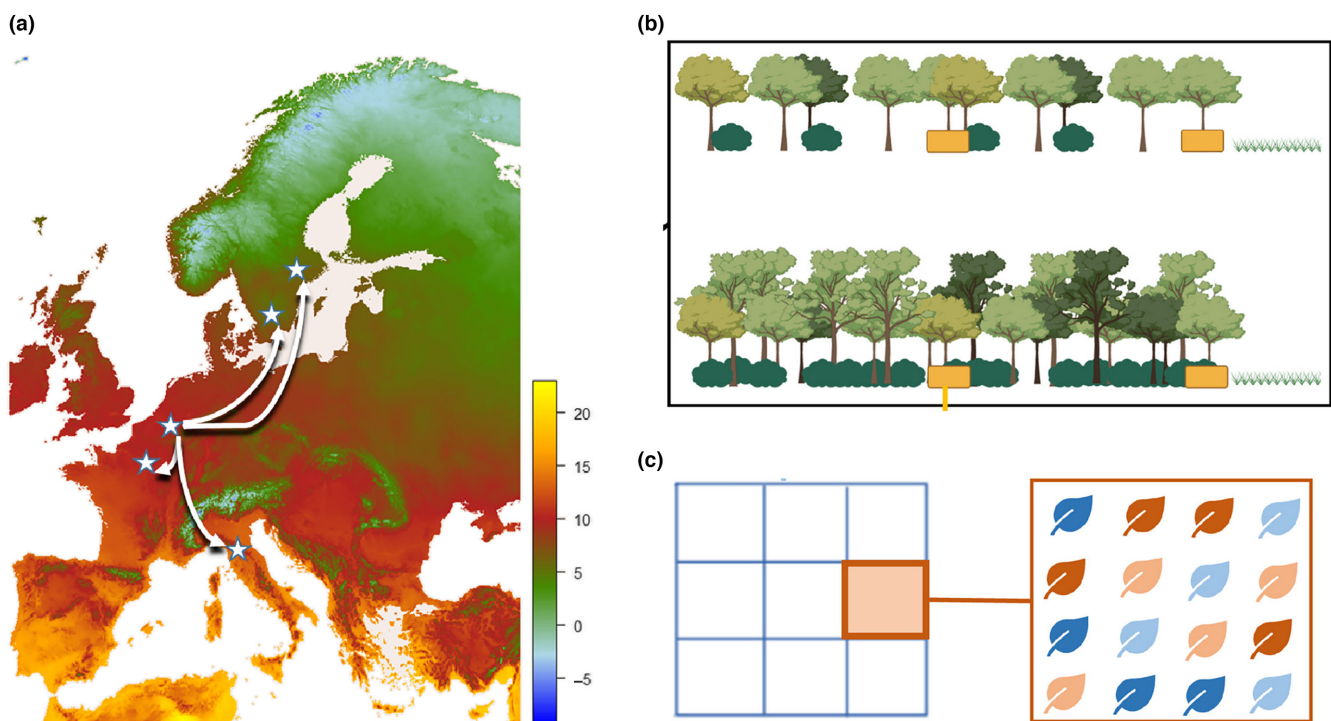


FIGURE 2 Design of the transplant experiment applied here. (a) The five studied regions covering Central and Southern Sweden, Belgium, France and Italy. The colours on the map show the mean annual temperature (°C) based on WorldClim 2 (Fick & Hijmans, 2017). (b) Each region contains four plots along two microclimatic gradients: two plots in a dense forest, two in an open forest. In each forest, one plot is situated at the forest edge and one in the forest interior. (c) Each plot contains nine mesocosms and each mesocosm contained 16 plants at the time of transplantation: four individuals of four different species in a randomized position. Two species per mesocosm were relatively more warm-adapted (red) and two relatively more cold-adapted (blue), and within each of these two pairs, one was a generalist (more transparent hue) and the other a forest specialist (darker hue). Tree symbols from BioRender.com.

Frenne, Baeten, et al., 2011; Verheyen et al., 2003). Both the geographic and thermal niche distribution of each species are plotted in Figure 3. According to the geographic distribution map, two species (*C. sylvatica* and *V. minor*) with a more southern distribution were transplanted close to or beyond their northern range edge.

Estimating plants' thermal niches often involves detailed eco-physiological measurements and experiments in field or laboratory conditions. Alternatively, the determination of realized climatic niches based on species' distributions is a reliable method for estimating a species' thermal tolerance (Vangansbeke et al., 2021) and has been widely employed in ecological niche modeling for many years (e.g., De Frenne et al., 2013; Haesen et al., 2023; Peterson, 2011). The thermal niche distribution for each species was plotted based on 1000 values of mean growing-season (April to September) temperature of the 1970–2000 period randomly drawn within each species' distribution in Europe (ClimPlant database available on Figshare at <https://doi.org/10.6084/m9.figshare.12199628>; Vangansbeke et al., 2021), which was then corrected to microclimate niche data based on a detailed map of forest microclimate temperature (ForestTemp database, Haesen et al., 2021). We selected the

1970–2000 climate data because species distribution maps were sourced from the atlases of Hultén and Fries (1986) and Meusel and Jäger (1992), which represent species distributions prior to the recent warm period. We assumed that the climate data for 1970–2000 were considerably more accurate than those from warmer, more recent periods such as 2000–2020, although temperatures at the end of the 1990s had already risen due to climate change (IPCC, 2001). The cold and warm limits of a given species were represented by computing the 0.05 and 0.95 percentiles of its thermal niche, respectively. The 0.95 percentile is a level commonly chosen in previous studies to describe thermal extremes while avoiding outliers (e.g., Li et al., 2020; Sunday et al., 2014; Webb et al., 2020). To test the sensitivity of our results to the choice of the warming tolerance, we also used the 0.99 percentile of the realized thermal niche (Figure S1). Based on the warm limit of the 12 species (Figure 3), the warm limit among the 12 species ranged from 16.13°C for *G. sylvaticum* to 19.08°C for *G. robertianum*. The three most cold-adapted species are *G. sylvaticum*, *A. nemorosa* and *O. acetosella*, and the three most warm-adapted species are *U. dioica*, *V. minor* and *G. robertianum*. The other species, ranked according to their thermal niche as

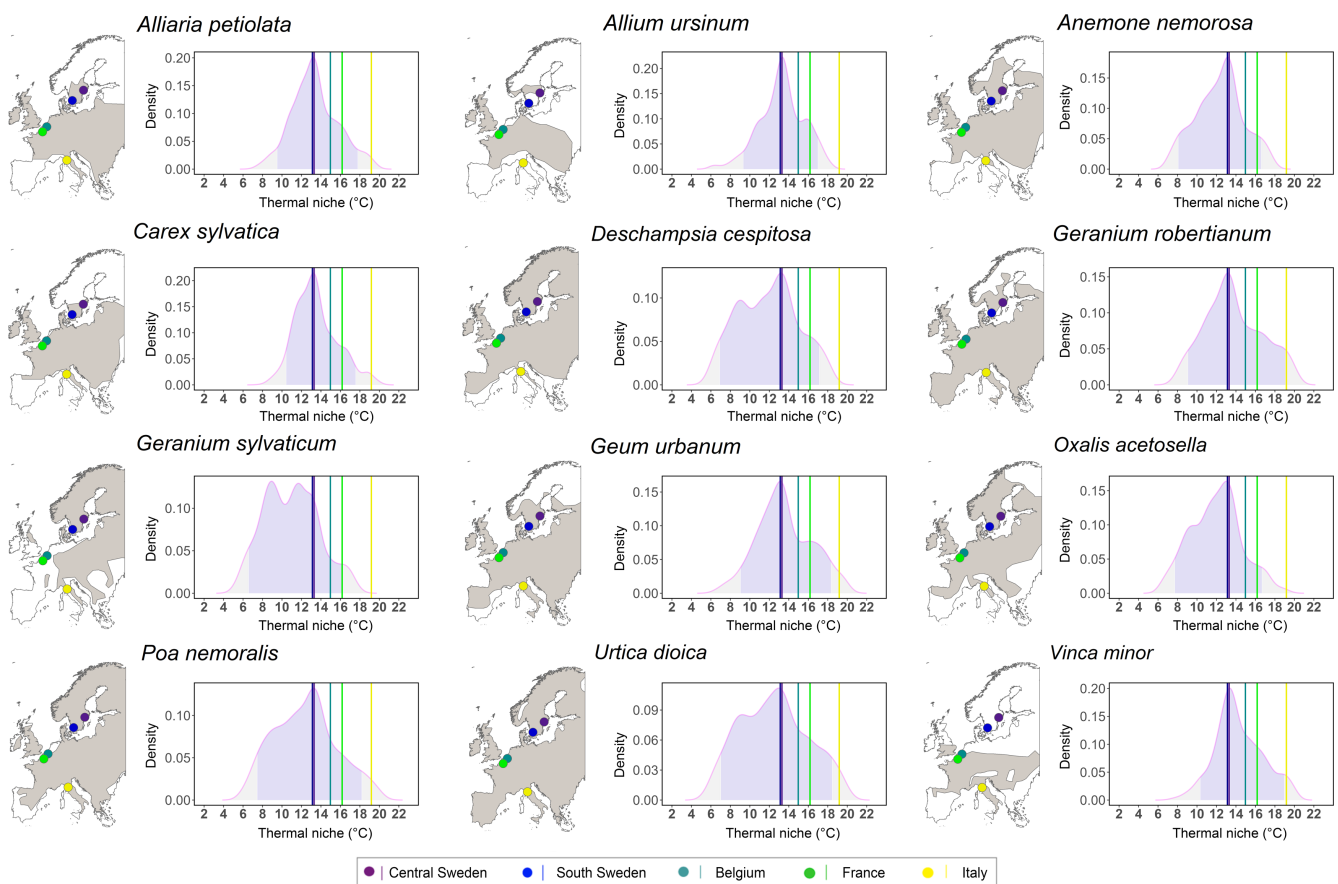


FIGURE 3 The geographical and thermal niche range of the 12 studied understory species. In each map, the grey area is the geographic distribution of a species, and the five circles indicate the five experimental regions. The density plot next to each map shows the microclimate-based thermal niche range of a species (data from the growing season). The grey shading in the density plot represents thermal niches that fall below a species' cold limit (5th percentile) or above its warm limit (95th percentile). The lines in each density plot are the mean microclimate temperatures (in-situ measured in the growing season) of the five studied regions, and the lines for Central and South Sweden are very close together due to their comparable temperatures during the experiment.

calculated here, are *A. ursinum*, *D. cespitosa*, *C. sylvatica*, *A. petiolata*, *P. nemoralis* and *G. urbanum*.

2.3 | Experimental design

A large-scale transplant experiment was installed in early spring 2019 across five regions located along a 1750 km long transect spanning the entire European temperature broadleaved forest biome (Figure 2a). In each region, four experimental plots were established with contrasting forest structure (open vs. dense) and distance to the forest edge (edge vs. interior) (Figure 2b), hereby capturing a major part of the natural variation in macroclimate and microclimate in European broadleaf forests. Dense forest stands typically had a well-developed shrub and tree layer, high basal area and canopy cover. Open forest stands were characterized by a high canopy openness and the absence of a shrub layer. In each forest stand, experimental plots were installed at c. 2 m from the south-facing forest edge and in the forest interior (minimal distance of 50 m from any forest edge). In total, 20 experimental plots (5 regions \times 2 forest types \times 2 plots per forest type) were established.

All experimental plots contained nine mesocosm communities (Figure 2c), each composed of four individuals (replicates) of four different species randomly planted in a rectangular grid of 4 \times 4. In total, the experiment encompassed 180 mesocosms (5 regions \times 2 forest types \times 2 plots per forest type \times 9 mesocosms per plot), 2880 individuals (180 mesocosms \times 4 species \times 4 individuals) and 240 individuals per species (12 replicates \times 20 experimental plots). Species were transplanted into mesocosm boxes (21.5 L plastic containers of 30 \times 40 cm with drainage holes covered by a root cloth) that contained the same potting soil everywhere (85% peat and 15% coconut fiber, containing slow-release fertilizer 15:8:11:2 of nitrogen, phosphorus, potassium, magnesium, 5–6.5 pH-KCl, Osmocote Exact Low Start 16–18 M, ICL Specialty Fertilizers, Geldermalsen, The Netherlands). Thus, any potential effects induced by differences in soil conditions were ruled out to exclusively study signals caused by gradients in macroclimate, microclimate, and forest density. The species *Alliaria petiolata*, *Geranium robertianum*, *Geranium sylvaticum*, and *Poa nemoralis* were grown from seeds and transplanted as seedlings. All other species were planted as mature individuals or as rhizomes derived from natural populations in Belgium (Gontrode).

2.4 | Plot temperature

Near-ground temperatures at the height experienced by understorey herbs (15 cm height) were measured every 15 min from mid-April, 2019 in the central mesocosm of each plot with TMS-4 loggers (TOMST, Prague, Czech Republic) (Maclean et al., 2021; Wild et al., 2019). We compiled 2 years of growing-season temperature data (April–September) spanning three growing seasons (May

2019–April 2021) and calculated the mean growing-season temperature for each plot (Wei et al., 2023). Since we did not have a complete month of temperature data in April 2019, we additionally included temperature data for April 2021 to have a fully balanced set of temperature data.

2.5 | Plant measurement

During the growing season (April–September) of 2019, 2020 and 2021, we recorded the survival and flowering probability (whether it flowered or not) for each individual in the experiment (Wei et al., 2023). For all surviving individuals, we measured the natural height (without stretching the plant) and estimated the cover (Pérez-Harguindeguy et al., 2013). Summer-flowering species were measured in July 2019, 2020 and 2021. Spring-flowering species were measured in April and May 2020 and 2021. We also counted the number of flowers or inflorescence units for each flowering individual.

2.6 | Data analysis

The warming tolerance of species *j* in plot *i* ($\Delta T_{\text{niche},ij}$) is a thermal vulnerability index and was calculated here following Deutsch et al. (2008):

$$\Delta T_{\text{niche},ij} = T_{\text{WLi}} - T_{\text{ISj}}$$

where T_{WLi} is the inferred growing-season warm limit (WL) temperature (0.95 percentile of the thermal niche range) of species *i* across its entire range in Europe, and T_{ISj} is the growing-season (April–September) mean in-situ (IS) forest temperature of plot *j*. Therefore, both T_{WLi} and T_{ISj} and were calculated considering the local microclimatic conditions of the focal plot and across the distribution of the focal species.

For each of the five performance indices we measured (i.e., survival, growth, ground cover, flowering probability and flower number), we first modeled the response of each performance index to ΔT_{niche} across all 12 species together, assuming both linear and flexible shape-curves using generalized linear mixed models (GLMMs) and generalized additive models (GAMMs), respectively, with “mesocosm”, “sampling year” and “species” as random intercept terms. We then modeled species-specific responses to ΔT_{niche} using GLMMs. Because data on flowering probability and flower number were not sufficient for certain species (e.g. *G. sylvaticum*, *A. petiolata*, *V. minor*, *G. robertianum*), we only modeled the responses of these two indices across species. In addition, we only modeled GAMMs across species to test whether the complex non-linear relationships can be captured based on the larger sample sizes when pooling species together (Wood, 2017). We used a binomial error distribution for survival and flowering and a Gaussian error distribution for growth, cover and flower number. To investigate whether the results remained robust irrespective of cutoff threshold (0.99 percentile vs. 0.95 percentile),

we also applied all the GLMMs and GAMMs to ΔT_{niche} , calculated using the 0.99 percentile of the realized thermal niche; the results were very similar indeed (Figure S1). For GLMMs, the “lme” function in lme4 R Packages was applied, and the “gamm” function in gamm4 package was used for GAMMs. Finally, we estimated across- and within-species responses to distance to forest edge, forest structure and macroclimate (mean site temperature of the five sites) using all two-way interactions in the GLMMs.

To additionally capture extreme values that might have a significant impact on plant performance, we also calculated ΔT_{niche} using the 0.95 percentile maximum value of the in situ plot growing season temperature (here, referred to as $\Delta T_{\text{niche_max}}$), and assessed its effects on species performance using the same statistical methods as described above (see Result S1; Figures S2 and S3).

3 | RESULTS

3.1 | ΔT_{niche} characteristics

From the coldest (Central Sweden) to the warmest (Italy) region (Figure 4a), the ΔT_{niche} ranged from -2 to $+6^\circ\text{C}$ among the 12 studied species. The mean ΔT_{niche} across all the species within a given region was significantly different between the five regions (except

for a non-significant difference between Central and South Sweden) based on Tukey test for pair-wise comparisons ($p < .05$), with the mean ΔT_{niche} values across species within a given region ranging from $+4.54 \pm 0.94^\circ\text{C}$ in the coldest region to $-1.52 \pm 1.10^\circ\text{C}$ in the warmest region. The warmest region of Italy (mean microclimate temperature of 19.16°C during the growing season) was $+1.5^\circ\text{C}$ warmer than the mean warm limits across all 12 species (17.66°C). Only for the most warm-adapted species (*V. minor* and *G. robertianum*) temperatures in Italy were close to the warm limit (ΔT_{niche} close to 0). The mean microclimate temperature in France (16.17°C in the growing season) was comparable to temperatures at the warm limit (ΔT_{niche} close to 0) for the most cold-adapted species (*G. sylvaticum*, *A. nemorosa* and *O. acetosella*).

When estimating ΔT_{niche} based on forest structure (dense vs. open) or distance to forest edge (Figure 4b,c), the ΔT_{niche} ranged from -1°C to $+4^\circ\text{C}$ among the 12 species. The mean ΔT_{niche} was lower at forest edge or in open forests in each species, due to a locally warmer microclimate. This was because, the ΔT_{niche} of a species was calculated as the temperature difference between its warm limit temperature and the plot temperature. As the warm limit of a species was fixed in the definition used here, the lower ΔT_{niche} observed at the forest edge was attributed to the higher in-situ measured temperature in forest edges than in forest interiors. The mean ΔT_{niche} across all 12 species for the edge-interior

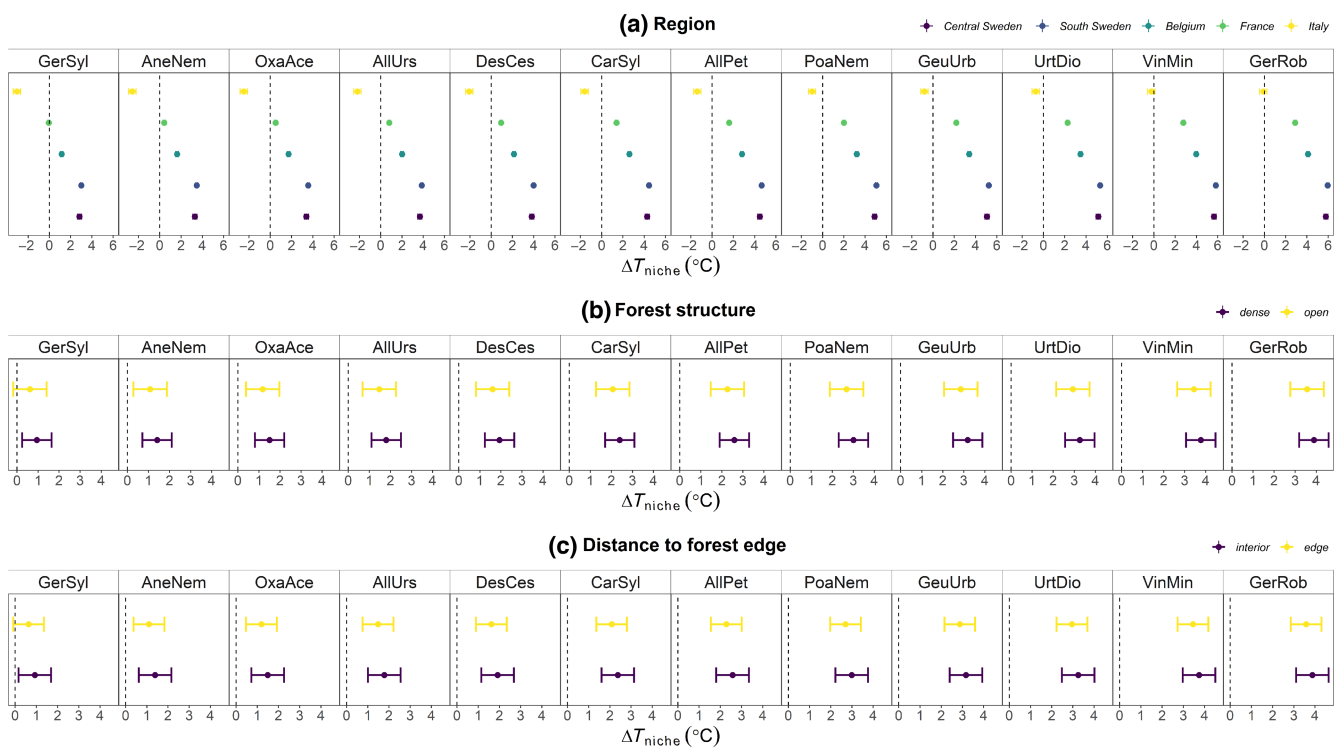


FIGURE 4 The mean and standard error (SE) of ΔT_{niche} value for each species depending on (a) the region along the latitudinal gradient, (b) forest structure (dense vs. open forests) and (c) distance to forest edge (edge vs. interior). Species are ordered along an “indicative gradient” based on the warmest limit of their thermal niches from cold to warm. This ordering does not take into account local adaptation. Species code: AllPet, *Alliaria petiolata*; AllUrs, *Allium ursinum*; AneNem, *Anemone nemorosa*; CarSyl, *Carex sylvatica*; DesCes, *Deschampsia cespitosa*; GerRob, *Geranium robertianum*; GerSyl, *Geranium sylvaticum*; GeuUrb, *Geum urbanum*; OxaAce, *Oxalis acetosella*; PoaNem, *Poa nemoralis*; UrtDio, *Urtica dioica*; VinMin, *Vinca minor*.

difference was -0.29°C , and for the open-dense difference, it was -0.33°C .

3.2 | Effects of ΔT_{niche} on the performance of understory plants

We found a linearly increasing percentage of ground cover, height and flowering probabilities in response to ΔT_{niche} across all 12 species (Figure 5b–d). For species survival and number of flowers (Figure 5a,e), we did not find a significant linear response, but a significant non-linear response to ΔT_{niche} .

At the species-specific level, patterns showed idiosyncratic responses to ΔT_{niche} depending on the species identity and the performance index (Figure S4). The five performance indices of the two cold-adapted species *G. sylvaticum* and *A. ursinum* showed consistently positive responses to ΔT_{niche} , and one species—*D. cespitosa*—showed consistently negative responses to ΔT_{niche} . On the contrary, the survival of the cold-adapted species *A. nemorosa* decreased but its height and flowering probability increased with ΔT_{niche} , and the survival of another cold-adapted species—*O. acetosella*—increased but its height decreased with ΔT_{niche} . In addition, with regards to most warm-adapted species, the five performance indices showed no statistically significant responses to ΔT_{niche} , except for two species, *G. urbanum* and *G. robertianum*, whose survival decreased with higher ΔT_{niche} .

3.3 | Responses of understory plants to micro- and macro-climate

Concerning the interaction effects of distance to forest edge/structure with macroclimate on species performance in general across all 12 studied species, the survival and height showed lower values at the forest edge than in the forest interior in warmer macroclimates. Meanwhile, all the five performance indices (except the flowering probability) were lower in open than in dense forests in a warmer macroclimate. The direction of species-specific responses to the interaction effect of distance to forest edge/structure with macroclimate was similar to the general pattern across all species (see more details in Result S2 and Table S1).

4 | DISCUSSION

Here, we demonstrated that the magnitude of ΔT_{niche} for several understory plant species was mainly affected by macroclimate, with the forest canopy playing a significant role in buffering the microclimate. In general, across all 12 studied species, our findings support the general hypothesis that plant performance (growth and reproduction) decreased when local temperature conditions are too close or even exceed the warmer limit of species (i.e., ΔT_{niche} decreases and becomes negative). However, species-specific responses may vary depending on the combination of the species identity and

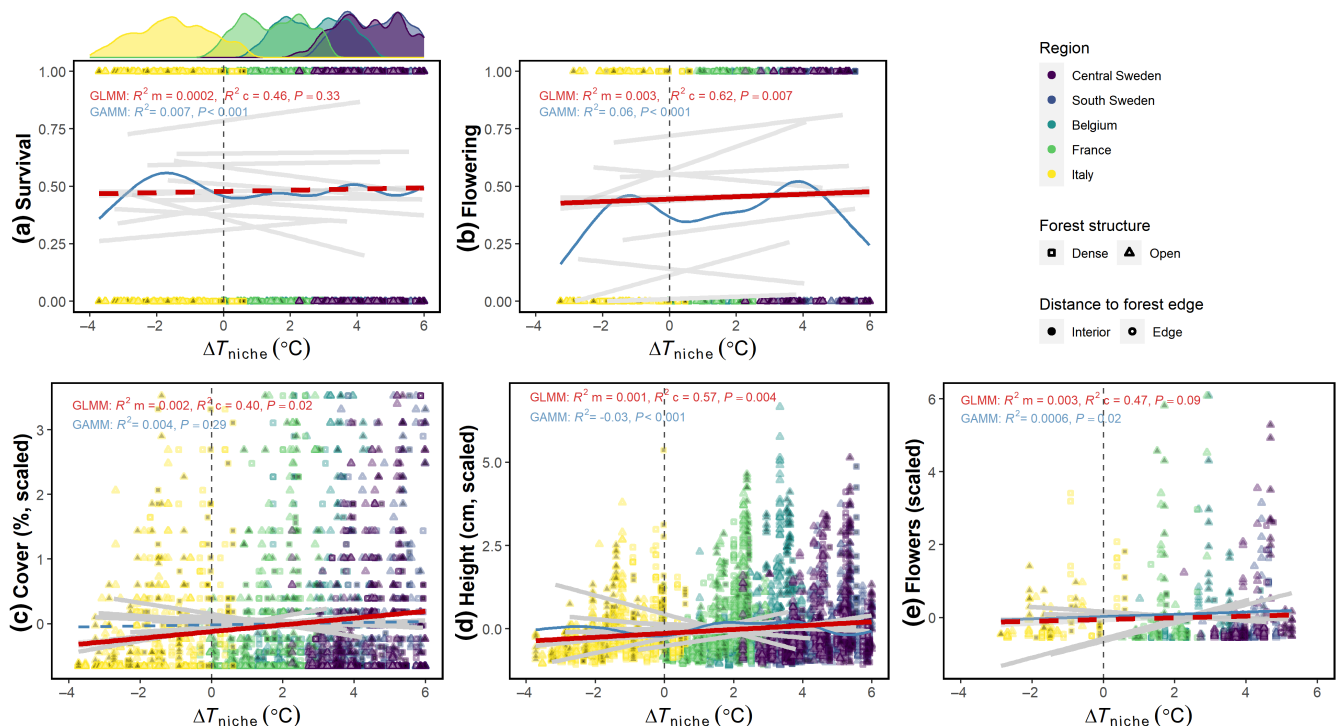


FIGURE 5 Responses of survival, percentage ground cover, plant height, flowering probabilities and the number of flowers per individual to ΔT_{niche} across all 12 species. The red lines indicate generalized linear mixed models (GLMMs), the blue lines generalized additive models (GAMMs), dashed lines indicate non-significant effects (with $p > .05$). Within-species responses are also indicated in grey lines (each line is the fit of the GLMM of one species). For survival, density side-plots were added to visualize the distribution of the data.

performance index. Finally, we highlighted the role of microclimate, particularly in dense forest structures, in providing potential transient microrefugia for understory species in warmer regions.

4.1 | ΔT_{niche} characteristics

Our study is the first that quantifies ΔT_{niche} of multiple understory plant species across various transplanted populations based on microclimate temperature data. The ΔT_{niche} index directly reflects the thermal distance to the warm limit of a given species' population at a given location. Specifically, our study demonstrated that the ΔT_{niche} of 12 understory plant species typical of European temperate forests, was strongly affected by the macroclimatic differences among regions and to a lesser extent, by microclimatic conditions within a given forest stand (cf. distance to the edge and stand structure). We found large differences in ΔT_{niche} (mean values ranging from -2 to $+6^{\circ}\text{C}$) among species, and the ΔT_{niche} values of all species were less positive than expected, which can likely be attributed to the warmer growing seasons experienced in 2019 and 2020 compared to the long-term climatic average (i.e., average climatology over the baseline period of 1979–2013). Moreover, the mean growing-season temperature of France during this study was similar to the temperature at the warm limit of the most cold-adapted species (e.g., *G. sylvaticum*, *A. nemorosa* and *O. acetosella*), and that of Italy was similar to the temperature at the warm limit of the most warm-adapted species in this study (*V. minor* and *G. robertianum*). Our finding that cold-adapted species are approaching their temperature limits while warm-adapted species still maintain a tolerance range has significant ecological implications. For example, cold-adapted species may face challenges in adapting to rising temperatures, leading to reduced fitness and potential population decline (Lenoir et al., 2010), which can contribute to decreased biodiversity and altered ecological interactions (Parmesan, 2006). Furthermore, the decline or loss of cold-adapted species may impact important ecosystem functions and services such as nutrient cycling and carbon sequestration (Franklin et al., 2016). Previous large-scale studies on estimating the thermal limits of species were mainly based on geographical range (i.e., ΔT distance) along latitude or altitude (e.g., Gazol et al., 2015; O'Sullivan et al., 2017). For example, the study by Feeley et al. (2020) based on an altitudinal gradient showed that cold species from highland forest communities had lower thermal optima and maxima compared to species from hotter lowland forests. Yet, based on our ΔT_{niche} quantification, the warm range limit was shown directly in terms of temperature conditions with ΔT_{niche} reaching zero or being negative when the in situ temperature is equal to or exceeds, respectively, the warm limit of the species' thermal niches. This represents a significant advance in our understanding of plant responses to warming, enabling more accurate forecasting of the temperature thresholds at which species are expected to exhibit reduced performance. Moreover, the concept of ΔT_{niche} provides a practical tool to predict and monitor warming impacts considering microclimate, which has been previously unexplored. For example, it helps identify which

species are closer to or exceed their warming tolerance and are more likely to be negatively influenced by warming at a certain location. This information could support effective conservation and management strategies to mitigate the negative effect of climate change on plant biodiversity and ecosystem functioning.

We found consistently lower ΔT_{niche} (i.e., less positive values) in forest edges and in open forests than in forest interiors and closed forests, respectively, for each species. This was due to the higher mean temperature conditions in forest edges or in open forests than in forest interiors or in closed forests, respectively, pointing out the microclimate buffering role of the forest canopy. These findings are very consistent with former studies showing that the maximum as well as the average temperature were cooler by around 2°C inside than outside forests across Europe (De Lombaerde et al., 2022; Haesen et al., 2021; Zellweger et al., 2019). Furthermore, we found that ΔT_{niche} was significantly lower in open than in dense forests but only in the warmest region of the studied latitudinal gradient (i.e., Italy). This is also consistent with previous findings that summer temperatures at weather stations and below the forest canopy differed less towards higher latitudes (Graae et al., 2012; von Arx et al., 2012).

4.2 | Effects of ΔT_{niche} on the performance of understory plants

Our study demonstrated that decreasing ΔT_{niche} towards the point at which local temperature exceeds the warmer limit of the focal species, resulted in decreased plant performance (except for survival and number of flowers) across species. Similar to our results, a decrease in seed viability, tree growth and heat tolerance with decreasing latitudes or elevations were observed in previous studies (Gazol et al., 2015; O'Sullivan et al., 2017; Slot et al., 2021; Verheyen et al., 2009). Thermal stress can change plant physiological processes (e.g., photosynthesis, metabolite production), phenology (e.g., timing of flowering), demography (e.g., rates of survival, growth and reproduction) and, ultimately, result in reduced growth and reproduction of plant species (Nievola et al., 2017; Urban, 2015; Warren et al., 2018). In particular, the mean April–September temperatures of our five studied regions fall within the warmer portion of each of the 12 studied species' thermal niche, as shown in Figure 3. Even plots located in the coldest region (Sweden) of our studied latitudinal gradient are close to the thermal optimum or in the warmer portion of the thermal niches of each of the 12 species analysed here. Therefore, the observed decreasing trend in plant performance as ΔT_{niche} decreases, was expected. Detecting the significant effects of ΔT_{niche} on plant growth and reproduction across species in our relatively short-term study is a important finding, as it suggests that the impact on these species is expected to increase over the long term.

However, an overall decrease in plant species survival with decreasing ΔT_{niche} was not detected in our study. Previous studies have shown that under rising temperatures, certain species are unable to survive or establish (Harsch et al., 2009; Kelly &

Goulden, 2008; Kueppers et al., 2017; Salzer et al., 2009; Shay et al., 2021); other studies have found a non-significant correlation between species survival or distribution changes and climate warming (e.g., Foster & D'Amato, 2015; Van Bogaert et al., 2011), despite generally steep temperature gradients (Beauregard & Blois, 2016; Lenoir & Svenning, 2015). Some previous studies, though focusing on tree species, also reported limited demographic declines and retraction in the distribution of many temperate trees under increasing climatic warming, suggesting sustained demographic resilience to climatic impacts (Carnicer et al., 2021; Dittmar et al., 2003; Granda et al., 2018; Hackett-Pain & Friend, 2017). Other studies suggest that plant mortality is a stochastic phenomenon (Coppi et al., 2022; Franklin et al., 1987) and there may be a time lag between episodic stressful conditions and mortality responses (Cailleret et al., 2017; Jump et al., 2017; Sanczuk et al., 2022). Yet, we also cannot exclude the possibility that there might be a delay in the response of species in terms of survival rate. Hence, a long-term study may be needed here to confirm or not our preliminary findings.

It is generally assumed that species which have originated in colder regions are sensitive to warming effects, and others from warmer regions are more tolerant to or favored by warming (Nievoła et al., 2017). The decreased survival of two warm-adapted species (i.e., *G. urbanum* and *G. robertianum*) with increasing ΔT_{niche} , and the increased survival, growth or reproductive performance of two relatively cold-adapted species (i.e., *G. sylvaticum* and *A. ursinum*) were consistent with this hypothesis. However, the cold-adapted species were not always sensitive to or positively affected by warming. The survival of some cold-adapted species (*A. nemorosa* and *D. cespitosa*) even showed negative responses to increasing ΔT_{niche} . Yet, the negative responses of cold-adapted species to warming could also be found in many previous studies. However, these studies have mainly focused on tree species and thermal niche optima. For example, several studies showed that the responses of cold-habitat species (Dahlberg et al., 2014; Greiser et al., 2019) to temperature were either lacking or positive, indicating no direct temperature limitation at the warm range margin of species. This suggests that factors other than warm temperatures, such as low precipitation, light limitations, biotic interactions, or a lack of nutrients, may play a role in determining a species performance within the thermal niche of species (Allen et al., 2015; Greiser et al., 2021; Normand et al., 2009; Soudzilovskaia et al., 2020). Some authors explained that a high degree of phenotypic plasticity could reduce the adverse effect of changing temperatures. Moreover, concerning previous studies on understory plants in Europe, *A. nemorosa* was the most commonly studied species among our 12 species. We found decreased survival of *A. nemorosa* to ΔT_{niche} corroborating results of previous studies (De Frenne, Brunet, et al., 2011; Depauw et al., 2022; Vangansbeke et al., 2022). Besides, only three species showed consistent responses of the five performance indices to ΔT_{niche} (*G. sylvaticum* and *A. ursinum* a positive response and *D. cespitosa* a negative response). On the other hand, there were species whose survival and growth showed contrasting responses among the indices we used to

measure plant performance, either with increased survival but decreased growth/flowering (*O. acetosella*) or vice versa (*A. nemorosa*; *G. robertianum*). Some previous studies (e.g. Benavides et al., 2015) mentioned that this might refer to survival-growth/reproduction trade-offs which may potentially counterbalance, at the species level, the negative effect of warming on survival, as long as the exposure to climate change does not exceed a certain threshold.

Finally, the idiosyncratic responses of species to warming were also detected in previous studies, in terms of emergence and survival, flower and leaf phenology or phylogenetic patterns (Buonaiuto & Wolkovich, 2021; Kueppers et al., 2017; Slot et al., 2021; Stahl et al., 2014). We suggest this might be because plants have thermal regulatory and adaptive strategies and plasticity. Plant species with similar warm limits along their thermal niche might have different leaf sizes, shapes and morphology and thus display divergent adaptation and plasticity to warming despite sharing the same warm limit (De Frenne, Brunet, et al., 2011). For example, some plant species can adapt to hot and dry conditions by reducing leaf area or developing thicker cuticles to keep moisture, or can reduce water use by growing deeper roots (Schenk & Jackson, 2002). Some may produce heat-shock proteins to protect photosynthesis from heat stress, or can bloom earlier during the vegetation period as temperatures warm up (Gasperini et al., 2023; Larcher, 2003; McDowell et al., 2008). This might induce different and unpredictable species-specific performance responses to increasing warming (Fauset et al., 2018; Leigh et al., 2017; Michaletz et al., 2015; Nievoła et al., 2017).

5 | CONCLUSIONS

Using a continental-extent transplant experiment, we showed that the observed variation in plant species warming tolerance (ΔT_{niche}) relative to their warm limit was mostly affected by macroclimatic differences between regions, with all studied species successively reaching their warm range limit ($\Delta T_{\text{niche}} = 0$) in the warmest regions of the studied latitudinal gradient. Yet, the lower ΔT_{niche} in forest edges and in open forests for each species indicated that microclimate buffering plays a role in determining plant species warming tolerance relative to their warm limit. In general, across all 12 studied species, we demonstrated decreased plant performance—reduced plant height, cover and flowering probability—with decreasing ΔT_{niche} . Warming may thus lead to a decrease in future plant performance at these species' warm range limits. While relationships across species offer valuable insights, we recognize that implications for plant performance may differ within species due to factors as local adaptation, genetic variability, and phenotypic plasticity. Further long-term research is required on within-species dynamics and their effects on plant performance in a warming climate. Finally, to our knowledge, our study is the first to reveal the role of microclimate, particularly dense forest structure, in relaxing the exposure to macroclimate warming that is likely to reduce the warming tolerance of understory plant species relative to their warm range limits. This highlights the importance of considering microclimate when studying the impact

of macroclimate warming, though the impact of microclimatic processes to mitigate macroclimate warming may be smaller than when moving from southern to northern Europe (macroclimate). Even though our study has already included a diverse set of common understory plant species of temperate forests across Europe to represent the thermal niche variation, we suggest studying the warming tolerance, through transplant experiments, of more plant species and take the potential of species' local adaptation into account to test our hypothesis on the potential and usefulness of ΔT_{niche} in predicting plant species performance under climate warming.

Our study suggests that to manage and conserve biodiversity under future climate warming, quantifying plant species' warming tolerance relative to their warm limits and protecting areas within their warm limit is essential. Moreover, conservation efforts should prioritize areas and habitats where the temperature is close to the warm limit of species' thermal niche (ΔT_{niche} close to 0), such as closed-canopy forests at the warm margin of cold-adapted plant species. Microclimate should be integrated into land management planning, conservation strategies, as well as into efforts to conserve and restore forest habitats as potential microrefugia for plant species at the warm margin of their range. This may only happen through coordinated and collaborative efforts between land managers, conservation organizations, and policymakers.

AUTHOR CONTRIBUTIONS

Liping Wei: Conceptualization; data curation; formal analysis; funding acquisition; methodology; writing – original draft; writing – review and editing. **Pieter Sanczuk:** Conceptualization; data curation; formal analysis; funding acquisition; methodology; writing – review and editing. **Karen De Pauw:** Conceptualization; data curation; formal analysis; funding acquisition; methodology; writing – review and editing. **Maria Mercedes Caron:** Data curation; writing – review and editing. **Federico Selvi:** Data curation; writing – review and editing. **Per-Ola Hedwall:** Data curation; writing – review and editing. **Jörg Brunet:** Data curation; writing – review and editing. **Sara A. O. Cousins:** Data curation; writing – review and editing. **Jan Plue:** Data curation; writing – review and editing. **Fabien Spicher:** Data curation; writing – review and editing. **Cristina Gasperini:** Data curation; writing – review and editing. **Giovanni Iacopetti:** Data curation; writing – review and editing. **Anna Orczewska:** Writing – review and editing. **Jaime Uria-Diez:** Data curation; writing – review and editing. **Jonathan Lenoir:** Conceptualization; data curation; methodology; writing – review and editing. **Pieter Vangansbeke:** Conceptualization; data curation; formal analysis; funding acquisition; methodology; writing – review and editing. **Pieter De Frenne:** Conceptualization; data curation; formal analysis; funding acquisition; methodology; writing – review and editing.

ACKNOWLEDGMENTS

LW, KDP, PV, PS, and PDF received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (ERC Starting Grant FORMICA 757833) and the international mobility project of National Natural

Science Foundation of China—Research Foundation Flanders (NSFC-FWO, No. 32211530482). LW was also supported by China Scholarship Council (CSC), and KDP was also supported by the Research Foundation Flanders (FWO) (K.D.P. ASP035-19).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The full dataset is accessible in figshare at: <https://doi.org/10.6084/m9.figshare.23055236> (Wei et al., 2023).

ORCID

Liping Wei  <https://orcid.org/0000-0002-4296-9851>
 Pieter Sanczuk  <https://orcid.org/0000-0003-1107-4905>
 Karen De Pauw  <https://orcid.org/0000-0001-8369-2679>
 Maria Mercedes Caron  <https://orcid.org/0000-0002-6216-695X>
 Federico Selvi  <https://orcid.org/0000-0002-3820-125X>
 Per-Ola Hedwall  <https://orcid.org/0000-0002-0120-7420>
 Jörg Brunet  <https://orcid.org/0000-0003-2667-4575>
 Sara A. O. Cousins  <https://orcid.org/0000-0003-2656-2645>
 Jan Plue  <https://orcid.org/0000-0002-6999-669X>
 Fabien Spicher  <https://orcid.org/0000-0002-9999-955X>
 Cristina Gasperini  <https://orcid.org/0000-0002-2713-010X>
 Giovanni Iacopetti  <https://orcid.org/0000-0002-1472-4435>
 Anna Orczewska  <https://orcid.org/0000-0002-7924-9794>
 Jaime Uria-Diez  <https://orcid.org/0000-0003-3749-0181>
 Jonathan Lenoir  <https://orcid.org/0000-0003-0638-9582>
 Pieter Vangansbeke  <https://orcid.org/0000-0002-6356-2858>
 Pieter De Frenne  <https://orcid.org/0000-0002-8613-0943>

REFERENCES

- Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, 6(8), art129. <https://doi.org/10.1890/ES15-00203.1>
- Angert, A. L., Sheth, S. N., & Paul, J. R. (2011). Incorporating population-level variation in thermal performance into predictions of geographic range shifts. *Integrative and Comparative Biology*, 51(5), 733–750. <https://doi.org/10.1093/icb/acr048>
- Barbati, A., Marchetti, M., Chirici, G., & Corona, P. (2014). European forest types and forest Europe SFM indicators: Tools for monitoring progress on forest biodiversity conservation. *Forest Ecology and Management*, 321, 145–157. <https://doi.org/10.1016/j.foreco.2013.07.004>
- Beauregard, F., & Blois, S. (2016). Rapid latitudinal range expansion at cold limits unlikely for temperate understory forest plants. *Ecosphere*, 7(11), e01549. <https://doi.org/10.1002/ecs2.1549>
- Benavides, R., Escudero, A., Coll, L., Ferrandis, P., Gouriveau, F., Hódar, J. A., Ogaya, R., Rabasa, S. G., Granda, E., Santamaría, B. P., Martínez-Vilalta, J., Zamora, R., Espelta, J. M., Peñuelas, J., & Valladares, F. (2015). Survival vs. growth trade-off in early recruitment challenges global warming impacts on Mediterranean mountain trees. *Perspectives in Plant Ecology, Evolution and Systematics*, 17(5), 369–378. <https://doi.org/10.1016/j.ppees.2015.06.004>
- Brown, J. H. (1984). On the relationship between abundance and distribution of species. *The American Naturalist*, 124(2), 255–279. <http://www.jstor.org/stable/2461494>

- Buonaiuto, D. M., & Wolkovich, E. M. (2021). Differences between flower and leaf phenological responses to environmental variation drive shifts in spring phenological sequences of temperate woody plants. *Journal of Ecology*, 109(8), 2922–2933. <https://doi.org/10.1111/1365-2745.13708>
- Cailleret, M., Jansen, S., Robert, E. M. R., Desoto, L., Aakala, T., Antos, J. A., Beikircher, B., Bigler, C., Bugmann, H., Caccianiga, M., Čada, V., Camarero, J. J., Cherubini, P., Cochard, H., Coyea, M. R., Čufar, K., Das, A. J., Davi, H., Delzon, S., ... Martínez-Vilalta, J. (2017). A synthesis of radial growth patterns preceding tree mortality. *Global Change Biology*, 23(4), 1675–1690. <https://doi.org/10.1111/gcb.13535>
- Carnicer, J., Vives-Inglá, M., Blanquer, L., Méndez-Camps, X., Rosell, C., Sabaté, S., Gutiérrez, E., Sauras, T., Peñuelas, J., & Barbeta, A. (2021). Forest resilience to global warming is strongly modulated by local-scale topographic, microclimatic and biotic conditions. *Journal of Ecology*, 109(9), 3322–3339. <https://doi.org/10.1111/1365-2745.13752>
- Chevalier, M., Broennimann, O., & Guisan, A. (2021). Using a robust multi-settings inference framework on published datasets still reveals limited support for the abundant centre hypothesis: More testing needed on other datasets. *Global Ecology and Biogeography*, 30(11), 2211–2228. <https://doi.org/10.1111/geb.13376>
- Clusella-Trullas, S., Garcia, R. A., Terblanche, J. S., & Hoffmann, A. A. (2021). How useful are thermal vulnerability indices? *Trends in Ecology & Evolution*, 36(11), 1000–1010. <https://doi.org/10.1016/j.tree.2021.07.001>
- Coppi, A., Lazzaro, L., & Selvi, F. (2022). Plant mortality on ultramafic soils after an extreme heat and drought event in the Mediterranean area. *Plant and Soil*, 471, 123–139. <https://doi.org/10.1007/s11104-021-05179-2>
- Cuesta, F., Tovar, C., Llambí, L. D., Gosling, W. D., Halloy, S., Carilla, J., Muriel, P., Meneses, R. I., Beck, S., Ulloa Ulloa, C., Yager, K., Aguirre, N., Viñas, P., Jácome, J., Suárez-Duque, D., Buytaert, W., & Pauli, H. (2019). Thermal niche traits of high alpine plant species and communities across the tropical Andes and their vulnerability to global warming. *Journal of Biogeography*, 47(2), 408–420. <https://doi.org/10.1111/jbi.13759>
- Dahlberg, C. J., Ehrlén, J., & Hylander, K. (2014). Performance of forest bryophytes with different geographical distributions transplanted across a topographically heterogeneous landscape. *PLoS One*, 9(11), e112943. <https://doi.org/10.1371/journal.pone.0112943>
- Dallas, T., Decker, R. R., & Hastings, A. (2017). Species are not most abundant in the centre of their geographic range or climatic niche. *Ecology Letters*, 20(12), 1526–1533. <https://doi.org/10.1111/ele.12860>
- De Frenne, P., Baeten, L., Graae, B. J., Brunet, J., Wulf, M., Orczewska, A., Kolb, A., Jansen, I., Jamoneau, A., Jacquemyn, H., Hermy, M., Diekmann, M., De Schrijver, A., De Sanctis, M., Decocq, G., Cousins, S. A. O., & Verheyen, K. (2011). Interregional variation in the floristic recovery of post-agricultural forests. *Journal of Ecology*, 99, 600–609. <https://doi.org/10.1111/j.1365-2745.2010.01768.x>
- De Frenne, P., Brunet, J., Shevtsova, A., Kolb, A., Graae, B. J., Chabrierie, O., Cousins, S. A., Decocq, G., De Schrijver, A., Diekmann, M., Gruwe, R., Heinken, T., Hermy, M., Nilsson, C., Stanton, S., Tack, W., Willaert, J., & Verheyen, K. (2011). Temperature effects on forest herbs assessed by warming and transplant experiments along a latitudinal gradient. *Global Change Biology*, 17(10), 3240–3253. <https://doi.org/10.1111/j.1365-2486.2011.02449.x>
- De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B. R., Zellweger, F., Aalto, J., Ashcroft, M. B., Christiansen, D. M., Decocq, G., De Pauw, K., Govaert, S., Greiser, C., Gril, E., Hampe, A., Jucker, T., Klings, D. H., Koelemeijer, I. A., Lembrechts, J. J., Marrec, R., ... Hylander, K. (2021). Forest microclimates and climate change: Importance, drivers and future research agenda. *Global Change Biology*, 27(11), 2279–2297. <https://doi.org/10.1111/gcb.15569>
- De Frenne, P., Rodríguez-Sánchez, F., Coomes, D. A., Baeten, L., Verstraeten, G., Vellen, M., Bernhardt-Römermann, M., Brown, C. D., Brunet, J., Cornelis, J., Decocq, G. M., Dierschke, H., Eriksson, O., Gilliam, F. S., Hédli, R., Heinken, T., Hermy, M., Hommel, P., Jenkins, M. A., ... Verheyen, K. (2013). Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences of the United States of America*, 110(46), 18561–18565. <https://doi.org/10.1073/PNAS.1311190110>
- De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B. R., Hylander, K., Luoto, M., Vellend, M., Verheyen, K., & Lenoir, J. (2019). Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution*, 3(5), 744–749. <https://doi.org/10.1038/s41559-019-0842-1>
- De Lombaerde, E., Vangansbeke, P., Lenoir, J., Van Meerbeek, K., Lembrechts, J., Rodríguez-Sánchez, F., Luoto, M., Scheffers, B., Haesen, S., Aalto, J., Christiansen, D. M., De Pauw, K., Depauw, L., Govaert, S., Greiser, C., Hampe, A., Hylander, K., Klings, D., Koelemeijer, I., ... De Frenne, P. (2022). Maintaining forest cover to enhance temperature buffering under future climate change. *Science of the Total Environment*, 810, 151338. <https://doi.org/10.1016/j.scitotenv.2021.151338>
- De Pauw, K., Sanczuk, P., Meeussen, C., Depauw, L., De Lombaerde, E., Govaert, S., Vanneste, T., Brunet, J., Cousins, S. A. O., Gasperini, C., Hedwall, P.-O., Iacopetti, G., Lenoir, J., Plue, J., Selvi, F., Spicher, F., Uria-Diez, J., Verheyen, K., Vangansbeke, P., & De Frenne, P. (2022). Forest understorey communities respond strongly to light in interaction with forest structure, but not to microclimate warming. *New Phytologist*, 233, 219–235. <https://doi.org/10.1111/nph.17803>
- Depauw, L., Hu, R., Dhungana, K. S., Govaert, S., Meeussen, C., Vangansbeke, P., Strimbeck, R., Graae, B. J., & De Frenne, P. (2022). Functional trait variation of *Anemone nemorosa* along macro- and microclimatic gradients close to the northern range edge. *Nordic Journal of Botany*, 2022(4), e03471. <https://doi.org/10.1111/njb.03471>
- Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 6668–6672. <https://doi.org/10.1073/pnas.0709472105>
- Diamond, S. E., Sorger, D. M., Hulcr, J., Pelini, S. L., Toro, I. D., Hirsch, C., Oberg, E., & Dunn, R. R. (2012). Who likes it hot? A global analysis of the climatic, ecological, and evolutionary determinants of warming tolerance in ants. *Global Change Biology*, 18, 448–456. <https://doi.org/10.1111/j.1365-2486.2011.02542.x>
- Dittmar, C., Zech, W., & Elling, W. (2003). Growth variations of common beech (*Fagus sylvatica* L.) under different climatic and environmental conditions in Europe—A dendroecological study. *Forest Ecology and Management*, 173(1–3), 63–78. [https://doi.org/10.1016/S0378-1127\(01\)00816-7](https://doi.org/10.1016/S0378-1127(01)00816-7)
- Eaton, E., Caudullo, G., Oliveira, S., & de Rigo, D. (2016). *Quercus robur* and *Quercus petraea* in Europe: Distribution, habitat, usage and threats. In J. San-Miguel-Ayanz, D. de Rigo, G. Caudullo, T. Houston Durrant, & A. Mauri (Eds.), *European atlas of forest tree species* (pp. 160–163). Publication Office of the European Union.
- Fauset, S., Freitas, H. C., Galbraith, D. R., Sullivan, M. J. P., Aidar, M. P. M., Joly, C. A., Phillips, O. L., Vieira, S. A., & Gloor, M. U. (2018). Differences in leaf thermoregulation and water use strategies between three co-occurring Atlantic forest tree species. *Plant, Cell & Environment*, 41(7), 1618–1631. <https://doi.org/10.1111/pce.13208>
- Feeley, K., Martínez-Villa, J., Perez, T., Silva Duque, A., Triviño Gonzalez, D., & Duque, A. (2020). The thermal tolerances, distributions, and performances of tropical montane tree species. *Frontiers in Forests and Global Change*, 3, 25. <https://doi.org/10.3389/ffgc.2020.00025>

- Fick, S. E., & Hijmans, R. J. (2017). WORLDCLIM 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302–4315. <https://doi.org/10.1002/joc.5086>
- Foster, J. R., & D'Amato, A. W. (2015). Montane forest ecotones moved downslope in northeastern USA in spite of warming between 1984 and 2011. *Global Change Biology*, 21(12), 4497–4507. <https://doi.org/10.1111/gcb.13046>
- Franklin, J., Serra-Diaz, J. M., Syphard, A. D., & Regan, H. M. (2016). Global change and terrestrial plant community dynamics. *Proceedings of the National Academy of Sciences of the United States of America*, 113(14), 3725–3734. <https://doi.org/10.1073/pnas.1519911113>
- Franklin, J. F., Shugart, H. H., & Harmon, M. E. (1987). Tree death as an ecological process. *Bioscience*, 37(8), 550–556. <https://doi.org/10.2307/1310665>
- Frazier, M. R., Huey, R. B., & Berrigan, D. (2006). Thermodynamics constrains the evolution of insect population growth rates: “Warmer is better”. *The American Naturalist*, 168(4), 512–520. <https://doi.org/10.1086/506977>
- Gasperini, C., Carrari, E., Govaert, S., Meeussen, C., De Pauw, K., Plue, J., Sanczuk, P., Vanneste, T., Vangansbeke, P., Iacopetti, G., & De Frenne, P. (2023). Trait variation in juvenile plants from the soil seed bank of temperate forests in relation to macro- and microclimate. *Applied Vegetation Science*, 26(3), e12739.
- Gazol, A., Camarero, J. J., Gutiérrez, E., Popa, I., Andreu-Hayles, L., Motta, R., Nola, P., Ribas, M., Sangüesa-Barreda, G., Urbinati, C., & Carrer, M. (2015). Distinct effects of climate warming on populations of silver fir (*Abies alba*) across Europe. *Journal of Biogeography*, 42(6), 1150–1162. <https://doi.org/10.1111/jbi.12512>
- Graae, B. J., De Frenne, P., Kolb, A., Brunet, J., Chabrerie, O., Verheyen, K., Pepin, N., Heinken, T., Zobel, M., Shevtsova, A., Nijs, I., & Milbau, A. (2012). On the use of weather data in ecological studies along altitudinal and latitudinal gradients. *Oikos*, 121(1), 3–19. <https://doi.org/10.1111/j.1600-0706.2011.19694.x>
- Granda, E., Alla, A. Q., Laskurain, N. A., Loidi, J., Sánchez-Lorenzo, A., & Camarero, J. J. (2018). Coexisting oak species, including rear-edge populations, buffer climate stress through xylem adjustments. *Tree Physiology*, 38(2), 159–172. <https://doi.org/10.1093/treephys/tpx157>
- Greiser, C., Ehrlén, J., Luoto, M., Meineri, E., Merinero, S., Willman, B., & Hylander, K. (2021). Warm range margin of boreal bryophytes and lichens not directly limited by temperatures. *Journal of Ecology*, 109(10), 3724–3736. <https://doi.org/10.1111/1365-2745.13750>
- Greiser, C., Ehrlén, J., Meineri, E., & Hylander, K. (2019). Hiding from the climate: Characterizing microrefugia for boreal forest understory species. *Global Change Biology*, 26(2), 471–483. <https://doi.org/10.1111/gcb.14874>
- Hackett-Pain, A. J., & Friend, A. D. (2017). Increased growth and reduced summer drought limitation at the southern limit of *Fagus sylvatica* L., despite regionally warmer and drier conditions. *Dendrochronologia*, 44, 22–30. <https://doi.org/10.1016/j.dendro.2017.02.005>
- Haesen, S., Lembrechts, J. J., De Frenne, P., Lenoir, J., Aalto, J., Ashcroft, M. B., Kopecký, M., Luoto, M., Maclean, I., Nijs, I., Niittynen, P., Hoogen, J., Arriga, N., Brůna, J., Buchmann, N., Čiliak, M., Collalti, A., De Lombaerde, E., Descombes, P., ... Van Meerbeek, K. (2021). ForestTemp—Sub-canopy microclimate temperatures of European forests. *Global Change Biology*, 27(23), 6307–6319. <https://doi.org/10.1111/gcb.15892>
- Haesen, S., Lenoir, J., Gril, E., De Frenne, P., Lembrechts, J. J., Kopecký, M., Macek, M., Man, M., Wild, J., & Van Meerbeek, K. (2023). Microclimate reveals the true thermal niche of forest plant species. *Ecology Letters*, 00, 1–13. <https://doi.org/10.1111/ele.14312>
- Harsch, M. A., Hulme, P. E., McGlone, M. S., & Duncan, R. P. (2009). Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters*, 12(10), 1040–1049. <https://doi.org/10.1111/j.1461-0248.2009.01355.x>
- Hengeveld, R. (1992). *Dynamic biogeography*. Cambridge University Press.
- Hultén, E., & Fries, M. (1986). *Atlas of North European vascular plants: North of the Tropic of Cancer*. Koeltz Scientific.
- Inouye, D. W. (2008). Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology*, 89(2), 353–362. <https://doi.org/10.1890/06-2128.1>
- IPCC. (2001). Climate change 2001: The scientific basis. In J. T. Houghton, Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, K. Maskell, & C. A. Johnson (Eds.), *Contribution of working group I to the third assessment report of the Intergovernmental Panel on Climate Change*. Cambridge University Press.
- Jump, A. S., Ruiz-Benito, P., Greenwood, S., Allen, C. D., Kitzberger, T., Fensham, R., Martínez-Vilalta, J., & Lloret, F. (2017). Structural overshoot of tree growth with climate variability and the global spectrum of drought-induced forest dieback. *Global Change Biology*, 23(9), 3742–3757. <https://doi.org/10.1111/gcb.13636>
- Kearney, M. R., Porter, W. P., & Huey, R. B. (2021). Modelling the joint effects of body size and microclimate on heat budgets and foraging opportunities of ectotherms. *Methods in Ecology & Evolution*, 12, 458–467. <https://doi.org/10.1111/2041-210X.13528>
- Kelly, A. E., & Goulden, M. L. (2008). Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 105(33), 11823–11826. <https://doi.org/10.1073/pnas.0802891105>
- Kingsolver, J. G., Diamond, S. E., & Buckley, L. B. (2013). Heat stress and the fitness consequences of climate change for terrestrial ectotherms. *Functional Ecology*, 27, 1415–1423. <https://doi.org/10.1111/1365-2435.12145>
- Kueppers, L. M., Conlisk, E., Castanha, C., Moyes, A. B., Germino, M. J., Valpine, P., Torn, M. S., & Mitton, J. B. (2017). Warming and provenance limit tree recruitment across and beyond the elevation range of subalpine forest. *Global Change Biology*, 23(6), 2383–2395. <https://doi.org/10.1111/gcb.13561>
- Larcher, W. (2003). *Physiological plant ecology* (4th ed.). Springer-Verlag.
- Leigh, A., Sevanto, S., Close, J. D., & Nicotra, A. B. (2017). The influence of leaf size and shape on leaf thermal dynamics: Does theory hold up under natural conditions? *Plant, Cell & Environment*, 40(2), 237–248. <https://doi.org/10.1111/pce.12857>
- Lenoir, J., Gégout, J. C., Dupouey, J. L., Bert, D., & Svenning, J. C. (2010). Forest plant community changes during 1989–2007 in response to climate warming in the Jura Mountains (France and Switzerland). *Journal of Vegetation Science*, 21, 949–964. <https://doi.org/10.1111/j.1654-1103.2010.01201.x>
- Lenoir, J., & Svenning, J.-C. (2015). Climate-related range shifts—A global multidimensional synthesis and new research directions. *Ecography*, 38(1), 15–28. <https://doi.org/10.1111/ecog.00967>
- Li, D., Yuan, J., & Kopp, R. E. (2020). Escalating global exposure to compound heat-humidity extremes with warming. *Environmental Research Letters*, 15(6), 064003. <https://doi.org/10.1088/1748-9326/ab7d04>
- Maclean, I. M. D., Duffy, J. P., Haesen, S., Govaert, S., De Frenne, P., Vanneste, T., Lenoir, J., Lembrechts, J. J., Rhodes, M. W., & Van Meerbeek, K. (2021). On the measurement of microclimate. *Methods in Ecology and Evolution*, 12(8), 1397–1410. <https://doi.org/10.1111/2041-210X.13627>
- Manthey, J., Campbell, L., Saupe, E., Soberón, J., Hensz, C., Myers, C., Owens, H., Ingenloff, K., Peterson, A., Barve, N., Lira-Noriega, A., & Barve, V. (2015). A test of niche centrality as a determinant of population trends and conservation status in threatened and endangered North American birds. *Endangered Species Research*, 26(3), 201–208. <https://doi.org/10.3354/esr00646>
- Marchin, R. M., Backes, D., Ossola, A., Leishman, M. R., Tjoelker, M. G., & Ellsworth, D. S. (2022). Extreme heat increases stomatal conductance and drought-induced mortality risk in vulnerable plant

- species. *Global Change Biology*, 28, 1133–1146. <https://doi.org/10.1111/gcb.15976>
- Martínez-Gutiérrez, P. G., Martínez-Meyer, E., Palomares, F., & Fernández, N. (2018). Niche centrality and human influence predict rangewide variation in population abundance of a widespread mammal: The collared peccary (*Pecari tajacu*). *Diversity and Distributions*, 24(1), 103–115. <https://doi.org/10.1111/ddi.12662>
- Martínez-Meyer, E., Díaz-Porras, D., Peterson, A. T., & Yáñez-Arenas, C. (2013). Ecological niche structure and rangewide abundance patterns of species. *Biology Letters*, 9, 20120637. <https://doi.org/10.1098/rsbl.2012.0637>
- McDowell, N., & Allen, C. (2015). Darcy's law predicts widespread forest mortality under climate warming. *Nature Climate Change*, 5, 669–672. <https://doi.org/10.1038/nclimate2641>
- McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D. G., & Yezzer, E. A. (2008). Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist*, 178, 719–739. <https://doi.org/10.1111/j.1469-8137.2008.02436.x>
- Meeussen, C., Govaert, S., Vanneste, T., Bollmann, K., Brunet, J., Calders, K., Cousins, S. A. O., de Pauw, K., Diekmann, M., Gasperini, C., Hedwall, P. O., Hylander, K., Iacopetti, G., Lenoir, J., Lindmo, S., Orczewska, A., Ponette, Q., Plue, J., Sanczuk, P., ... de Frenne, P. (2021). Microclimatic edge-to-interior gradients of European deciduous forests. *Agricultural and Forest Meteorology*, 311, 108699. <https://doi.org/10.1016/j.agrformet.2021.108699>
- Mellert, K. H., Ewald, J., Hornstein, D., Dorado-Liñán, I., Jantsch, M., Taeger, S., Zang, C., Menzel, A., & Kölling, C. (2016). Climatic marginality: A new metric for the susceptibility of tree species to warming exemplified by *Fagus sylvatica* (L.) and Ellenberg's quotient. *European Journal of Forest Research*, 135(1), 137–152. <https://doi.org/10.1007/s10342-015-0924-9>
- Meusel, H., & Jäger, E. J. (1992). *Vergleichende Chorologie der zentral-europäischen Flora, Karten* (Vol. III). VEB Gustav Fischer.
- Michaletz, S. T., Weiser, M. D., Zhou, J., Kaspari, M., Helliker, B. R., & Enquist, B. J. (2015). Plant thermoregulation: Energetics, traits-environment interactions, and carbon economics. *Trends in Ecology & Evolution*, 30, 714–724. <https://doi.org/10.1016/j.tree.2015.09.0>
- Mölder, A., Meyer, P., & Nagel, R. V. (2019). Integrative management to sustain biodiversity and ecological continuity in Central European temperate oak (*Quercus robur*, *Q. petraea*) forests: An overview. *Forest Ecology and Management*, 437, 324–339. <https://doi.org/10.1016/j.foreco.2019.01.006>
- Morin, X., & Chuine, I. (2006). Niche breadth, competitive strength and range size of tree species: A trade-off based framework to understand species distribution. *Ecology Letters*, 9(2), 185–195. <https://doi.org/10.1111/j.1461-0248.2005.00864.x>
- Moritz, C., & Agudo, R. (2013). The future of species under climate change: Resilience or decline? *Science*, 341(6145), 504–508. <https://doi.org/10.1126/science.1237190>
- Nievela, C. C., Carvalho, C. P., Carvalho, V., & Rodrigues, E. (2017). Rapid responses of plants to temperature changes. *Temperature*, 4(4), 371–405. <https://doi.org/10.1080/23328940.2017.1377812>
- Normand, S., Treier, U. A., Randin, C., Vittoz, P., Guisan, A., & Svenning, J.-C. (2009). Importance of abiotic stress as a range-limit determinant for European plants: Insights from species responses to climatic gradients. *Global Ecology and Biogeography*, 18(4), 437–449. <https://doi.org/10.1111/j.1466-8238.2009.00451.x>
- Osorio-Olvera, L., Yáñez-Arenas, C., Martínez-Meyer, E., & Peterson, A. T. (2020). Relationships between population densities and niche-centroid distances in North American birds. *Ecology Letters*, 23(3), 555–564. <https://doi.org/10.1111/ele.13453>
- O'sullivan, O. S., Heskell, M. A., Reich, P. B., Tjoelker, M. G., Weerasinghe, L. K., Penillard, A., Zhu, L., Egerton, J. J. G., Bloomfield, K. J., Creek, D., Bahar, N. H. A., Griffin, K. L., Hurrey, V., Meir, P., Turnbull, M. H., & Atkin, O. K. (2017). Thermal limits of leaf metabolism across biomes. *Global Change Biology*, 23(1), 209–223. <https://doi.org/10.1111/gcb.13477>
- Parnesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, 37, 637–669. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110100>
- Parnesan, C., & Hanley, M. E. (2015). Plants and climate change: Complexities and surprises. *Annals of Botany*, 116(6), 849–864. <https://doi.org/10.1093/aob/mcv169>
- Pearman, P. B., Randin, C. F., Broennimann, O., Vittoz, P., van der Knaap, W. O., Engler, R., Le Lay, G., Zimmermann, N. E., & Guisan, A. (2008). Prediction of plant species distributions across six millenia. *Ecology Letters*, 11(4), 357–369. <https://doi.org/10.1111/j.1461-0248.2007.01150.x>
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., ... Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61, 167–234. <https://doi.org/10.1071/BT12225>
- Peterson, A. T. (2011). Ecological niche conservatism: A time-structured review of evidence. *Journal of Biogeography*, 38, 817–827. <https://doi.org/10.1111/j.1365-2699.2010.02456.x>
- Pincebourde, S., & Casas, J. (2019). Narrow safety margin in the phyllosphere during thermal extremes. *Proceedings of the National Academy of Sciences of the United States of America*, 116, 5588–5596. <https://doi.org/10.1073/pnas.1815828116>
- Potter, K. A., Arthur Woods, H., & Pincebourde, S. (2013). Microclimatic challenges in global change biology. *Global Change Biology*, 19(10), 2932–2939. <https://doi.org/10.1111/gcb.12257>
- Salzer, M. W., Hughes, M. K., Bunn, A. G., & Kipfmüller, K. F. (2009). Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. *Proceedings of the National Academy of Sciences of the United States of America*, 106(48), 20348–20353. <https://doi.org/10.1073/pnas.0903029106>
- Sanczuk, P., De Lombaerde, E., Haesen, S., Van Meerbeek, K., Van der Veken, B., Hermy, M., Verheyen, K., Vangansbeke, P., & De Frenne, P. (2022). Species distribution models and a 60-year-old transplant experiment reveal inhibited forest plant range shifts under climate change. *Journal of Biogeography*, 49(3), 537–550. <https://doi.org/10.1111/jbi.14325>
- Santini, L., Pironon, S., Maiorano, L., & Thuiller, W. (2019). Addressing common pitfalls does not provide more support to geographical and ecological abundant-centre hypotheses. *Ecography*, 42(4), 696–705. <https://doi.org/10.1111/ecog.04027>
- Schenk, H. J., & Jackson, R. B. (2002). The global biogeography of roots. *Ecological Monographs*, 72, 311–328. [https://doi.org/10.1890/0012-9615\(2002\)072\[0311:TGBOR\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2002)072[0311:TGBOR]2.0.CO;2)
- Sexton, J. P., McIntyre, P. J., Angert, A. L., & Rice, K. J. (2009). Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics*, 40(1), 415–436. <https://doi.org/10.1146/annurev.ecolsys.110308.120317>
- Shay, J. E., Pennington, L. K., Mandussi Montiel-Molina, J. A., Toews, D. J., Hendrickson, B. T., & Sexton, J. P. (2021). Rules of plant species ranges: Applications for conservation strategies. *Frontiers in Ecology and Evolution*, 9, 700962. <https://doi.org/10.3389/fevo.2021.700962>
- Slot, M., Cala, D., Aranda, J., Virgo, A., Michaletz, S. T., & Winter, K. (2021). Leaf heat tolerance of 147 tropical forest species varies with elevation and leaf functional traits, but not with phylogeny. *Plant, Cell & Environment*, 44(7), 2414–2427. <https://doi.org/10.1111/pce.14060>
- Soberón, J., & Arroyo-Peña, B. (2017). Are fundamental niches larger than the realized? Testing a 50-year-old prediction by Hutchinson.

- PLoS One, 12(4), e0175138. <https://doi.org/10.1371/journal.pone.0175138>
- Soudzilovskaia, N. A., Vaessen, S., Barcelo, M., He, J., Rahimlou, S., Abarenkov, K., Brundrett, M. C., Gomes, S. I. F., Merckx, V., & Tedersoo, L. (2020). FungalRoot: Global online database of plant mycorrhizal associations. *New Phytologist*, 227(3), 955–966. <https://doi.org/10.1111/nph.16569>
- Stahl, U., Reu, B., & Wirth, C. (2014). Predicting species' range limits from functional traits for the tree flora of North America. *Proceedings of the National Academy of Sciences of the United States of America*, 111(38), 13739–13744. <https://doi.org/10.1073/pnas.1300673111>
- Sunday, J. M., Bates, A. E., Kearney, M. R., Colwell, R. K., Dulvy, N. K., Longino, J. T., & Huey, R. B. (2014). Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences of the United States of America*, 111(15), 5610–5615. <https://doi.org/10.1073/pnas.1316145111>
- Urban, M. C. (2015). Accelerating extinction risk from climate change. *Science*, 348(6234), 571–573. <https://doi.org/10.1126/science.aaa4984>
- Van Bogaert, R., Haneca, K., Hoogesteger, J., Jonasson, C., De Dapper, M., & Callaghan, T. V. (2011). A century of tree line changes in sub-Arctic Sweden shows local and regional variability and only a minor influence of 20th century climate warming. *Journal of Biogeography*, 38(5), 907–921. <https://doi.org/10.1111/j.1365-2699.2010.02453.x>
- Vangansbeke, P., Máliš, F., Hédli, R., Chudomelová, M., Vild, O., Wulf, M., Jahn, U., Welk, E., Rodríguez-Sánchez, F., & De Frenne, P. (2021). ClimPlant: Realized climatic niches of vascular plants in European forest understoreys. *Global Ecology and Biogeography*, 30(6), 1183–1190. <https://doi.org/10.1111/geb.13303>
- Vangansbeke, P., Sanczuk, P., Govaert, S., De Lombaerde, E., & De Frenne, P. (2022). Negative effects of winter and spring warming on the regeneration of forest spring geophytes. *Plant Biology*, 24(6), 950–959. <https://doi.org/10.1111/plb.13443>
- Verheyen, K., Adriaenssens, S., Gruwez, R., Michalczyk, I. M., Ward, L. K., Rosseel, Y., Van den Broeck, A., & García, D. (2009). *Juniperus communis*: Victim of the combined action of climate warming and nitrogen deposition? *Plant Biology*, 11(Suppl. 1), 49–59. <https://doi.org/10.1111/j.1438-8677.2009.00214.x>
- Verheyen, K., Honnay, O., Motzkin, G., Hermy, M., & Foster, D. R. (2003). Response of forest plant species to land-use change: A life-history trait-based approach. *Journal of Ecology*, 91, 563–577.
- von Arx, G., Dobbertin, M., & Rebetez, M. (2012). Spatio-temporal effects of forest canopy on understory microclimate in a long-term experiment in Switzerland. *Agricultural and Forest Meteorology*, 166–167, 144–155. <https://doi.org/10.1016/j.agrformet.2012.07.018>
- Warren, R., Price, J., VanDerWal, J., Cornelius, S., & Sohl, H. (2018). The implications of the United Nations Paris Agreement on climate change for globally significant biodiversity areas. *Climatic Change*, 147, 395–409. <https://doi.org/10.1007/s10584-018-2158-6>
- Webb, T. J., Lines, A., & Howarth, L. M. (2020). Occupancy-derived thermal affinities reflect known physiological thermal limits of marine species. *Ecology and Evolution*, 10, 7050–7061. <https://doi.org/10.1002/ece3.6407>
- Wei, L., Sanczuk, P., De Pauw, K., Mercedes Caron, M., Selvi, F., Hedwall, P.-O., Brunet, J., Cousins, S., Plue, J., Spicher, F., Gasperini, C., Iacopetti, G., Orczewska, A., Uria-Diez, J., Lenoir, J., Vangansbeke, P., & De Frenne, P. (2023). Data from: Predicting forest plant responses to climate change based on species' thermal safety margins relative to their warm limits. *Figshare*. <https://doi.org/10.6084/m9.figshare.23055236>
- Wild, J., Kopecký, M., Macek, M., Šanda, M., Jankovec, J., & Haase, T. (2019). Climate at ecologically relevant scales: A new temperature and soil moisture logger for long-term microclimate measurement. *Agricultural and Forest Meteorology*, 268, 40–47. <https://doi.org/10.1016/j.agrformet.2018.12.018>
- Wood, S. N. (2017). *Generalized additive models: An introduction with R*. CRC Press.
- Zellweger, F., Coomes, D., Lenoir, J., Depauw, L., Maes, S. L., Wulf, M., Kirby, K. J., Brunet, J., Kopecký, M., Máliš, F., & Schmidt, W. (2019). Seasonal drivers of understorey temperature buffering in temperate deciduous forests across Europe. *Global Ecology and Biogeography*, 28(12), 1774–1786. <https://doi.org/10.1111/geb.12991>
- Zellweger, F., De Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-Römermann, M., Baeten, L., Hédli, R., Berki, I., Brunet, J., Van Calster, H., Chudomelová, M., Decocq, G., Dirnböck, T., Durak, T., Heinken, T., Jaroszewicz, B., Kopecký, M., Máliš, F., ... Coomes, D. (2020). Forest microclimate dynamics drive plant responses to warming. *Science*, 368(6492), 772–775. <https://doi.org/10.1126/science.aba6880>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Wei, L., Sanczuk, P., De Pauw, K., Caron, M. M., Selvi, F., Hedwall, P.-O., Brunet, J., Cousins, S. A. O., Plue, J., Spicher, F., Gasperini, C., Iacopetti, G., Orczewska, A., Uria-Diez, J., Lenoir, J., Vangansbeke, P., & De Frenne, P. (2023). Using warming tolerances to predict understory plant responses to climate change. *Global Change Biology*, 30, e17064. <https://doi.org/10.1111/gcb.17064>