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RESEARCH ARTICLE

Ecological indicator values of understorey plants perform poorly to infer forest microclimate temperature

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Abstract

Question: Ecological indicator values (EIVs) reflect species' optimal conditions on an environmental gradient, such as temperature. Averaged over a community, they are used to quantify thermophilization stemming from climate change, i.e. the reshuffling of communities toward more warm-adapted species. In forests, understorey plant communities do not keep up with global warming and accumulate a climatic debt. Although the causes are still debated, this thermal lag may be partly explained by forest microclimate buffering. For the first time, we test whether community means of EIVs are able to capture microclimate (here, under forest canopies) temperature across, or also within forests.

Location: 157 forest plots across three French deciduous forests covering a large macroclimatic gradient.

Methods: To assess whether EIVs can be used to infer the mean and range of microclimate temperature in forests, we measured understorey air temperature for ca. 1 year (10 months) with sensors located 1 m above the ground. We surveyed bryophytes and vascular plants within 400-m² plots, and computed floristic temperature from ordinal-scale EIVs (Ellenberg, Julve) and degree-scale EIVs (ClimPlant, Bryophytes of Europe Traits) for both temperature and continentality, i.e. temperature annual range. Finally, we fitted linear models to assess whether EIVs could explain the mean and range of microclimate temperature in forests.

Results: Vascular plant and bryophyte communities successfully reflected differences in mean annual temperatures across forests but largely failed to do so for microclimate variation within forests. Bryophytes did not perform better than vascular plants to infer microclimate conditions. The annual range of microclimate temperatures was poorly associated with ordinal-scale EIVs for continentality but was positively correlated with degree-scale EIVs for annual range within lowland forests, especially for vascular plant communities.

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Conclusion: Overall, the capabilities of EIVs to infer microclimate was inconsistent. Refined EIVs for temperature are needed to capture forest microclimates experienced by understorey species.

KEYWORDS

bryophytes, buffering, community temperature index, ecological indicator values, forest flora, global warming, microclimate, plant community, thermophilization, vascular plants

1 | INTRODUCTION

Plant species cannot grow everywhere: their presence reflects the environment, and evidences some of its abiotic properties. This knowledge has been used for millennia by humankind to interpret pedoclimatic conditions, for instance, to spot humid or dry, rich or poor soils for agriculture and forestry purposes. Ecologists have formalized this knowledge and quantified it into “ecological indicator values” (EIVs; Ellenberg, 1974), used to reflect the environmental conditions associated with a given species, indicating its optimum within its realized niche (Diekmann, 2003). Averaged over a floristic community, with species sometimes weighted by their abundance, they allow ecologists to infer, or “bioindicate”, environmental conditions such as nutrient availability or temperature.

Heinz Ellenberg was the first to design a list of EIVs for the main plant species of Western Central Europe, more particularly Germany (Ellenberg, 1974). His EIVs, in an ordinal scale from 1 to 9, have later been adapted for other geographic situations. For example, Julve adapted them for France (Julve, 2015). Ellenberg's EIVs and their derivatives are still actively used by ecologists, frequently in forest systems (Zolotova et al., 2023). These ordinal-scale EIVs from Ellenberg or Julve are mainly based on expert knowledge and field observations, whereas new sets of “biogeographic” EIVs are statistically derived from spatial occurrences and distribution maps covering large spatial extents, such as EcoPlant (Gégout et al., 2005) and ClimPlant (Vangansbeke et al., 2021). Contrary to the original ordinal-scale EIVs, these new EIVs are on a continuous scale, usually in degrees Celsius for temperature.

Plant EIVs are widely used as proxies for environmental conditions, and to infer spatial and temporal vegetation dynamics (Diekmann, 2003; Pinto et al., 2016; Hutsemékers et al., 2023). Plant EIVs for temperature can be averaged across species within a given plant community to obtain a community mean of temperature EIV, or “floristic temperature” (also called the community temperature index; Richard et al., 2021). In the context of global warming, this floristic temperature is used to evaluate thermophilization, i.e. the replacement of cold-tolerant or mesophilic species by more warm-adapted species (Lenoir et al., 2010; De Frenne et al., 2013; Martin et al., 2019). Ecosystems that experienced more warming have already responded with increased thermophilization (Gottfried et al., 2012; Pacheco-Riaño et al., 2023). Although thermophilization has taken place over the past decades in many plant communities, it often has not kept pace with climate change, resulting in a thermal

“lag” or “climatic debt”, which is especially pronounced in lowland forest understories (Bertrand et al., 2011; Lenoir et al., 2022; but see Pacheco-Riaño et al., 2023). This thermal lag may be driven by species persistence and tolerance to thermal and water stress (Bertrand et al., 2016), but is often thought to be partly determined by the buffering capacity of forest microclimates (De Frenne et al., 2013; Zellweger et al., 2020; Richard et al., 2021). Here, we define microclimate as the proximal climatic conditions to which organisms are exposed, whereas macroclimate refers to large-scale and free-air conditions, as measured by standardized weather stations (De Frenne & Verheyen, 2016; Bramer et al., 2018). Under the canopy of most forests, buffered temperature conditions are recorded with a reduced range of temperatures compared with macroclimate temperatures, i.e. lower maxima and higher minima (De Frenne et al., 2021). This buffering effect in forests is caused by two main mechanisms during the day: interception of solar radiation and transpiration by trees (De Frenne et al., 2021). At night, canopies slow the return of infrared radiation to the atmosphere. Forests may, therefore, hold the response of understorey plant communities to climate change, at least as long as the canopy stays closed (Lenoir et al., 2010; Zellweger et al., 2020; Christiansen et al., 2022). Forest cover also has a cooling effect on understorey floristic temperatures at a landscape scale (Borderieux et al., 2023).

Plant EIVs have been confronted with corresponding field measurements for light, soil reaction, moisture and nitrogen (Diekmann, 2003; Szymura et al., 2014; Depauw et al., 2021), but to our knowledge, not yet for temperatures inside forests. Therefore, it is unclear whether EIVs for temperature mean and range are solely able to reflect macroclimate (i.e. differences across different forests) or also microclimate gradients (i.e. differences within one forest). The question of how microclimates track macroclimate change remains open (De Frenne et al., 2021). If EIVs could be linked to microclimate temperature from sensors placed directly in the habitat of interest, we could use floristic surveys in forests to model microclimate and microclimate warming. We might even reconstruct microclimates of the past from historical floristic surveys, using transfer functions (Bertrand et al., 2016; Pacheco-Riaño et al., 2023) similarly to paleoecological studies (Paus, 2013). The big advantage would be that vegetation inventories are abundant and may date back a century; contrary to the relatively recent and scarce in situ temperature measurements in forests.

Amid the understorey flora, bryophytes are more cryptic and harder to identify than their vascular relatives, and are therefore



TABLE 1 Characteristics of the three studied forests, from ONF (National Forest Office) data with a weather station located near each of the three forests (Figure 1).

	Aigoual	Blois	Mormal
Surface (ha)	2,469 ^a	2,749	9,137
Dominant trees	<i>Fagus sylvatica</i>	<i>Quercus petraea</i>	<i>Quercus robur</i> / <i>Fagus sylvatica</i>
Climate influences	Mountainous and Mediterranean	Oceanic	Oceanic and continental
Elevation (m)	829–1,565	94–141	140–175
Tabsolute min (C°)	−14.8	−12.0	−15.1
Tmean min (C°)	3.7	7.1	5.7
T mean (C°)	6.9	11.3	9.7
Tmean max (C°)	11.1	16.4	14.3
Tabsolute max (C°)	33.8	40.1	36.7
Annual rainfall (mm)	1,853	744	930
Number of rainy days (>1 mm) per year	143	179	211

Note: Climatic parameters were averaged over the period 1996–2004.

Abbreviation: T, Temperature.

^aThe complete surface of Aigoual forest is 16,123 ha; but we focused on a central area of about 2,000 ha. The surface and range of elevation presented in this table is for this study area, not the complete forest.

much less studied (Kiebacher et al., 2023; Kutnar et al., 2023). However, they may be better indicators of microclimates than vascular plants for several reasons. First, bryophytes are much smaller than vascular plants. Although large species require a relatively large “physical space niche”, so that their realized niche may be accurately described by environmental factors at resolutions of tens to hundreds of meters, smaller species occupy smaller physical spaces that are characterized by specific micro-environmental features (Aarssen et al., 2006; Potter et al., 2013). Second, their spores are often less limited by dispersal than vascular seeds (Vanderpoorten et al., 2019), which may translate into a better capacity to bioindicate environmental conditions favorable to their development. Third, bryophytes are poikilohydric, i.e. their water status completely depends on their environment and they directly rely on rainfall for water uptake, rendering them especially sensitive to subtle variations in climatic conditions (Fenton & Frego, 2005; Mills & Macdonald, 2005; He et al., 2016). Finally, bryophytes are highly sensitive to warm and extreme microclimate temperatures, and may thus represent valuable monitors of microclimate (Hylander et al., 2002). Temperate bryophyte species, for instance, typically die when exposed to temperatures above 30°C (Furness & Grime, 1982), making them better indicators of global warming than vascular plants (Becker Scarpitta et al., 2017; Kiebacher et al., 2023).

With this study, we aimed to compare temperature records from microclimate sensors against temperature estimates from bioindication, and thus assess whether plant EIVs can be used to infer microclimate temperature in the understory of temperate deciduous forests. We considered both mean annual temperature and temperature annual range because the latter might be more relevant to qualify forest microclimate buffering than mean conditions, over a 10-month period (which we, for simplicity, hereafter refer to as annual). We compared the predictive power of two types of EIVs—ordinal-scale vs degree-scale EIVs—for both vascular plants

and bryophytes and assessed whether local heterogeneities within the survey area (rocks, humid area or compacted ground) may blur bioindication. We hypothesize that: (a) plant EIVs are able to characterize the mean and range of temperature variation across forest sites (located in different macroclimates) as well as within forests (microclimates); (b) bryophytes are better indicators of microclimate temperature than vascular plants; and (c) removing species associated with a local heterogeneity will marginally improve the predictive power of plant EIVs on microclimate temperature.

2 | METHODS

2.1 | Study area and sampling design

The study focuses on three state forests in France: Mormal, Blois and Aigoual. These three forests belong to the RENECOFOR national network of long-term monitoring of forest ecosystems (onf.fr/renecofor; Ulrich, 1995) and were chosen because of their contrasting macroclimate and dominant tree species, and because a long-term weather station was installed in open conditions nearby, or within a clearing inside the focal forests (Table 1; Figure 1). Blois is dominated by sessile oak (*Quercus petraea*), Mormal by pedunculate oak (*Quercus robur*) and beech (*Fagus sylvatica*). Both are lowland forests, whereas Aigoual is a mountainous forest dominated by beech. The three forests have poor, acidic soils. All three are managed by the National Forest Office (ONF) as even-aged forest stands, except for some stands in Aigoual which are not managed for reasons of accessibility or conservation.

We surveyed a total of 157 plots: 53 in Aigoual, 52 in Blois and 52 in Mormal (Figure 1; Appendix S1). Each plot consists of a 400-m² surface of vegetation survey, centered on a microclimate sensor. Plots were sampled alongside a forest cover and structure

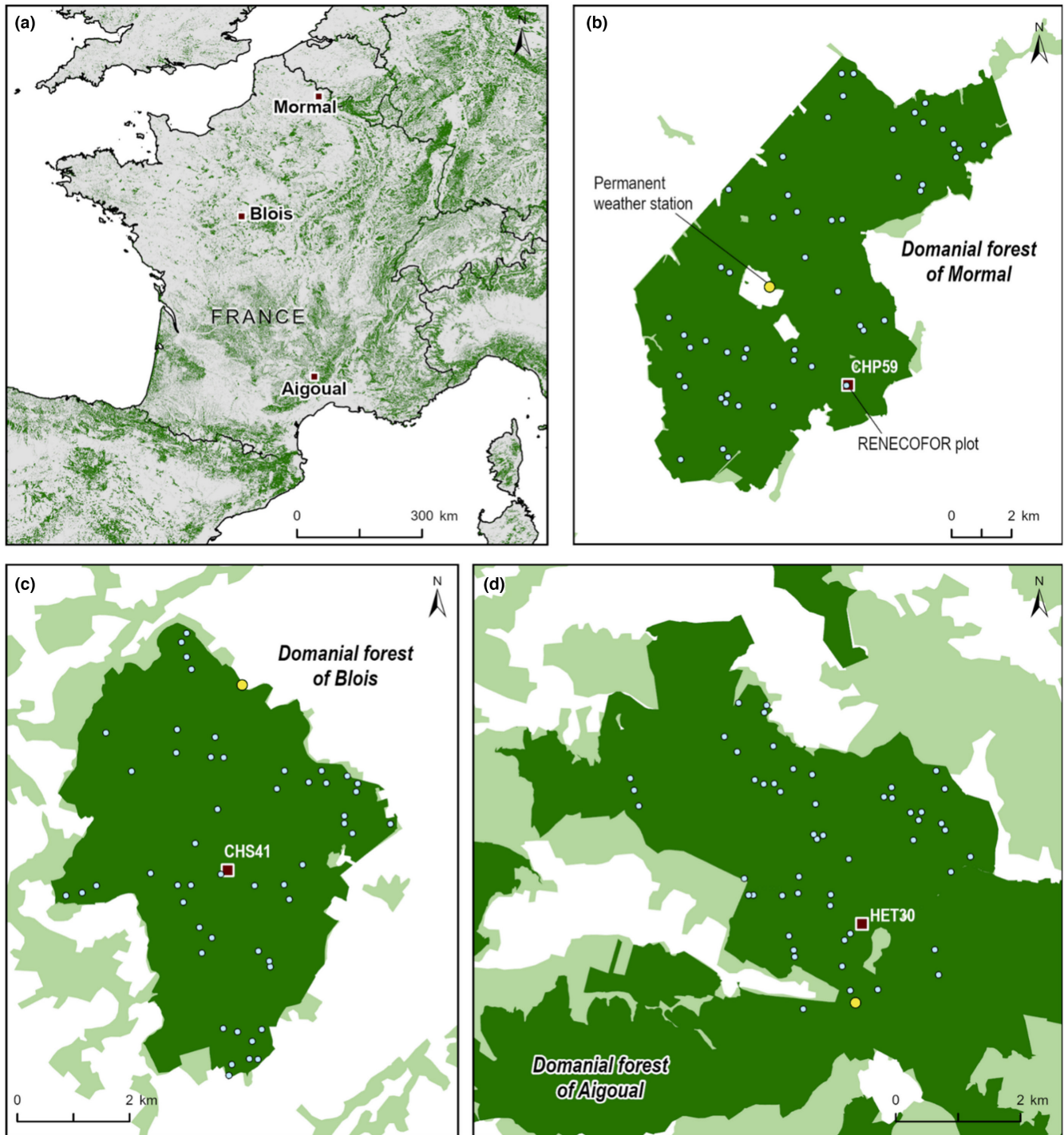


FIGURE 1 Sampling design, with the three forests located in France at contrasting latitudes. (a) Forest cover is outlined in green (Corine Land Cover 2018, <https://land.copernicus.eu/pan-european/corine-land-cover>), and darker green for the three studied forests: Mormal (b), Blois (c) and Aigoual (d). The blue and yellow dots represent study plots, the yellow dots in each forest being equipped with a weather station as well as microclimate sensors.

gradient, from very dense forests to open areas, in clearings or after tree harvest, and from young regeneration stages to mature forests (Appendix S1): thickets ($n=15$), saplings ($n=14$), pole stands ($n=24$), young stands ($n=22$), adult stands ($n=39$), old stands ($n=16$), irregular stands ($n=7$), seed trees ($n=3$), open ($n=5$), isolated trees ($n=4$) and coppices ($n=8$).

2.2 | Temperature measurements

Hourly microclimate temperatures were measured using Onset® HOBO® Pendant data loggers UA-001-64, which contain commonly used sensors in ecological studies (Bramer et al., 2018) with a manufacturer-reported accuracy of $\pm 0.53^{\circ}\text{C}$ from 0 to

50°C, and a resolution of 0.14°C at 25°C. The sensor represented the center of each of our 157 plots. Each sensor was attached on the north side of a tree trunk (George et al., 2015), at 1 m above ground level. Sensors were hung inside homemade white PVC shields, measuring 10 cm × 15 cm (Zellweger et al., 2019; Gril et al., 2023), aiming to minimize overheating from direct radiation. To compare microclimates across forests, we selected a common time of continuous measurements across the three forests representing a 10-month period, from 9 July 2021 to 9 May 2022. Covering an entire year was not possible because of some sensors malfunctioning in the field. For the sake of simplicity, this period is hereafter referred to as “annual”, although the whole of June and parts of May and July are lacking. For each sensor, we calculated the mean annual temperature conditions experienced by plants in the forest understorey. We then computed statistics of the daily minimum and maximum temperatures, and derived the 5th and 95th percentiles over the whole period so that we could compute the microclimate temperature quasi-annual range.

As to macroclimate, we obtained hourly temperature records from three local weather stations operated by RENECOFOR, located in open environments near each studied forest (Figure 1). Macroclimate temperatures were measured in standardized radiation shields, at a height of 1.5 m. We used this macroclimate temperature for two reasons: (a) to check whether our microclimate gradient across the three studied forests corresponds to a macroclimate gradient (Figure 2); and (b) to compare the mean macroclimate temperature for 2021, which covers most of the period we focus on, with the mean temperature for previous years (1979–2013), to control for the temporal mismatch between our measurements and the timescale used to assess some of our EIVs (Appendix S2). Based

on the distribution of yearly mean macroclimate temperatures, the year 2021 had a temperature very close to the mean macroclimatic records from 1979 to 2013 in each forest.

2.3 | Floristic inventories

Floristic surveys were carried out on 400-m² circular plots (equivalent to a radius of 11.3 m) around each temperature sensor, a commonly used and adequate surface for bioindication with EIVs in forests (Otýpková, 2009; Pinto et al., 2016). Species occurrences were recorded from mid-May to the beginning of July 2021, so that the three studied forests were sampled during approximately the same phenological stage: Blois first, then Mormal and finally Aigoual. Both bryophytes and herbaceous vascular plants, including woody plants lower than 50 cm, were identified at species level (species identified at genus or family level were not considered in the current analysis). All bryophytes were collected and identifications were checked in the laboratory. We recorded whenever a species occurred only on a local heterogeneity of the surveyed vegetation plot, either on a rock, a humid area (ditch, stream or puddle) or an area of compacted ground (such as skid trails and silvicultural paths, ancient or in activity).

2.4 | Floristic temperatures

Floristic temperatures were computed separately for vascular plants and bryophytes, using ordinal-scale and degree-scale EIVs representing either mean annual temperature or temperature annual range (see Table 2 for a list of EIVs).

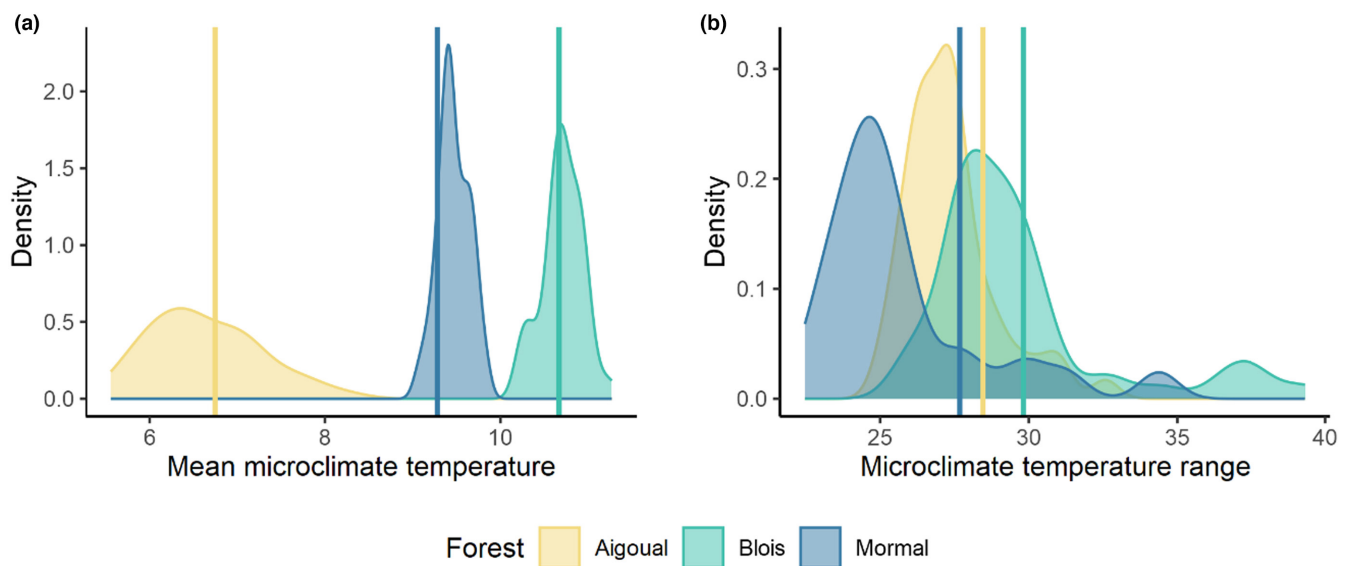


FIGURE 2 Distribution of mean annual temperature (a) and temperature annual range (b) in °C, recorded by microclimate sensors deployed between 9 July 2021 and 9 May 2022 across three forests in France (Aigoual, $n = 53$; Blois, $n = 52$; Mormal, $n = 52$). The vertical line depicts the equivalent macroclimate values from a local weather station.

TABLE 2 List of plant ecological indicator values (EIVs) used as predictors of microclimate temperature in this study, along with the database and source from which they were extracted.

Group	EIV	Description	Database	Source
Vascular plants	T_mean_ord_vasc	Julve's temperature T	Baseflore	Julve (2015)
	T_range_ord_vasc	Julve's continentality K		
	T_mean_deg_vasc	WorldClim's T mean	ClimPlant	Vangansbeke et al. (2021)
	T_range_deg_vasc	WorldClim's T range		
Bryophytes	T_mean_ord_bryo	Ellenberg's temperature T	BET	van Zuijlen et al. (2023)
	T_range_ord_bryo	Ellenberg's continentality K		
	T_mean_deg_bryo	CHELSA's T mean		
	T_range_deg_bryo	CHELSA's T range		

Note: The names of EIVs we use in this study indicate whether they represent temperature mean or range, are in ordinal or degree scale, and apply to vascular plants or bryophytes.

Abbreviation: T, Temperature.

2.4.1 | Vascular plants

As ordinal-scale EIVs for vascular plants, we used Julve's temperature and continentality indices, from the French Baseflore database (Julve, 2015). For the mean temperature index (hereafter T_mean_ord_vasc), each species is attributed an "Ellenberg-like" value (Appendix S3), ranging from 1 (alpine and high-altitude plants typically found at a mean annual temperature of around 0°C) to 9 (thermophilous Mediterranean to sub-desertic plants typically found at a mean annual temperature of around 18°C). Similarly, the continentality index (hereafter T_range_ord_vasc) ranges from 1 (marine to maritime conditions corresponding to a temperature annual range around 8°C) to 9 (hypercontinental conditions corresponding to a temperature annual range around 40°C).

To compare with degree-scale EIVs, we used the ClimPlant database (Vangansbeke et al., 2021). Temperature preferences were inferred by Vangansbeke et al. using atlas distribution maps related to a macroclimatic grid, in this case WorldClim's (Fick & Hijmans, 2017). Mean values over the 1970–2000 period were used. Among available temperature variables in the ClimPlant database, we selected mean annual temperature (hereafter T_mean_deg_vasc), and minimum and maximum temperatures, for which we used the 5th and 95th percentile to calculate temperature annual range (hereafter T_range_deg_vasc).

2.4.2 | Bryophytes

For bryophytes, we used the new Bryophytes of Europe Traits (BET) database (van Zuijlen et al., 2023), with ordinal-scale and degree-scale EIVs matching the ones used above for vascular plants. The BET database includes EIVs adapted from Ellenberg, and subsequently included in databases such as BryForTrait (Bernhardt-Römermann et al., 2018), for mean annual temperature (ranging from 1 for cold alpine-nival conditions to 9 for extreme warmth conditions; hereafter T_mean_ord_bryo) and for continentality (ranging from 1 for extreme oceanic to 9 for extreme continental; hereafter

T_range_ord_bryo). It also includes statistic-based values for mean annual temperature (BIO1) and the temperature annual range (BIO7) in degrees Celsius, built from IUCN occurrence data overlaid on CHELSA macroclimatic raster layers over the 1979–2013 period (Karger et al., 2017). These were respectively calculated as the mean of daily mean air temperatures over 1 year (hereafter T_mean_deg_bryo), and the difference between the maximum temperature of the warmest month and the minimum temperature of the coldest month (hereafter T_range_deg_bryo).

2.4.3 | Computation of floristic temperature

Across our three forests and 157 plots, we recorded 3,769 occurrences of 338 species of vascular plants and 2,181 occurrences of 145 species of bryophytes. The average number of species (after excluding genus and family-level recordings) per plot was 21.0 for vascular plants and 12.2 for bryophytes. All analyses were performed with R (version 4.2.2; R Core Team, R Foundation for Statistical Computing, Vienna, AT).

Our set of EIVs for T_mean_ord_vasc and T_range_ord_vasc covered almost all vascular plant occurrence records (97.3%) with one exception, the "group of species" *Rubus fruticosus*. As for T_mean_deg_vasc and T_range_deg_vasc, they covered 94.5% of vascular plant occurrence records. EIVs for T_mean_ord_bryo covered 74.1% of bryophyte occurrence records and 90.6% for T_range_ord_bryo, whereas T_mean_deg_bryo and T_range_deg_bryo, covered 99.2% of bryophyte occurrence records.

In each plot, we computed floristic temperatures based on species occurrences and their associated EIVs. Although averaging ordinal values has been criticized, it is the usual way of dealing with EIVs and is recommended by many authors to obtain surrogates for measured environmental variables (Diekmann, 2003). Floristic temperatures were calculated as simple arithmetic means of the EIVs (Käfer & Witte, 2004). We also calculated floristic temperatures weighted by abundance for vascular species, but similarly to Szymura et al. (2014), the resulting correlations were lower than when based

on occurrences only, and are therefore not included in the main text (see Appendix S4 for the methods and results using weighted floristic temperatures). The same procedure was repeated, but excluding the occurrences of species that were restricted to local ground heterogeneities (rock, humid area or compacted ground, see Appendix S5 for results). We used the function “functcomp” from the *FD* package to compute floristic temperatures (R Core Team, R Foundation for Statistical Computing, Vienna, AT) (Laliberté et al., 2022).

2.5 | Statistical analyses

The correlation between temperature values measured by microclimate sensors and floristic temperature was quantified using simple linear models and linear mixed-effects models. We considered either mean annual temperature or temperature annual range, measured by microclimate sensors, as the response variable. Given the nature of the response variables, Gaussian distribution was chosen using the functions “descdist” and “fitdist” of the *fitdistrplus* package (Delignette-Muller & Dutang, 2015). We independently ran models for each taxonomic group (bryophytes or vascular plants) and each EIV group (ordinal-scale or degree-scale), either: (a) within each forest separately, or (b) across all three forests together. For global models across all three forests, we used both a simple linear model and a mixed-effects model with the forest site as a random intercept effect, and floristic temperature as the fixed effect. The mixed-effects modeling approach allowed us to compare the variability explained by the fixed effect (floristic temperature) alone vs fixed and random effects together. Although a mixed-effects model accounts for the nested structure of our data, we were especially interested in the amount of microclimate variability that could be explained by floristic temperature, within and across sites. Therefore, these two types of models give us complementary information. Linear mixed-effects models were fitted using the “lmer” function from the *lme4* package (Bates et al., 2015). Residuals of all models were visually checked for normality and homoscedasticity, using the “plot_model” function from the *sjPlot* package (Lüdtke, 2021). In the figures and appendices, asterisks indicate statistically significant results based on *p*-values: ns, not significant; **p* < 0.05; ***p* < 0.01; and ****p* < 0.001 (for the actual *p*-values, see Appendix S6).

3 | RESULTS

Between 9 July 2021 and 9 May 2022, hourly microclimate temperatures ranged from −8.6 to 40.8°C in Blois forest, from −8.7 to 34.5°C in Mormal forest, and from −9.4 to 32.0°C in Aigoual forest. Over this entire period, the mean annual microclimate temperature ranged from 10.2 to 11.3°C (mean ± SD: 10.7 ± 0.2°C) in Blois, from 9.1 to 9.8°C (9.5 ± 0.2°C) in Mormal, and from 5.6 to 8.3°C (6.6 ± 0.6°C) in Aigoual (Figure 2a). The annual range of microclimate temperature ranged from 25.9 to 39.3°C (29.7 ± 3.1°C) in

Blois, from 22.5 to 34.4°C (25.7 ± 2.7°C) in Mormal, and from 25.0 to 32.6°C (27.4 ± 1.5°C) in Aigoual (Figure 2b). Interestingly, in Blois and Mormal, the measured range was thus larger within than between forests. The differences in microclimates across forests can be related to a macroclimate gradient, as shown by weather station records over the same period, especially for the mean annual temperature (Figure 2).

Mixed-effects models across all three forests explained the vast majority of microclimate temperature by the random intercept term, i.e. the forest. The conditional R^2 (proportion of variance explained by both fixed and random effects) ranged between 93.9% and 94.9%, whereas the marginal R^2 (proportion of variance explained by the fixed effect only, i.e. floristic temperature) only reached a maximum of 2.6% (Appendix S6). This means that once we discriminate forests, floristic temperature does not bring much information to explain microclimate temperature.

We then focused on the outputs of simple linear models (see Appendix S6 for *p*-values). Along the entire latitudinal gradient covered by all three forests, the annual mean and range of temperature measured by microclimate sensors were significantly correlated with their respective floristic temperature, as inferred from vascular plant species composition (Figure 3). By contrast, the correlation was much lower or even non-significant when considered within each forest separately. Across all three forests, floristic $T_{\text{mean_ord_vasc}}$ and $T_{\text{mean_deg_vasc}}$ increased with mean annual microclimate temperature ($R^2=0.77$ and 0.50, respectively), as well as within Aigoual forest ($R^2=0.11$ and 0.08) (Figure 3a,b). Floristic $T_{\text{range_ord_vasc}}$ increased with annual range of microclimate temperature among forests ($R^2=0.10$), and decreased within Blois forest along with $T_{\text{range_deg_vasc}}$ ($R^2=0.18$ and 0.58 respectively). In Aigoual forest, floristic $T_{\text{range_ord_vasc}}$ decreased with increasing annual range of microclimate temperature ($R^2=0.14$), whereas in Mormal forest, floristic $T_{\text{range_deg_vasc}}$ increased ($R^2=0.41$; Figure 3c,d).

Similar to vascular plants, the mean and range value of microclimate temperature were significantly and positively correlated with bryophyte floristic temperature along the gradient covered by all three forests (except floristic $T_{\text{range_ord_bryo}}$), whereas the correlation was mostly lower or non-significant within each forest considered separately (Figure 4). Floristic $T_{\text{mean_ord_bryo}}$ and $T_{\text{mean_deg_bryo}}$ increased with increasing mean annual microclimate temperature among forests ($R^2=0.65$ and 0.42 respectively; Figure 4a,b). In Aigoual forest, the $T_{\text{range_ord_bryo}}$ increased with mean annual microclimate temperature ($R^2=0.21$). Floristic $T_{\text{range_deg_bryo}}$ had a very limited explanatory power on the annual range of microclimate temperature ($R^2=0.06$), whereas floristic $T_{\text{range_ord_bryo}}$ values did not explain any variation at all among forests. However, temperature annual range increased with floristic $T_{\text{range_ord_bryo}}$ and $T_{\text{range_deg_bryo}}$ within Mormal forest ($R^2=0.21$ and 0.23 respectively; Figure 4c,d).

Equivalent analyses were conducted on floristic temperatures calculated after removing occurrence records of vascular plants or bryophytes associated with local ground heterogeneities that may represent specific microhabitat conditions (rock, humid area

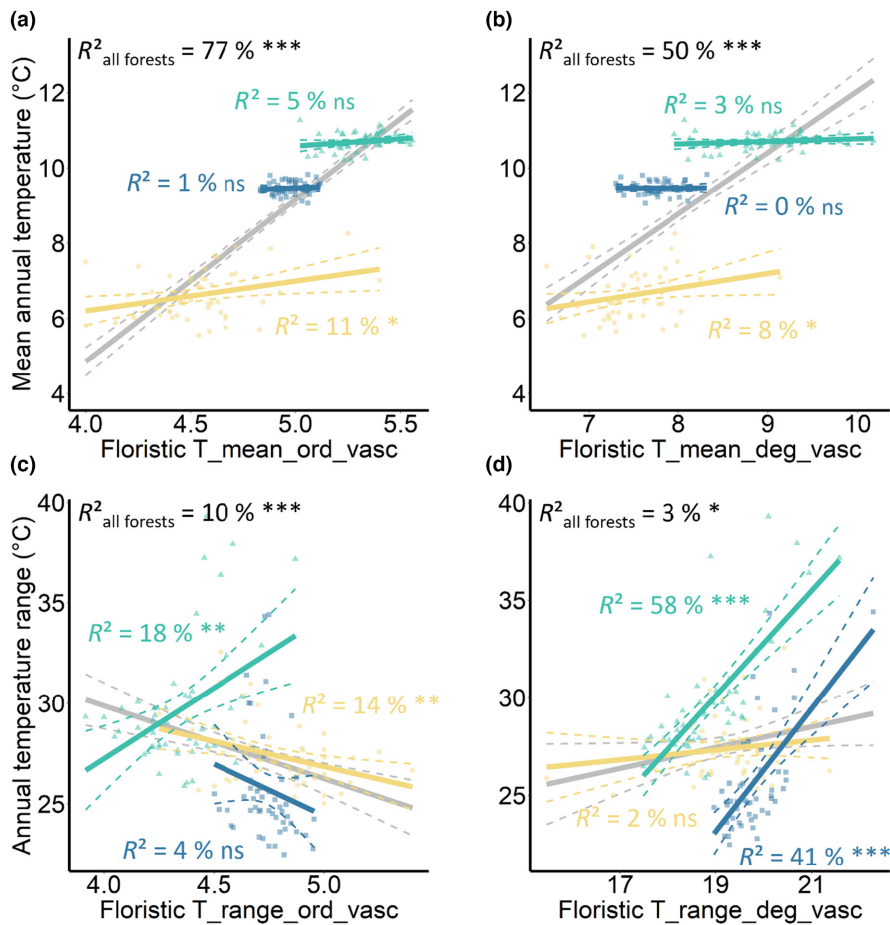


FIGURE 3 Correlations between measured microclimate temperature and vascular plant floristic temperature, for the annual mean (a, b) and range (c, d). R^2 values and significance are computed based on linear regressions for each forest separately (yellow: Aigoual; green: Blois; dark blue: Mormal). The global R^2 value is computed based on linear regression for all forests together (gray). Floristic temperatures are community means: T_{mean_ord_vasc} is the community mean of Julve's temperature, T_{range_ord_vasc} of Julve's continentality, T_{mean_deg_vasc} of WorldClim's T mean, and T_{range_deg_vasc} of WorldClim's T range. The source of each floristic temperature, either ordinal or degree-scale, is listed in Table 2.

or compacted ground; 17.3% of all records of vascular plants and 28.3% of bryophytes). The results remained the same or yielded slightly lower correlations when forests were considered separately (Appendix S5).

4 | DISCUSSION

4.1 | Floristic temperature does not capture microclimate temperature within forests

Unsurprisingly, and in accordance with previous studies (Marcenò & Guarino, 2015; Chytrý et al., 2018; Tichý et al., 2023), floristic temperature was positively correlated with the complete gradient of mean annual microclimate temperature across our three forests with contrasted macroclimates, even though we compared only three different sites in France. Ordinal-scale EIVs (Julve's or Ellenberg's T) performed better than degree-scale EIVs (from the ClimPlant or BET databases), for vascular plants and bryophytes alike, at capturing differences in microclimatic mean annual temperature among forests. Julve's EIVs are adapted to France, and Ellenberg's to a neighboring country, which might explain their better correlations compared with indices accounting for European-wide or global distributions.

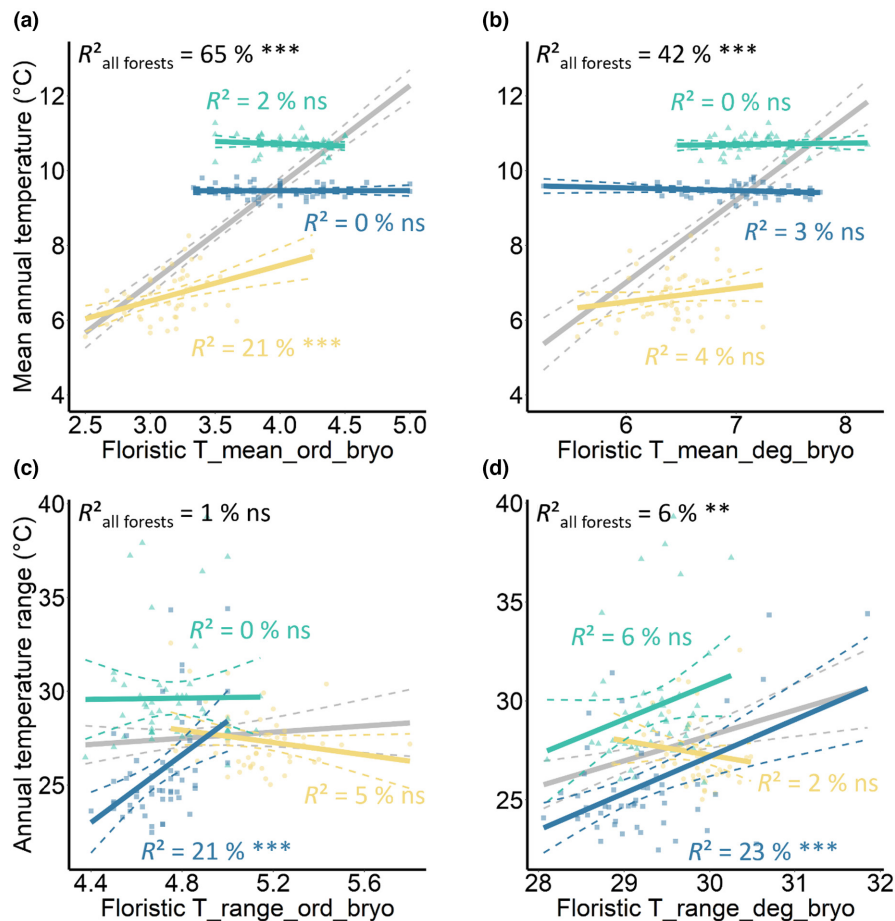
Consistent with our findings, although we used microclimate measurements, Tichý et al. (2023) recently standardized Ellenberg-like

temperature EIVs at a European scale, and they obtained an R^2 value of 46% by fitting a linear regression between temperature inferred from 364,104 vegetation surveys across Europe and their respective mean summer macroclimate temperature extracted from CHELSA (Karger et al., 2017). In addition, Chytrý et al. (2018) adapted Ellenberg's EIVs for temperature to the Czech flora and obtained a correlation value of 0.66 between floristic temperature and mean July temperature interpolated from weather stations. Interestingly, they purposely removed major microclimate effects by selecting plots in open areas away from trees, and with a slope less than 5% to minimize the effect of topography.

Importantly, and contrary to our first hypothesis, the correlations between floristic temperature and mean annual temperature conditions measured by microclimate sensors were very low, or even non-significant when considering the variation in mean annual microclimate temperatures observed within each of the three studied forests separately. Mixed-effects models also showed that floristic temperature did not improve the modeling of microclimate temperature, once we account for the forest. This suggests that temperature EIVs, either using ordinal scale or degree scale, are not good indices to infer microclimate variations within forests, but rather reflect differences across forests. This might have been expected, however, because temperature EIVs were originally based on macroclimate, not microclimate (De Frenne et al., 2013; Zellweger et al., 2020). Yet contrary to our results, two studies found an increase of floristic



FIGURE 4 Correlations between measured microclimate temperature and bryophyte floristic temperature, for the annual mean (a, b) and range (c, d). R^2 values and significance are computed based on linear regressions for each forest separately (yellow: Aigoual; green: Blois; dark blue: Mormal). Global R^2 value is computed based on linear regression for all forests together (gray). Floristic temperatures are community means: $T_{\text{mean_ord_bryo}}$ is the community mean of Ellenberg's temperature, $T_{\text{range_ord_bryo}}$ of Ellenberg's continentality, $T_{\text{mean_deg_bryo}}$ of CHELSA's T mean, and $T_{\text{range_deg_vasc}}$ of CHELSA's T range. The source of each ordinal or degree-scale floristic temperature is listed in Table 2.



temperature after clear-cutting management or storm-induced gaps within boreal and temperate forest canopies, perhaps because of a different sampling gradient of structure (Dietz et al., 2020; Christiansen et al., 2022).

Removing plants associated with a local heterogeneity within plots (humid area, compacted ground or rock), which we thought may have different microclimates altering the bioindication signal, did not improve the fit of regressions, either for bryophytes or for vascular plants. Also contrary to our expectations, bryophytes did not perform better than vascular plants as microclimate indicators, perhaps being related to even smaller scale variations in temperature and humidity close to the ground and within microhabitats than vascular plants (Kiebacher et al., 2023). There was one exception in Aigoual forest, where Ellenberg's temperature EIVs for bryophytes had a better relationship with mean microclimate temperature than the equivalent Julve's EIVs for vascular plants. This could be because of a higher diversity in bryophytes than in vascular plants in most of the plots in Aigoual forest. The relation for the mountainous plots in Aigoual generally diverged from Blois and Mormal, which could be explained by the fact that they differed not only by forest structure, but also in terms of topographic features such as slope and aspect, causing further topoclimate and microclimate complexities, as well as in the adiabatic lapse rate along elevation (Maclean et al., 2015).

To our knowledge, few studies have directly compared local temperature measurements from microclimate sensors with floristic

temperatures, and none have done so within gradients of forest microclimates. Gottfried et al. (2012) did correlate the floristic temperature (weighted by abundance) of a thermic vegetation indicator based on altitudinal ranks with temperature measured by sensors placed 10-cm deep in the soil, more specifically the mean of daily minimum temperatures of June. The global Spearman rho coefficient was 0.52, but varied widely between the different European mountain regions, from 0.89 to an insignificant correlation. However, the latter study did not focus on forest microclimate variations within a given macroclimate, and elevation would surely be the prime driver of their temperature variations, similar to the results we obtained for the Aigoual forest.

4.2 | Temperature range may be predicted by degree-scale EIVs within lowland forests

Mean annual temperature conditions are not as important as extreme temperatures for many understory species (Ashcroft & Gollan, 2012; Macek et al., 2019). A dense forest stand may have the same mean annual temperature as a more open forest stand nearby, or even an open meadow located next to the forest, although considerably more buffered against temperature extremes throughout the year; which is why we also tested the annual range of microclimate temperature.

Floristic temperature for annual temperature range had no (for bryophytes) to very low (for vascular plants) explanatory power on the observed variation in the annual measured range of microclimate temperature across the three forest sites. The correlation within each forest was also mostly low or non-significant, possibly because we only focused on a single (almost complete) year and not on a long-term average. In the mountainous region of the Aigoual forest, the low correlation may be due to the shorter gradient of temperature annual range. Fitting a model along a short gradient of environmental variation critically limits the strength of bioindication (Szymura et al., 2014). By contrast, a notable exception among these non-significant results, the annual range of microclimate temperature was highly correlated with floristic temperature within the two lowland forests of Blois and Mormal using degree-scale EIVs for vascular plants, whereas ordinal-scale EIVs had much lower and inconsistent predictive ability on the annual range of microclimate temperature.

Julve's or Ellenberg's ordinal-scale EIVs for continentality (K) have an equivocal meaning, because the concept of continentality not only integrates daily and seasonal ranges of temperatures, but also of precipitation and humidity. Continentality is less well-defined and less used than other EIVs (Berg et al., 2017). These ordinal-scale EIVs may be biased by an incomplete vision of their authors, although Ellenberg's or Julve's K and T EIVs rely not only on expert knowledge, but also on mapped distributions of species. Degree-scale, or "biogeographic" EIVs are not exempt from errors and may also be biased; for instance, a given species may be excluded by dispersal limitation, edaphic conditions or biotic factors from a climatically suitable area, which will then wrongly be considered as unsuitable. Therefore, fundamental climatic niches are usually wider than realized ones (Soberón & Arroyo-Peña, 2017; Sanczuk et al., 2022), which are the ones used to derive EIVs. However, our results on vascular plants demonstrate a clear, if not direct link between a degree-scale EIV and microclimate measurements of temperature annual range in lowland forests, which might open up new opportunities for quantifying the buffering effect in lowland forests using plant communities.

4.3 | Why can EIVs not predict forest microclimate temperatures?

Apart from ClimPlant's degree-scale temperature range (floristic T_range_ord_vasc) in lowland forests, we showed that the relationship between temperature EIVs and microclimate temperature is not consistent, limiting the possibility of using current ordinal-scale or degree-scale EIVs to infer or reconstruct forest microclimate temperature; that is, using a "transfer function", as termed by paleoecologists and ecologists (Bertrand et al., 2011; Paus, 2013; Pacheco-Riaño et al., 2023).

There are three main possible explanations for the low correlation we observed between measured microclimate temperatures and floristic temperatures. First, although variation in microclimate

conditions shapes community composition in vascular plants (Zellweger et al., 2020; Haesen et al., 2023) and bryophytes (Fenton & Frego, 2005; Man et al., 2022), forest plants may not respond primarily to microclimate temperatures (Bertrand et al., 2016; Schall & Heinrichs, 2020). Other non-climatic factors are assumed to play an increasing role at small spatial resolutions (Pearson & Dawson, 2003). Shifting from large spatial extents to fine spatial grains thus raises the question of the relevance of the variables that operate along different combinations of spatial grains and extents (Bruehlheide et al., 2018). Beyond stochasticity, species occurrences are related to more than one parameter, and confounding effects could have obscured the bioindication signal, because other abiotic factors such as soil acidity, humidity, or landscape connectivity may be predominant in community assembly rules (Diekmann, 2003; Borderieux et al., 2023). Plants may also respond with delay to past land-use and management conditions (Lenoir et al., 2022). Biotic interactions such as competition or mutualism may further complicate species coexistence and the resulting plant community composition (Sanczuk et al., 2022).

Second, the response of plants to microclimate differs from their response to macroclimate temperature (Haesen et al., 2023). Species could, theoretically, bioindicate microclimate temperature, but most likely after a complete redesign of temperature EIVs; for instance, using the linear relationship between macroclimate and microclimate temperatures (Gril et al., 2023). Temperature mean or range (continentality) has a special status among EIVs, because these climatic EIVs are not representative of local (microclimate) temperature conditions, and instead were built from macroclimatic or topoclimatic (the layering of successive vegetation belts along elevational gradients in mountain regions) conditions. Combining available microclimate maps of understorey temperature at the continental scale of Europe (Haesen et al., 2021) with vegetation plot data from the European Vegetation Archive (EVA) (Chytrý et al., 2016), it should now be possible to estimate new, refined temperature EIVs for forest plant species.

Third, some specialist plant species may be better bioindicators of local environmental conditions than others, having a narrower ecological niche, whereas generalist species may be indifferent or tolerate a large range of environmental conditions (Diekmann, 2003). Therefore, specific species of vascular plants or bryophytes with narrow thermal tolerance may be better microclimate indicators than the whole community (Haesen et al., 2023).

4.4 | Using plant communities to track macro- and microclimatic changes in forests

Climate change reshuffles plant communities toward more warm-adapted species, creating novel species assemblages, and this ongoing thermophilization process is usually quantified by EIVs averaged at the community level (De Frenne et al., 2013; Govaert et al., 2021; Richard et al., 2021). A concern sometimes raised is the circularity of reasoning when ecologists explain vegetation patterns with plant

EIVs (Diekmann, 2003; Schall & Heinrichs, 2020), but establishing a link between bioindication and local temperature measurements does not suffer from this issue, nor does quantifying the thermophilization of plant communities over time.

Current macroclimate and floristic temperature are not at equilibrium within forest understories, and the thermal lag or climatic debt of forest plant communities relative to macroclimatic conditions is steadily increasing over time (Richard et al., 2021). This lag is either perceived (a) as a major risk (Bertrand et al., 2016), as many species may go locally extinct whenever the debt is “paid off”, especially in case of brutal canopy openings such as timber harvesting or windstorms; or (b) as a chance for species to get additional time to adapt to warmer conditions (Zellweger et al., 2020). Understorey communities are mainly composed of perennial species with a long lifespan. Their capacity to withstand warming may cause the thermal lag in forest communities (Bertrand et al., 2016; Martin et al., 2019; Schall & Heinrichs, 2020), and this is especially pronounced for vascular plants, whereas bryophytes may be more sensitive and responsive (Becker Scarpitta et al., 2017; Kiebacher et al., 2023; but see Govaert et al., 2021). Alternatively, this thermal lag may be explained by microclimate buffering under dense canopies (De Frenne et al., 2013; Zellweger et al., 2020). If so, one would expect temperature EIVs to be a useful tool for evaluating thermophilization in response to microclimate changes, discriminating between trajectories of canopy opening or closing over time (Dietz et al., 2020; Christiansen et al., 2022). We found a few low, but sometimes significant correlations between floristic and measured temperature within forests, across a gradient of microclimate buffering by the canopy. Yet no direct relationship could be established, questioning the relative importance of microclimate buffering in explaining the macroclimatic debt in forests.

We mostly found very similar results for both bryophytes and vascular plants, two contrasting ecological groups (Becker Scarpitta et al., 2022; Kutnar et al., 2023), strengthening our point. However, confirmation by larger-scale studies, both in space and time, is needed. At a European level, future studies may use the newly available harmonized EIVs (Vangansbeke et al., 2021; Dengler et al., 2023; Tichý et al., 2023) together with vegetation plot data from EVA (Chytrý et al., 2016) and high-resolution maps of understorey temperature (Haesen et al., 2021) to confirm or deny our findings at a larger spatial extent.

AUTHOR CONTRIBUTIONS

JL, RM, FS, EG, EGM and GD conceived the research idea. EG, GV, FS, VLR, BB, JL and RM conducted the field study. AV and FS checked bryophyte species identifications. RM analyzed the data with inputs from EG, FS, GV and JL. EG led the writing with significant contributions from all co-authors.

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DATA AVAILABILITY STATEMENT

The R script and associated data are published online on Figshare: <https://doi.org/10.6084/m9.figshare.25151459.v1> Raw temperature time series and plant community composition data were submitted to the international SoilTemp database (www.soiltempproject.com/) and will be available upon request.

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SUPPORTING INFORMATION

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

Appendix S1. Plot location (coordinates in WGS84), elevation and forest structure.

Appendix S2. The mean temperature of 2021 compared to 1979–2013 macroclimate records.

Appendix S3. Meaning of Julve's temperature and continentality coefficients for vascular plants, from the Baseflore database (Julve 2015).

Appendix S4. Weighting vascular plant species by their abundance.

Appendix S5. Results after removing species associated to local heterogeneities—vascular plants and bryophytes.

Appendix S6. Details of model outputs—correlations between measured and floristic temperature, with linear models (LM) or linear mixed models (LMM).

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