

## RESEARCH ARTICLE

# The affinity of vascular plants and bryophytes to forest microclimate buffering

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## Abstract

1. With recent advances in technology and modelling, ecologists are increasingly advised to use microclimate, not the usual coarse scale macroclimate based on weather stations, to better reflect the proximal conditions that species experience. This is especially relevant in forest ecosystems, where natural disturbances and management create substantial heterogeneity in microclimates. Under dense canopies, species may experience buffered (less extreme) microclimate temperatures relative to macroclimate, as well as increased relative humidity, reduced light and wind.
2. Focusing on understorey plants, we investigated species response curves to the buffering capacity of the canopy layer, measured as the log-transformed slope parameter of the microclimate to macroclimate linear relationship. If lower or higher than zero, microclimate temperatures are buffered or amplified, respectively, relative to macroclimate.
3. During leaf-on conditions (July–September 2021), we measured hourly microclimate temperatures in 157 plots across three temperate deciduous forests with contrasted macroclimates. We used paired hourly macroclimate measurements from nearby weather stations to derive the slope parameter, quantifying microclimate buffering.
4. We surveyed vascular plant and bryophyte communities in 400m<sup>2</sup> plots centred on our microclimate sensors. Species were classified into three groups of forest affinity: core specialists; edge specialists; and generalists. We fitted generalized linear mixed-effects models, by forest affinity group and by species, to obtain logistic response curves of the probability of occurrence against microclimate buffering. The species' optimum was computed as the microclimate effect that maximizes the species' probability of presence.
5. We found contrasted microclimate preferences: Most bryophytes as well as the vascular plants classified as forest core specialists had an optimum in microclimate buffering, while forest edge specialists and generalists among vascular plants had

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an optimum in microclimate amplification. As canopies undergo increased disturbance frequency and intensity, more generalists and less forest core specialists might thus be expected in understorey communities, especially for bryophytes.

6. *Synthesis.* Understorey plants have a species-specific affinity to the forest microclimate, which we quantify for the first time. The investigation of species response curves to microclimate processes—buffering or amplification—can improve our understanding of the ecology of understorey plants, and help us anticipate their redistribution under climate change.

#### KEYWORDS

climate change, forest affinity, forest management, herbaceous layer, microclimate buffering, mosses and liverworts, plant–climate interactions, species response curves, temperature extremes, understorey floristic communities

## 1 | INTRODUCTION

Species often have ‘bell-shaped’ response curves to environmental gradients, with an optimum and a tolerance, ranging for instance between cold and warm limits to their survival and development (Austin, 1980; Lancaster & Humphreys, 2020; Normand et al., 2009). Climate variables are essential parameters to characterize the niche of a species and its implementation in species distribution models (Lembrechts, Lenoir, et al., 2019; Thuiller et al., 2005), especially to investigate future species' risks of extinction and redistribution (Lenoir et al., 2020; Román-Palacios & Wiens, 2020). Whether the coarsely resolved climatic grids most often used in biodiversity models are enough, or should instead be downscaled to high-resolution maps accounting for the effect of local environmental features on microclimates, has, however, become an increasing area of concern (Lembrechts, Nijs, & Lenoir, 2019; Lenoir et al., 2017). In forests, the microclimate experienced by understorey plant communities largely differs from the one measured in free-air conditions by weather stations (De Frenne et al., 2019). Understorey plants were shown to respond particularly slowly to global warming, which has been related to the microclimate effect of forest canopies (De Frenne et al., 2013; Zellweger et al., 2020). Indeed, forest plants rather depend on the proximal microclimate than on the regional macroclimate, so that incorporating microclimate temperature in species distribution models enhances their accuracy (Haesen, Lenoir, et al., 2023; Klinges et al., 2024; Lembrechts, Nijs, & Lenoir, 2019).

Forest plants are adapted to the specific conditions of the forest environment (Neufeld & Young, 2014). Understories usually have a deep shade that limits photosynthesis, but plants can benefit from a higher stability in humidity, wind conditions and temperature (Michalet et al., 2023; Valladares et al., 2016). Temperature maxima are typically lower and minima are higher inside forests compared to free-air conditions: This is called the buffering effect (De Frenne et al., 2021; Gril, Spicher, et al., 2023). Vegetation and especially trees are causing this dampening of temperature extremes, mainly by shadow and transpiration (De Frenne et al., 2021). Importantly, the forest microclimate is not only about temperature: under

canopies, incoming light and wind are reduced, and relative humidity is increased (De Frenne et al., 2021). The effects of these climatic variables are particularly hard to disentangle (De Pauw et al., 2022) and the present study does not intend to do so. Here, we refer to the forest microclimate buffering as a moderation of temperature extremes, correlating with gradients of other microclimatic variables (lower light and wind, higher relative humidity) as well.

The buffering capacity of the forest depends on forest structure: high, dense and vertically complex forests have a more buffered microclimate (Frey et al., 2016; Gril, Laslier, et al., 2023; Kovács et al., 2017). An amplification effect can alternatively be observed when trees are small or scattered, generating large canopy gaps with low air mixing but high light penetration (Carnicer et al., 2019; Gril, Laslier, et al., 2023; Vandewiele et al., 2023). Whenever forest management modifies canopy structure, it impacts microclimate (Greiser et al., 2018) and thus the plants of the understorey layer (Christiansen et al., 2022).

The understorey layer accounts for <1% of the plant biomass on average, but 80% of plant diversity in temperate forest (Gilliam, 2007), and plays a substantial role for forest regeneration, food chain, productivity and nutrient cycling (Deng et al., 2023; Landuyt et al., 2019). Within the understorey layer, vascular plants and bryophytes, two contrasting taxonomic groups, are expected to differ in their response to environmental changes (Kutnar et al., 2023). Bryophytes are particularly sensitive to microclimate because of their strong reliance on atmospheric precipitation. Lacking roots, bryophytes directly depend on rainfall for water uptake, while their poikilohydric condition involves that they cannot regulate their water content (Mills & Macdonald, 2005). All temperate bryophyte species investigated so far are highly sensitive to even moderately warm temperatures, and die when kept hydrated at temperatures above 30°C (Furness & Grime, 1982; He et al., 2016). Therefore, variation in microclimatic conditions plays a crucial role in shaping the variation of bryophyte distributions at fine spatial resolutions (Hylander et al., 2002; Man et al., 2022).

Understorey species can be qualified as either forest specialist or generalist species, based on their habitat preferences, or

affinities (Bernhardt-Römermann et al., 2018; Heinken et al., 2022). Forest specialists can be divided into two categories: forest core specialists preferring closed canopies, and forest edge specialists growing in edges or clearings. Generalists are not only found in forests but also in open areas. They may be equally found in forest and open areas, or prefer open areas while being able to persist under the closing canopy of secondary forests or highly disturbed canopies. Ancient forests are more likely to host forest specialists, often late successional species with slow colonization capacities, such as *Brachypodium sylvaticum*, *Deschampsia cespitosa* or *Lamium galeobdolon* (Pellissier et al., 2013; Verheyen & Hermy, 2001). In contrast, generalists are often early successional species, efficient at colonizing gaps and secondary forests when there is sufficient light for rapid growth, such as *Ajuga reptans*, *Anthoxanthum odoratum* or *Cytisus scoparius* (Govaert et al., 2020; Heinken et al., 2022). Forest specialists are adapted to thick leaf litter layers, characteristic of dense forests, and to the deep shade cast by trees and shrubs, either by phenological adaptation for shade-avoiders, that is, vernal species completing most of their yearly cycle in spring before the foliation of the overstorey, or by morphological and ecophysiological adaptations for shade-tolerant species, that is, strategies to capture as much light as possible depending on their environment, such as an architecture that minimizes self-shading, high chlorophyll contents or flexible specific leaf area (Chelli et al., 2021; Decocq & Hermy, 2003; Neufeld & Young, 2014).

Because of these ecological differences, forest specialists and generalists may differ in their respective affinity to the forest microclimate (Govaert et al., 2020; Müller et al., 2019). Forest core specialists were shown to prevail over generalists under very dense canopy cover (Depauw et al., 2021; Sanczuk et al., 2023), suggesting a potential preference for buffered habitats. Here, we test the idea that beyond microclimate temperature, forest plants may show different affinities to the microclimate buffering or amplification (Figure 1). We hypothesize that (i) there is a gradient in microclimate preference from forest specialists to generalists, forest specialists having their optima in buffered microclimates and generalists in amplified microclimates, and similarly, (ii) forest bryophytes will prefer buffered over amplified environments, even more so than forest specialists among the vascular plants. With the approach we used here, we aim to go beyond the categories of forest specialist versus generalist, and instead provide a quantitative metric of species' optimum to rank species according to their affinity to the forest microclimate.

## 2 | MATERIALS AND METHODS

We recorded microclimate temperature in 157 plots within three forests, and related it to a macroclimate reference (weather station) to obtain the microclimate buffering or amplification effect (Figure 1a,b). We built 'response curves' sensu Austin (1980) and ter Braak and Looman (1986), that is, modelling species probability of presence along an environmental gradient. We related this buffering

capacity of the canopy to species records in each plot (presence-absence data), to obtain a response curve for each species and each group of forest affinity, separately for vascular plants and bryophytes (Figure 1c). Finally, we focused on testing whether the proportion of forest core specialists at the community level is related to microclimate buffering or amplification.

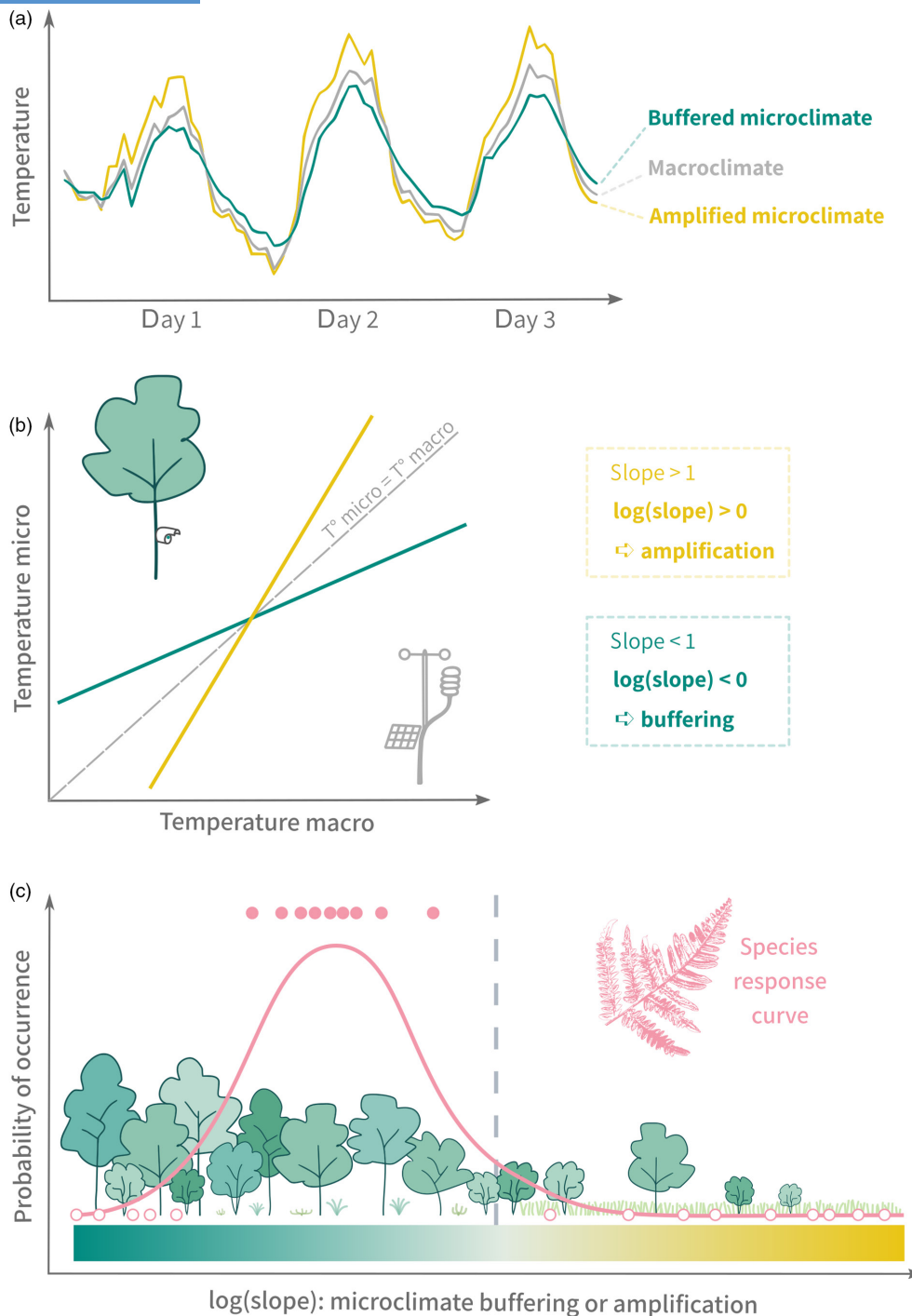
### 2.1 | Study area and sampling design

We selected three sites from the French national network of long-term monitoring of forest ecosystems (RENECOFOR; onf.fr/renecofor; Ulrich, 1995) located in Mormal, Blois and Aigoual forests to cover a range of macroclimatic conditions. Studying more than one region is recommended to detect general patterns of vegetation response beyond site-specific features (Müller et al., 2019). These state forests managed by the French National Forest Office (ONF) are equipped with a long-term weather station in nearby open conditions, or within a clearing inside the focal forests (Figure 2). The three forests differ in macroclimate and dominant tree species. Blois forest is dominated by sessile oak (*Quercus petraea*) and located in the oceanic domain, Mormal forest is dominated by pedunculate oak (*Quercus robur*) and beech (*Fagus sylvatica*) and located in the semi-continental domain, while the Aigoual forest is dominated by beech and located at the crossroad of several bioclimatic influences, including Mediterranean climate (Joly et al., 2010). Blois and Mormal are lowland forests (elevation <200m), while Aigoual is a mountainous forest (elevation from 1000 to 1500m). All three forest sites have acidic soils and are mostly managed for wood production as regular 'high forests', except in a few stands in Aigoual forest, not entirely managed for conservation or accessibility reasons (due to steep mountain slopes). We surveyed 53 plots in Aigoual, 52 in Blois and 52 in Mormal, for a total of 157 plots (Figure 2). Plots were selected to cover a gradient of forest structures and silvicultural stages, from treeless clearings to dense closed-canopy forests, and from regeneration stages to mature stands.

### 2.2 | Data acquisition

#### 2.2.1 | Microclimate and macroclimate temperature measurements

We measured local air temperature (hereafter microclimate temperature) hourly in each of the 157 plots, using Onset® HOBO® Pendant data loggers UA-001-64. These temperature sensors have a manufacturer-reported accuracy of  $\pm 0.53^{\circ}\text{C}$  from 0 to  $50^{\circ}\text{C}$ , and are often used in ecological studies (Bramer et al., 2018). We attached sensors at the centre of each plot, on the north side of tree trunks or wooden poles at a 1-m height above the ground (George et al., 2015). We hung them within homemade  $10 \times 15 \text{ cm}$  white PVC shields to minimize the effect of direct solar radiation (Gril, Spicher, et al., 2023; Zellweger et al., 2019). Because we are chiefly interested in the buffering effect of

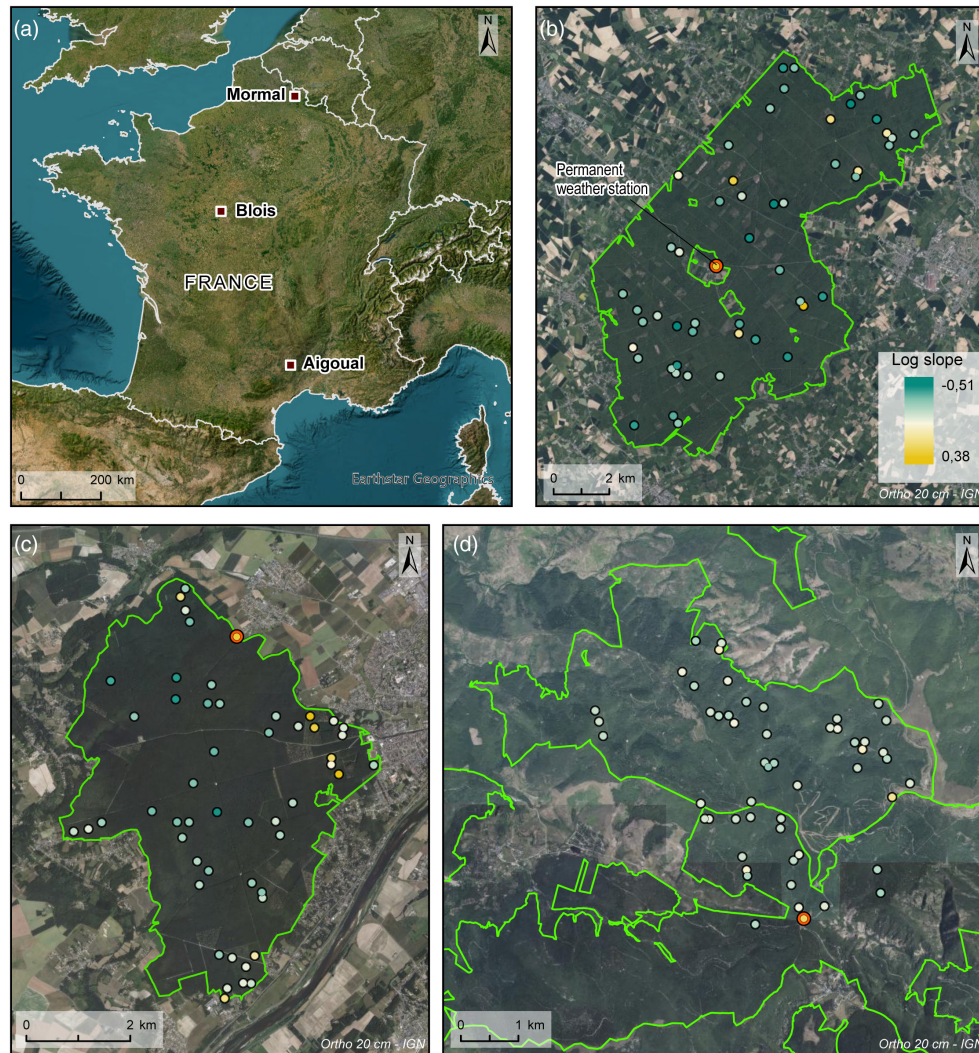


**FIGURE 1** Relating the buffering versus amplification effect of forest canopies to understory plant distributions. (a) We measured hourly microclimate temperature in several plots ( $n=157$ ), as well as temperature from a macroclimate reference (weather station) for each forest. (b) For each plot, we derived the slope parameter of the linear relationship between microclimate and macroclimate. A slope value lower than one (or  $\log(\text{slope}) < 0$ ) means that the microclimate temperature is buffered relative to the macroclimate, and a slope value higher than one ( $\log(\text{slope}) > 0$ ) means that the microclimate temperature is amplified. (c) We used species presence or absence (full and empty pink dots, respectively) at each plot to fit species response curves to the microclimate buffering versus amplification effect. For instance, the fictive species depicted here shows a clear preference towards a buffered microclimate.

temperate deciduous forests, especially pronounced during the leaf-on period (Gril, Spicher, et al., 2023), we focused on the period from the 9th of July to the end of September 2021.

Hourly macroclimate temperatures were recorded during the same period from standardized weather stations, located in open

grassland areas close to or within each forest (Figure 2). The temperature sensor was shielded and placed at 1.5m above ground, a common height to record macroclimate temperature (Bramer et al., 2018). To obtain the reference macroclimate corrected for elevation differences, we applied an adiabatic lapse rate of



**FIGURE 2** Sampling design consisting in (a) 157 plots of 400 m<sup>2</sup> each and spread across three forests: (b) Mormal ( $n=52$ ); (c) Blois ( $n=53$ ); and (d) Aigoual ( $n=53$ ). The boundary of each forest is outlined in green. Plot colour reflects proximal microclimatic conditions, from microclimate buffering ( $\log\_slope < 0$ , in green) to amplification ( $\log\_slope > 0$ , in yellow), a parameter that we extracted from a linear regression between hourly microclimate temperature recorded in each plot, and in a nearby weather station (represented by a red dot) as the macroclimate reference (Gril, Laslier, et al., 2023; Gril, Spicher, et al., 2023).

-0.56°C/100m for each plot based on the difference of elevation to the nearby weather station (Rolland, 2003).

### 2.2.2 | Floristic surveys

Species presence-absence of the herbaceous and bryophyte layers was recorded in circular plots of 11.3-m radius around each temperature sensor, corresponding to a surface area of 400 m<sup>2</sup>, as commonly implemented in forest inventories (e.g. Kutnar et al., 2023). We included all herbs and woody plants with a maximum height of 50 cm (Tinya et al., 2019), as well as terricolous and saxicolous bryophytes. Bryophyte specimens were systematically sampled in each plot for subsequent identification in the laboratory. Field surveys were carried out from mid-May to early July 2021 in Blois, Mormal, then Aigoual, in order to study vegetation at a similar phenological stage.

## 2.3 | Data processing

All analyses were conducted in R version 4.1.2 (R Core Team, 2021). We used the 'tidyverse' package to handle data preparation and visualization (Wickham et al., 2019).

### 2.3.1 | Computing microclimate buffering or amplification

To quantify how microclimate temperature is buffered or amplified relative to macroclimate, we used the slope parameter of the linear relationship between hourly measurements of microclimate and macroclimate (De Frenne et al., 2021; Gril, Spicher, et al., 2023; Rita et al., 2021). This integrative parameter describes the buffering (slope < 1) or amplification

(slope > 1) capacity of the target habitat where microclimate sensors are installed (Figure 1a,b). With a log-transformation of the slope parameter, a value of 0 means a neutral effect of forest canopy on temperature, while negative and positive values, respectively, indicate buffering and amplification. We used the method developed by Gril, Laslier, et al. (2023) and Gril, Spicher, et al. (2023) to compute the slope by fitting a separate simple linear model for each plot relating hourly microclimate temperature to the matching hourly macroclimate temperature recorded by the nearby weather station specific to each forest (see Appendix S1 for a visualization of each regression). We extracted the slope (the coefficient) of this regression and used its log-transformation (log\_slope hereafter) as our main explanatory variable in subsequent analyses, to describe the forest microclimate effect.

### 2.3.2 | Assigning forest affinity groups

Species were classified into three groups depending on their forest affinity, according to two recent classifications from the EuForPlant database for European vascular plants (Heinken et al., 2022) and the BryForTraits database for bryophytes (Bernhardt-Römermann et al., 2018), the latter originally stemming from Schmidt et al.'s (2011). Forest specialists are plants that occur mainly in forests. We distinguished specialists preferring forest cores with a closed canopy (group 1.1 for vascular plants or 1 for bryophytes), from specialists preferring forest edges or openings (group 1.2 or 2). Forest generalists can occur inside and outside forests, and are either indifferent to forest cover (group 2.1 or 3) or prefer open areas, but can survive in forests too (group 2.2 or 4). We pooled these two latter categories into a single 'generalist' group. We did not include the group of 'open landscape' plants from Heinken et al.'s (2022). The final forest affinity groups used in this study are thus core specialists, edge specialists and generalists (see Appendix S2 for the full list of species). Only vascular plants and bryophytes identified at the species level and with information on their forest affinity are considered in the subsequent analyses of this study (i.e. 98% of 3.355 and 94% of 2.035 records for vascular plants and bryophytes, respectively).

For vascular plants, the forest group depends on the focal region in the EuForPlant database, as species may shift their forest affinity across Europe. We thus assigned a forest affinity group depending on the region that plants were observed in: the French Atlantic region for species recorded in Blois and Mormal forests and the French mountainous region for species recorded in Aigoual forest (see the list of 16 species with a changing forest affinity group in Appendix S3). Bryophytes have a single forest affinity group per species in the BryForTrait database. For bryophytes, we also attributed a substrate preference to each species: rocks; soil; or indifferent.

### 2.3.3 | Modelling species response curves and the proportion of core specialists

Species presence/absence records were used as response variables in generalized linear mixed-effects models to fit response curves along the gradient of microclimate buffering to amplification (Figure 1c). Only species with a minimum of 10% presences and 10% absences in at least one forest were selected, that is, at least five presences and five absences (since we have 52 or 53 plots per forest), resulting in 126 vascular and 64 bryophyte species.

We fitted logistic mixed-effects regression models, with a binomial family and a logit-link function, using the first- and second-order polynomial terms of the log\_slope parameter as fixed-effect variables. First, we pooled all vascular plant (or bryophyte) species together to test for significant differences in the mean response curve of each forest affinity group. We fitted two logistic mixed-effects regression models (one for vascular plants and one for bryophytes), with forest affinity included as a fixed-effect variable in interaction with the first- and second-order polynomial term of the log\_slope parameter. Second, we fitted one logistic mixed-effects regression model per species. For models at the species level, the forest (i.e. a factor variable with three levels: Blois; Mormal; or Aigoual) was added as a random intercept term to account for variability across sites, only if the species was present in more than one forest. For the two models across vascular plant or bryophyte species, we not only added forest but also species as two separate random intercept terms.

We computed the microclimate optimum of each species, by selecting the log\_slope value that maximized its predicted probability of presence. We visually classified some species response curves as inconclusive, when an artefact of the model caused the response curve to look U-shaped (thus without a reliable optimum value), representing six species of vascular plants and 12 species of bryophytes. For these species, no optimum value could be derived.

Third, we modelled the proportion of forest core specialists relative to other forest affinity groups within each plot, separately for vascular plants and bryophytes. We used generalized linear mixed-effects models for proportion data, using a binomial family and a logit-link function, the response variable being a two-column matrix holding information on the number of forest core specialists in one column and the number of species in other forest affinity groups in the other column. The only fixed effect variable was the log\_slope parameter with forest as a random intercept term.

We used the *glmer* function from the 'lme4' package to fit all generalized linear mixed-effects models (Bates et al., 2015). The *tab\_model* function from the 'sjPlot' package was used to print model parameters and their significance, and the *ggpredict* function from the 'ggeffects' package to plot model predictions (Lüdtke, 2018, 2021). All data and codes are freely available online (see the data availability section).

### 3 | RESULTS

#### 3.1 | Response curves by forest affinity group

For vascular plants, we found a clear shift from a preference for slightly buffered conditions in core specialists to clearly amplified temperature fluctuations in edge specialists and generalists (Figure 3; Appendix S4a). Each group had a significantly different response curve from other groups, as evidenced by the significant interaction term between the forest affinity variable and the first- or second-order polynomial term of the  $\log\_slope$  parameter. By contrast, for bryophytes, only forest core specialists consistently differed from generalists in their response curve to temperature buffering (Figure 3; Appendix S4b). Random intercept terms (i.e. forest and species) explained the major part of the observed variability (the marginal  $R^2$  value for fixed effects being only 5.5% and 4%, and the conditional  $R^2$  value being 31% and 33%, for vascular plants and bryophytes, respectively).

#### 3.2 | Species response curves

Species exhibited contrasted responses to the forest microclimate effect (Figures 4 and 5, Appendix S5). We found that 45% of vascular plant species ( $n=57$ ; e.g. *Oxalis acetosella*, *Rubus idaeus*) and 70% of bryophyte species ( $n=45$ ; e.g. *Lophocolea heterophylla*, *Isoetecium myosuroides*, *Lescurea incurvata* or *Dicranella heteromalla*) had their optimum (i.e. maximum probability of occurrence) at negative values of the  $\log\_slope$  parameter, corresponding to buffered temperature conditions. In contrast, 47% of vascular plant species ( $n=59$ ; e.g. *Stachys sylvatica*, *Galeopsis tetrahit* or *Dactylis glomerata*) and only 5% of bryophyte species ( $n=3$ ; *Pseudoscleropodium purum*, *Brachythecium rutabulum* and *Campylopus introflexus*) had their optimum at positive values of the  $\log\_slope$  parameter, corresponding to amplified microclimate temperatures. A remaining 3% of vascular plants ( $n=4$ ; e.g. *Poa nemoralis*) and 5% of bryophytes ( $n=4$ ; e.g. *Pohlia lutescens* and *Dicranum scoparium*) preferred a neutral effect of microclimate, or 'coupling' to macroclimate temperature variations (i.e.  $\log\_slope=0\pm 0.01$ ). The variation of optima was important within each of the investigated forest affinity groups, especially for vascular plants, for which some forest core specialist species like *Luzula pilosa* had their optimum in highly amplified conditions (see Appendix S6). The substrate preference of bryophyte species (soil, rocks or indifferent) did not appear to explain their microclimate preference (see Appendix S7).

#### 3.3 | Proportion of forest core specialists

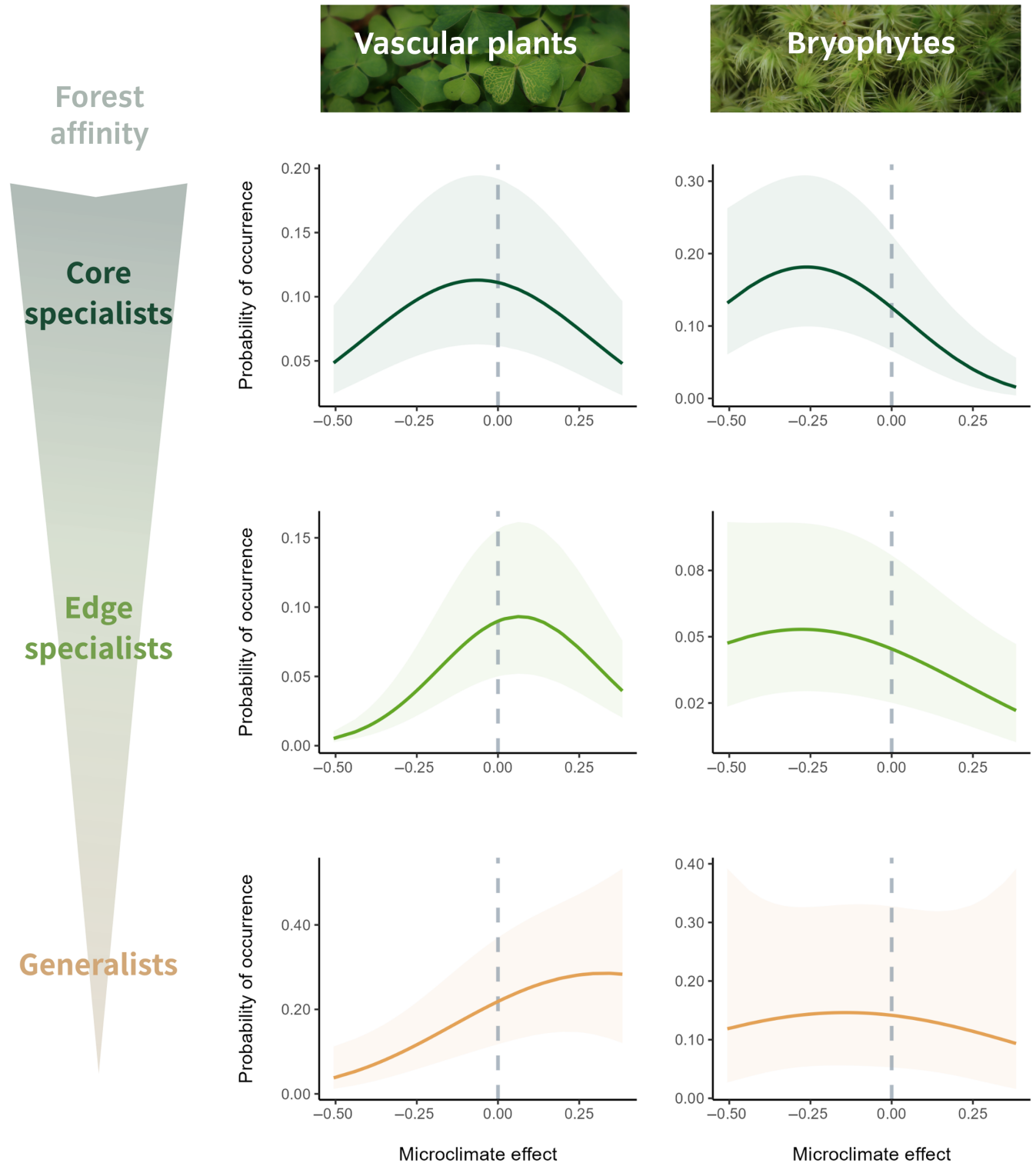
At the community level, we found that the proportion of forest core specialists was negatively correlated with the gradient of temperature buffering to amplification (Figure 6; Appendix S8). While

the proportion of forest specialists within understorey plant communities reached around 40%–50% under highly buffered temperature fluctuations ( $\log\_slope < -0.25$ ), it was mostly below 25% under amplified temperature fluctuations ( $\log\_slope > 0$ ). Forest as a random intercept had little impact on this relationship, as demonstrated by a very similar marginal and conditional  $R^2$  (5% and 5.2% for vascular plants; 3.2% and 5.9% for bryophytes, respectively). The coefficient was slightly higher for vascular plants than for bryophytes (estimates of  $-2.56$  and  $-2.05$ , respectively, but confidence intervals overlap).

### 4 | DISCUSSION

#### 4.1 | Forest plants' affinities to microclimate buffering or amplification

The buffering or amplification metric we focus on is unitless, and relative to the fluctuations of macroclimate temperature (Gril, Spicher, et al., 2023). We found that understorey vascular plants and bryophytes show different affinities to this microclimate effect, quantified as the  $\log$ -transformed slope of the linear relationship between microclimate and macroclimate. Although based on temperature only, the buffering or amplification effect actually conveys a lot more information than just relative temperature stability, as it also reflects other climatic factors connected to the buffering effect of forest canopies, that is, wind, relative humidity and especially light (De Frenne et al., 2021). Shade is indeed one of the main drivers for the spatial arrangement of species in the forest understorey (De Pauw et al., 2022; Valladares et al., 2016). Because closed canopies are more likely to buffer temperature fluctuations over time, our buffering gradient is likely capturing a light gradient as well (Depauw et al., 2021; Neufeld & Young, 2014). Therefore, one may wonder whether the responses to microclimate buffering are not simply responses to light availability. To investigate this possibility, we related our metric of the microclimate effect to a proxy of light conditions, canopy cover, computed from hemispherical photographs. This supplementary analysis (described in Appendix S9) demonstrates that although canopy cover and microclimate buffering are indeed related, with forest stands having a low canopy cover being likely to have an amplified microclimate temperature, they have a complicated relationship and are not at all redundant. For a similar canopy cover (around 80%–90%), the microclimate effect can range from neutral (i.e. coupling) to highly buffered. Thus, our species response curves to the microclimate effect represent a new and complementary information on plant ecology compared to existing species response curves to light availability. Studies that manage to decouple the intertwined effect of light and temperature on understorey plants are scarce and ideally require complex experimental set-ups (De Pauw et al., 2022). Instead, our integrative metric may allow us to evaluate the impact of the forest microclimate gradient as a whole, using only one easily measured parameter in the field that can be easily compared against a standard reference available worldwide,

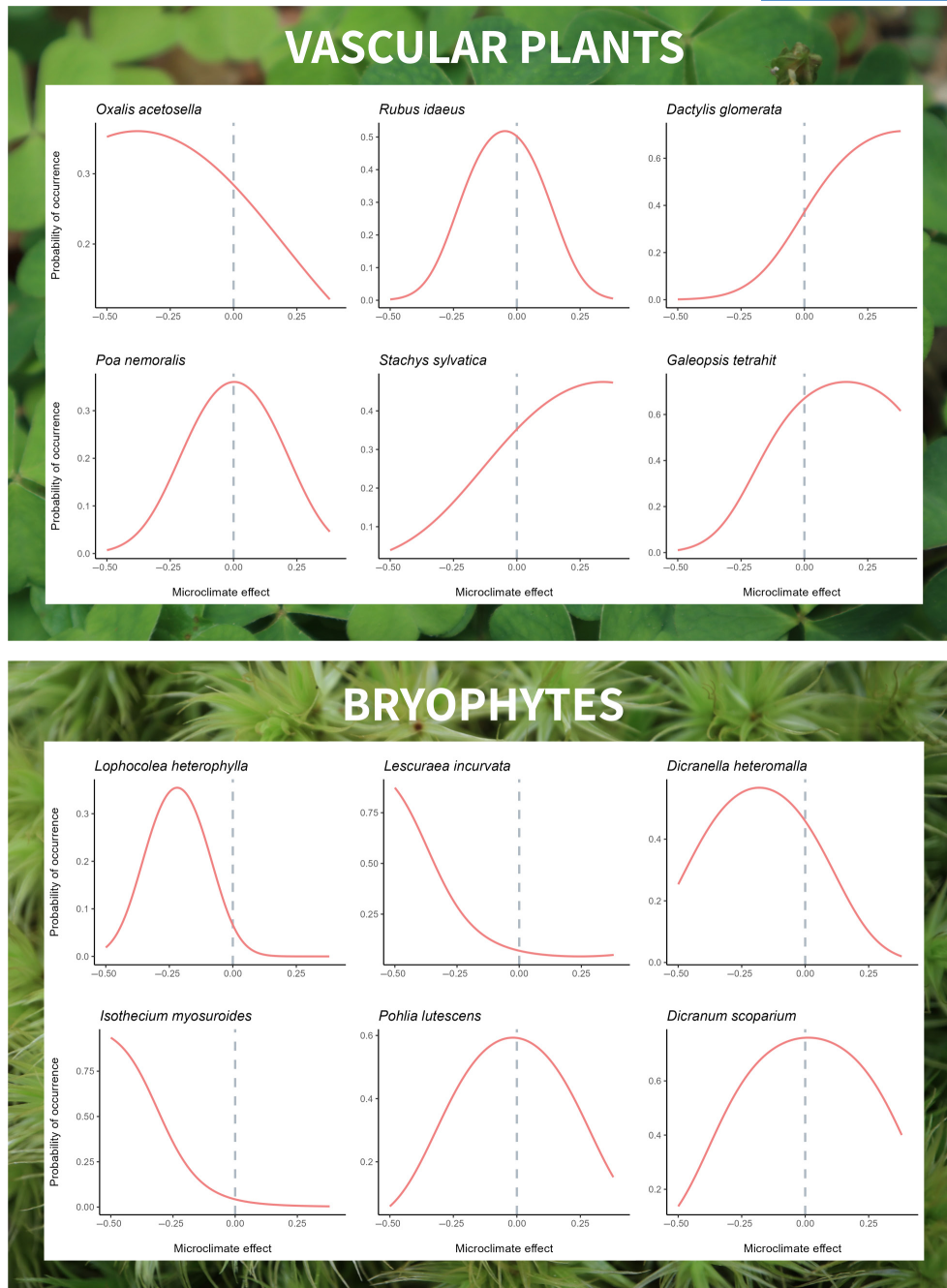


**FIGURE 3** Mean response curves of vascular plant (left) and bryophyte (right) species to a gradient of microclimate buffering ( $\log_{\text{slope}} < 0$ ) to amplification ( $\log_{\text{slope}} > 0$ ), depending on their forest affinity group (core specialist, edge specialist, generalist). Two separate generalized linear mixed-effects models were fitted, one for vascular plants and one for bryophytes, with forest and species as random intercept terms.

namely temperature. Although we already know that these different microclimate variables are correlated, additional studies are needed to disentangle the contribution of light, relative humidity or wind gradients to the microclimate buffering effect.

The novelty of our work is the use of a metric capturing the buffering or amplification of microclimatic temperature fluctuations relative to an international standard reference instead of temperature itself (mean, minimum, maximum or range), as usually

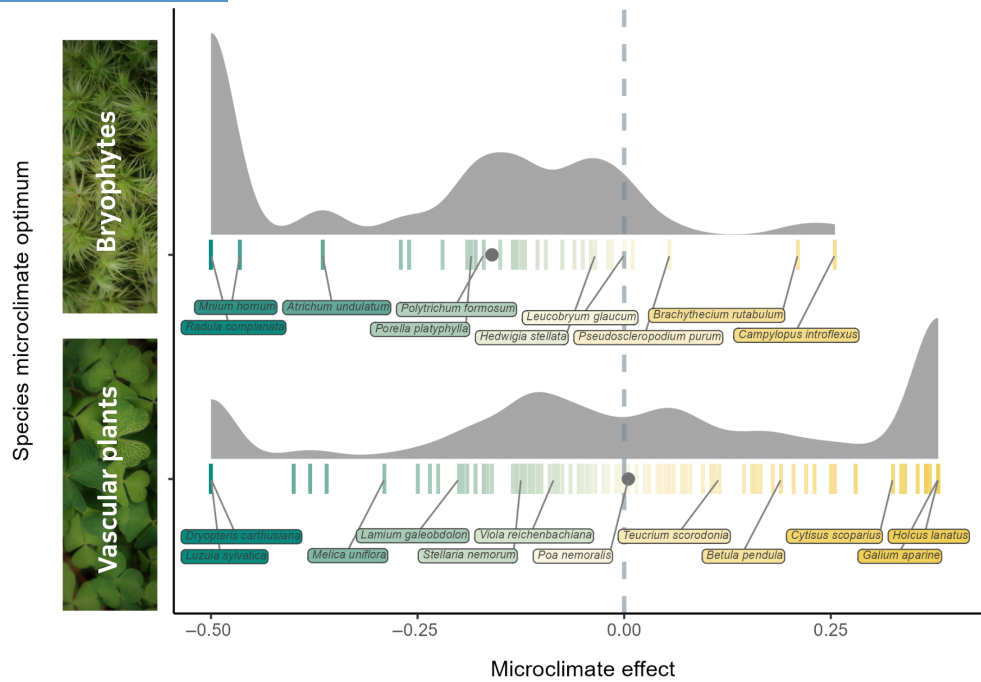




**FIGURE 4** Illustrative cases of understory species responses to microclimate temperature buffering ( $\log\_slope < 0$ ), coupling ( $\log\_slope = 0$ ) or amplification ( $\log\_slope > 0$ ) relative to macroclimate for a selection of six vascular plants (above) and six bryophytes (below). From the literature, the species depicted here are forest core specialists, edge specialists and generalists in the left, central and right columns, respectively.

done to investigate species thermal response curves. Maybe even more than mean conditions, organisms are affected by proximal temperature fluctuations and extremes that compromise their survival (Niu et al., 2014; Suggitt et al., 2011). In temperate forests, maximum microclimate temperature shapes vascular plants and bryophytes communities (Macek et al., 2019; Man et al., 2022). While the mean temperature may differ between forest understories and free-air conditions, the chief difference is on the stability of temperatures. Under forest canopies, extreme

temperatures are usually buffered by physical and physiological processes, that is, the interception of solar radiation and the transpiration of trees (De Frenne et al., 2021). This is, however, not always the case: Plant species can also experience amplified (more extreme) microclimate temperatures in forest openings or young stands (Gril, Laslier, et al., 2023; Vandewiele et al., 2023). Mobile species such as anteaters, birds or butterflies can target buffered habitats to decrease thermoregulation costs (Alessandrini et al., 2022; Carnicer et al., 2019; Giroux et al., 2023), but plants

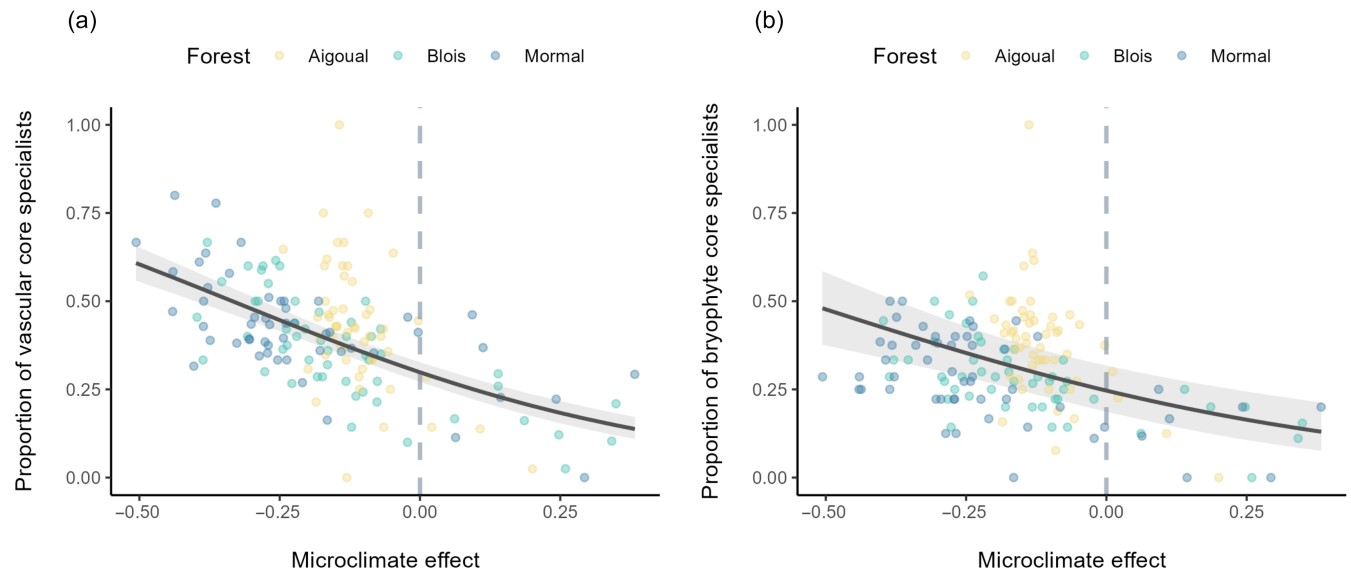


**FIGURE 5** Ranking of understory plant species according to their preferences for microclimate buffering ( $\log\_slope < 0$ ), coupling ( $\log\_slope = 0$ ) or amplification ( $\log\_slope > 0$ ). The ranking is based on the optimum value for each species, extracted from logistic response curves. This optimum is computed as the microclimate effect that maximizes the probability of presence of each species. The names of a few species are outlined. The grey area represents the relative distribution of all optima, and the two grey circles represent the mean microclimate optimum for bryophytes (above, 64 species), and for vascular plants (below, 126 species).

cannot: Either they are able to survive the microclimate temperature regime in which they are rooted, or they locally disappear. Plants growing in thermally stable or buffered habitats may have an advantage compared to plants growing in thermally unstable habitats undergoing extreme temperature fluctuations (Furness & Grime, 1982; Woods et al., 2021). Daily or annual temperature range directly impacts plant survival and metabolism such as photosynthesis (Chabot & Chabot, 1977); therefore, temperature range is a common bioclimatic index used in many species distribution models (e.g. Gardner et al., 2019), albeit these do not capture microclimatic fluctuations. The information brought by the buffering or amplification effect is complementary to the usual investigations focusing on plant thermal tolerance (Lancaster & Humphreys, 2020).

Although promising, our approach has limits. Plant species do not only respond to climate but also to edaphic, dispersal and landscape constraints (Borderieux et al., 2023), which may bias some of our species response curves. Past land-use effects can persist after decades or centuries and leave imprints on forest bryophyte and vascular communities, which are not always at equilibrium with their environment (Christiansen et al., 2023; Lenoir et al., 2022; Müller et al., 2019). Biotic interactions are also at play, as dense canopies tend to increase the competition for below-ground resources, and modify species interactions in complex ways (Sanczuk et al., 2022; Valladares et al., 2016). The observed responses we reported may thus be due to a direct preference

of a given species for buffered or amplified temperature fluctuations, but also to indirect effects involving a complex interplay between the focal species and predators, competitors or facilitators (Greiser et al., 2021). Moreover, we did not investigate intra-specific variation, although two far-apart populations of a similar species may have different responses to microclimate, for example, in Aigoual versus Mormal forests (Chelli et al., 2021; Merinero et al., 2020; Wasof et al., 2013). Future studies could focus on more sites to test whether species adjust their response curves across a large climatic gradient, especially at their northern and southern range limits (Depauw et al., 2022; Haesen, Lembrechts, et al., 2023). Besides, species may display different response curves to the same environmental gradient depending on their ontogenic life stage, from germination to adulthood (Valladares et al., 2016). In particular, we included tree seedlings, which may have different thermal exposure and requirements compared to adult trees (Caron et al., 2021). Finally, we focused on species presence-absence data, as a binary 'life-or-death' situation. However, microclimate conditions may also positively or negatively impact plant ecophysiological performance, growth and reproduction (Christiansen et al., 2023; Cubino et al., 2021; Hylander, 2005; Neufeld & Young, 2014; Stewart & Mallik, 2006). Future studies could focus on the impact of microclimate buffering or amplification on plant functional traits such as height or specific leaf area, depending on whether species are forest specialists or generalists (Chelli et al., 2021; De Pauw et al., 2022).



**FIGURE 6** Proportion of forest core specialists within vascular (a) and bryophyte (b) plant communities along the gradient of buffered ( $\log\_slope < 0$ ) or amplified ( $\log\_slope > 0$ ) temperature fluctuations. Observations are coloured by forest, used as a random intercept term in both models.

#### 4.2 | Specialists versus generalists: Bryophytes and vascular plants have different response curves to microclimate buffering or amplification

We found very contrasting optima to the buffering or amplification of microclimatic temperature fluctuations across forest plant species. Vascular plants and bryophytes have species-specific responses to microclimate (Godefroid et al., 2006; Haesen, Lembrechts, et al., 2023; Moen & Jonsson, 2003). In accordance with our first hypothesis and despite within-group variation, we reported a progressive shift of microclimate preferences from buffering to amplification along the forest affinity gradient for vascular plants. Previous studies showed that vascular plant species respond differently to microclimate gradients depending on their forest affinity, with specialists preferring more buffered temperatures than generalists (Govaert et al., 2020; Sanczuk et al., 2023). Yet, contrary to our hypothesis, forest edge specialists had an intermediate response and preferred slightly amplified thermal environments. This could be due to their preferred habitat, as edges and openings impair microclimate buffering and can even amplify local temperatures (Blonder et al., 2018; Hofmeister et al., 2019; Meeussen et al., 2021). For this reason, we suggest that forest core and edge specialists should not be grouped into a single 'forest specialist' group in future microclimate investigations.

Interestingly, vascular plants differed from bryophytes, as the latter almost systematically preferred buffered microclimates. Only a few bryophyte species (3 out of 64) preferred amplified microclimate temperatures, all classified as forest generalists. In line with our hypothesis and other studies, bryophytes classified as forest specialists preferred more stable thermal environments

(Furness & Grime, 1982; Hylander, 2005; Koelemeijer et al., 2023; Vanderpoorten et al., 2004). Yet, even generalist bryophytes with low forest affinity showed an optimum within microclimate buffering, although many could tolerate some amplified conditions with lower forest cover as well (Stewart & Mallik, 2006). In fact, the poikilohydric ecology of bryophytes brings about a major limitation on growth, restricted to wet periods. The necessity to achieve a certain water content to permit metabolic activity leads to photosynthesis mostly taking place during rainy or cloudy weather, so that even species of intensively insulated habitats are functionally shade plants (Marschall & Proctor, 2004). Therefore, in line with the present results, the vast majority of bryophyte species thrive in buffered environments.

It is worth noting that the forest specialist group for vascular plants includes both shade-avoidant and shade-tolerant species (Decocq & Hermy, 2003). Shade-avoiders like *Adoxa moschatellina* or *Anemone nemorosa* are vernal geophytes that complete their cycle very early in the year, and may be less directly concerned by the buffering effect of canopies during summer (Neufeld & Young, 2014). Yet, buffered forest stands could also protect plants from frost damage under cold weather, especially species that emerge early in the growing season. Future studies should also use temperature data from the winter and spring period to better understand the response of these vernal forest species. Shade-avoidant specialist species may nonetheless respond to the summer buffering gradient because of their exclusion from amplified habitats, where temperature regimes are more extreme, more light reaches the understorey and generalist species can outcompete them (Govaert et al., 2021; Sanczuk et al., 2023). Even if many seem to have a more or less pronounced preference for buffered temperatures, vascular plants of the forest core specialist group can often be found in amplified environments, for example, within forest meadows or young stands (Chelli

et al., 2021; Tinya et al., 2019). Here, most of our plots are managed as even-aged high forests, with a shelterwood system for regeneration. The fact that forest core specialists prevailed in mature, buffered stages of our managed forests proves that they can survive, as adult plants or in the soil seed bank, some amplified, unfavourable prior conditions during forest regeneration and early succession stages, or that they can recolonize from nearby mature stands. Under amplified temperature conditions, the growth and abundance of bryophytes or vascular plants that are specialists of forest cores might decrease, but they may persist until canopies close again (Christiansen et al., 2022; Fenton & Frego, 2005). Forest plant specialists might tolerate openings, potentially being more limited by the frequency than by the severity of canopy disturbances (Decocq et al., 2004). This would explain why thinning does not necessarily decrease the number of vascular forest specialists in ancient forests (Govaert et al., 2020). This is especially true for bryophytes, wherein species considered as indicators of ancient forests (e.g. *Antitrichia curtispindula*, *Frullania tamarisci*) did not exhibit an optimum under the most buffered conditions, but instead in situations of coupled macro-microclimate variations ( $\log\_slope=0$ ). In fact, such species would have adapted to the partly open environment of ancient forests due to the historical impact of large, now extinct grazing and browsing herbivores (Rose, 1992).

Understorey communities are often described as resilient to disturbances, able to return in a matter of years or decades to pre-disturbance conditions after heavy timber harvesting (Gilliam, 2007; but see Mercier et al., 2019), even if some sensitive species may be excluded, especially bryophytes (Müller et al., 2019). Interestingly for ecological and conservation applications, we generated a quantitative assessment of species affinity to the forest microclimate, beyond an assignment to discrete classes of forest generalist or specialist. Actually, response curves are very species-specific and far from being consistent within a forest affinity group (Appendix S6), calling for further refinement of our index from a larger sample across wider biogeographic ranges to obtain a reliable forest microclimate optimum for each understorey plant species.

### 4.3 | Future forest microclimates: The fate of forest understorey species under management and climate change

Assessing plant responses and vulnerability to forest management and climate change is an objective shared by many ecologists and conservationists, and our results confirm that forest microclimates are key to that endeavour (Christiansen et al., 2022; De Frenne et al., 2021; Zellweger et al., 2020). For bryophytes as well as vascular plants, the more thermally buffered the forest, the higher the proportion of core specialists, in line with previous results (Gasparini et al., 2021; Govaert et al., 2020; Müller et al., 2019). As canopies undergo increased disturbance regimes with climate change, more generalists and less forest core specialists are thus expected in

understorey communities (Sanczuk et al., 2023), with a risk of homogenization at the landscape level.

Microclimate buffering should be incorporated in forest management strategies (Aussenac, 2000; Hylander et al., 2022; von Arx et al., 2013). Maintaining forest cover and limiting canopy disturbances could counterbalance the negative impacts of climate change on forest understorey plants (De Lombaerde et al., 2022; Govaert et al., 2021; Thom et al., 2020). Forests may conserve biodiversity in the understorey as microrefugia, if their canopy stays stable through time (Finocchiaro et al., 2023; Lenoir et al., 2017; Zellweger et al., 2020). Continuous cover and uneven-aged management are increasingly advised to limit the impact of the temporal discontinuity induced by clear-cutting (Boch et al., 2013; Máliš et al., 2023; Tinya et al., 2019). Retention forestry can accommodate both forest generalists and specialists, but some forest core specialists will be excluded because of insufficient buffering (Fedrowitz et al., 2014). To conserve most of these forest core specialists, our results confirm the need to keep large, high and dense forest stands with a high buffering capacity (Govaert et al., 2020; Sanczuk et al., 2023; Zellweger et al., 2020), even if increasing canopy cover may not be enough to mitigate climate change impacts on forest core specialists (Naqinezhad et al., 2022). Forests in protected areas with no or reduced management may be more thermally buffered than most managed forests (Frey et al., 2016; Máliš et al., 2023; Xu et al., 2022). Old-growth forests provide within-stand heterogeneity with small gaps due to individual tree mortality, while even-aged management creates more microclimate heterogeneity at the landscape level with different silvicultural stages (Menge et al., 2023; Schall et al., 2018). A mosaic of buffered and amplified microclimates may be the best option to promote forest biodiversity, by accommodating for species over the whole microclimate buffering to amplification gradient (Greiser et al., 2018; Hylander et al., 2022; Pincebourde et al., 2016). However, while disturbed forests often have higher species richness, it is not necessarily a relevant metric for conservation because species colonizing openings are mostly generalists (Boch et al., 2013; Tinya et al., 2019). Homogeneous and closed canopies of even-aged stands will only favour some forest core specialists, and under the deep shade of our most buffered stand, most of the forest species we analysed would be disfavoured or excluded, including many forest specialists (Gasparini et al., 2021; Vanderpoorten et al., 2004). Selection management or gap-cutting may allow both forest edge and core specialists, if not generalists, to coexist (Müller et al., 2019; Tinya et al., 2019). Different structures and management trajectories will locally mitigate or enhance the effects of climate change on plant communities through microclimate (De Frenne et al., 2013; Greiser et al., 2018; Menge et al., 2023; Naqinezhad et al., 2022; Tinya et al., 2021), and thus promote an evolutionary diversification of understorey plants, desirable for resilience (Møller et al., 2023).

### AUTHOR CONTRIBUTIONS

Eva Gril and Jonathan Lenoir conceived the study. Jonathan Lenoir coordinated and obtained the funding for the project. Eva Gril, Fabien Spicher, Boris Brasseur, Ronan Marrec, Vincent Le Roux and

Jonathan Lenoir collected the data. Alain Vanderpoorten, Eva Gril, Fabien Spicher and Jonathan Lenoir identified plant species. Emilie Gallet-Moron, Eva Gril and Fabien Spicher managed the database. Eva Gril and Jonathan Lenoir analysed the data. Eva Gril created the visuals, with Emilie Gallet-Moron for the maps. Eva Gril wrote the manuscript, with editing and commenting from all.

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## CONFLICT OF INTEREST STATEMENT

None.

## PEER REVIEW

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## DATA AVAILABILITY STATEMENT

The R script and data are available online on figshare: <https://doi.org/10.6084/m9.figshare.25358488> (Gril et al., 2024).

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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.** Regressions to obtain the slope parameter describing microclimate temperature buffering or amplification for Mormal (59, blue), Blois (41, green) and Aigoual (30, yellow).

**Appendix S2.** List of vascular plant and bryophyte species per group of forest affinity, with their occurrence in each forest.

**Appendix S3.** List of 22 vascular plant species with a different affinity to forest depending on the region.

**Appendix S4.** Response of vascular plants and bryophytes to microclimate by forest affinity, model parameters and significance.

**Appendix S5.** Microclimate optima, by species of vascular plants and bryophytes.

**Appendix S6.** Microclimate optima by forest affinity group, for vascular plants and bryophytes.

**Appendix S7.** Microclimate optima of bryophytes species, depending on their preferred substrate.

**Appendix S8.** Proportion of forest core specialists.

**Appendix S9.** Relating microclimate temperature buffering or amplification to light availability.

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