

# Cool topoclimates promote cold-adapted plant diversity in temperate mountain forests.

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## Abstract

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26 Climate strongly influences the composition and diversity of forest plant  
27 communities. Recent studies have highlighted the role of tree canopies in shaping understory  
28 thermal conditions at small spatial scales (i.e. microclimate), especially in lowland forests.  
29 In mountain forests, however, the influence of topography in environmental conditions (i.e.,  
30 topoclimate) is ought to also influence plants' perceived temperature. Understanding how  
31 topography and canopies interactively affect understory temperature is key to identifying  
32 stable refugia that could shelter cold-adapted forest specialist plants under climate change.

33 Here we report on growing season understory temperatures using 48 loggers in  
34 contrasting topographic features and canopy of a mid-range mountain valley spanning from  
35 475 m a.s.l. to 1203 m a.s.l. in the Vosges Mountains (NE France). We disentangle the relative  
36 importance and the effects of topography vs. canopy in determining local temperatures. We  
37 then evaluate how topography and canopy-induced variation in temperature drive plant  
38 community composition and richness in 306 floristic surveys across the studied mountain  
39 valley.

40 Our results show that topography outweighed canopy cover in explaining growing  
41 season understory temperatures. Regardless of canopy, the daily mean temperature of the  
42 growing season in south-facing ridges was 1.5 °C (CI: 0.62 - 2.38°C) warmer than shaded  
43 valley bottoms, while dense canopies cooled temperatures by 0.5 °C (CI: 0.02 - 0.98 °C)  
44 compared to less dense canopies. Topoclimate explained community composition as much  
45 as elevation and was the only significant predictor of species richness. Cold topoclimate  
46 harbored 30% more species than the average species richness across our plots. This increase  
47 in species richness was explained by an increase of cold-adapted species, both forest  
48 specialist and generalist species.

49 Our findings highlight a stronger role of topography compared to canopy cover on  
50 community composition in mountain forests via topoclimatic cooling of north-facing slopes  
51 and valley bottoms. The importance of topographic features to explain temperature cooling  
52 and diversity underpins their role as present and likely future microrefugia.

### 53 **Keywords**

54 Community ecology, forest, topoclimate, microclimate, topography, climatic refugia,  
55 diversity, understory vegetation.

## 56 1. Introduction

57 The study of topography influences on vegetation has fascinated ecologists for more  
58 than 150 years (Johnston *et al.*, 1848), and has further gained in relevance in the context of  
59 the 21<sup>st</sup> century climate warming (Ashcroft, 2010; Dobrowski, 2011; IPCC, 2021; Lenoir *et*  
60 *al.*, 2017). Species distribution and climatic conditions are often modeled at a coarse  
61 resolution (typically 1 km or coarser), and thereby fail to capture local variation of climate  
62 at finer grains (Franklin *et al.*, 2013) :for instance, the topoclimate shaped by terrain (i.e.  
63 slope and aspect mainly) and the forest-induced microclimate (Bramer *et al.*, 2018; De  
64 Frenne *et al.*, 2021; Kemppinen *et al.*, 2023). Enhanced predictive power obtained by using  
65 smaller grain climatic data confirms that species physiological limits are better captured by  
66 topography and forest microclimate (Haesen *et al.*, 2023). Given that these factors can  
67 attenuate warm macroclimate temperatures, their study is key to identify areas where local  
68 conditions are continually buffered in a warmer future (Ashcroft, 2010; De Frenne *et al.*,  
69 2021; Haesen *et al.*, 2023; Hannah *et al.*, 2014). Such areas, refugia, are of utmost  
70 importance as they can host source populations of cold-adapted species endangered by  
71 climate change. Protection offered by these refugia can be disrupted in when it is induced  
72 by tree canopies whereas topography-induced buffering is more stable (Ashcroft, 2010;  
73 Hylander *et al.*, 2022). As these buffer components coexist in temperate mountainous  
74 forests, determining which buffering process is at play will allow to better predict and map  
75 sources of biodiversity persistence.

76 Variation in aspect can create contrasting local temperatures as slopes oriented to  
77 the equator receive more solar radiation, and west-facing slopes receive radiation during  
78 the warmest period of the day. As a result, southwest-facing slopes in northern hemisphere  
79 mountains display warmer mean temperatures, longer growing seasons and shorter snow  
80 cover durations (Ashcroft *et al.*, 2008; Davis *et al.*, 2019; Rita *et al.*, 2021; Rolland, 2003).  
81 The physical properties of air also interact with topographic features such as hydrological  
82 basins (McLaughlin *et al.*, 2017), valley bottoms and sinks. This phenomenon creates local  
83 areas of cold and dense air pooling that decouple, i.e. remove any correlation, between  
84 local conditions from the regional climate (Gudiksen *et al.*, 1992; Pastore *et al.*, 2022), thus  
85 creating topographic refugia (Dobrowski, 2011). These temperature variations are observed  
86 on a moderate scale, from fifty to hundreds of meters, and will be called hereafter  
87 topoclimate (Lenoir *et al.*, 2013). To focus on moderate scale and magnitude variation in  
88 temperature, we exclude from our definition of topoclimate the lapse rate induced from  
89 elevation, as this process has a much stronger effect on temperature, comparable to  
90 macroclimatic variation (Lenoir *et al.*, 2013; Rolland, 2003).

91 The topoclimate interacts with what we define as forest-induced microclimate (with  
92 smaller scale variation, from a meter to 25 m) to jointly determine the understory  
93 temperature experienced by forest organisms (De Frenne *et al.*, 2021). Canopy shading and  
94 evapotranspiration lead to an overall decrease of temperature throughout the year,

95 exacerbated in summer by a buffering of high temperatures compared to open-air (De Frenne  
96 *et al.*, 2021; Zellweger, Coomes, *et al.*, 2019). These buffering effects are apparent and  
97 well documented in temperate lowland forests, but their relative importance in contrast to  
98 elevation and topography is less known, and current evidence has not reached consensus  
99 (Macek *et al.*, 2019; Vandewiele *et al.*, 2023). In temperate mountain forests, we expect  
100 that topography (elevation excluded) displays more variability than canopy cover, placing it  
101 as the main driver of understory temperature and thus community composition.

102 Community composition was proven to respond to canopy cover in lowland forests.  
103 This is evidenced by the decrease of the average thermal optimum of the present species (a  
104 proxy of species' affinity to climate) in forests where tree canopy is densifying (De Frenne  
105 *et al.*, 2013; Dietz *et al.*, 2020; Richard *et al.*, 2021) and where colder understory  
106 temperatures are predicted (Zellweger *et al.*, 2020). This sheltering of cold-adapted species  
107 by a dense canopy needs to be compared with the sheltering provided by topography in  
108 mountain forests, as topographical refugia are likely to offer longer-term buffering of  
109 temperature, whereas canopy cover is prone to sudden perturbation (dieback, windfall, etc.)  
110 (Ashcroft, 2010; Finocchiaro *et al.*, 2023). Topographic refugia also harbor cold-adapted  
111 flora and host populations of species outside their expected climatic range (Ellis & Eaton,  
112 2021; Finocchiaro *et al.*, 2023; Haesen *et al.*, 2023; Macek *et al.*, 2019). Less know is how  
113 variation in temperature owing to topography and canopy cover can influence local diversity.  
114 No change in diversity will indicate a reshuffling of community with microclimate, however  
115 we expect an increase in diversity as a moderate cooling can relieve cold-adapted species  
116 stress and competition without inducing dieback in species not adapted to cold conditions.  
117 In temperate mountain forests, it is possible that the sheltering provided by topography  
118 resembles the effect of canopy (e.g. lower maximum temperature, higher humidity). To test  
119 this hypothesis, we will also study the species' characteristics, expecting an increase of  
120 forest specialists that could demonstrate that topoclimate can mimic understory conditions  
121 of dense forests.

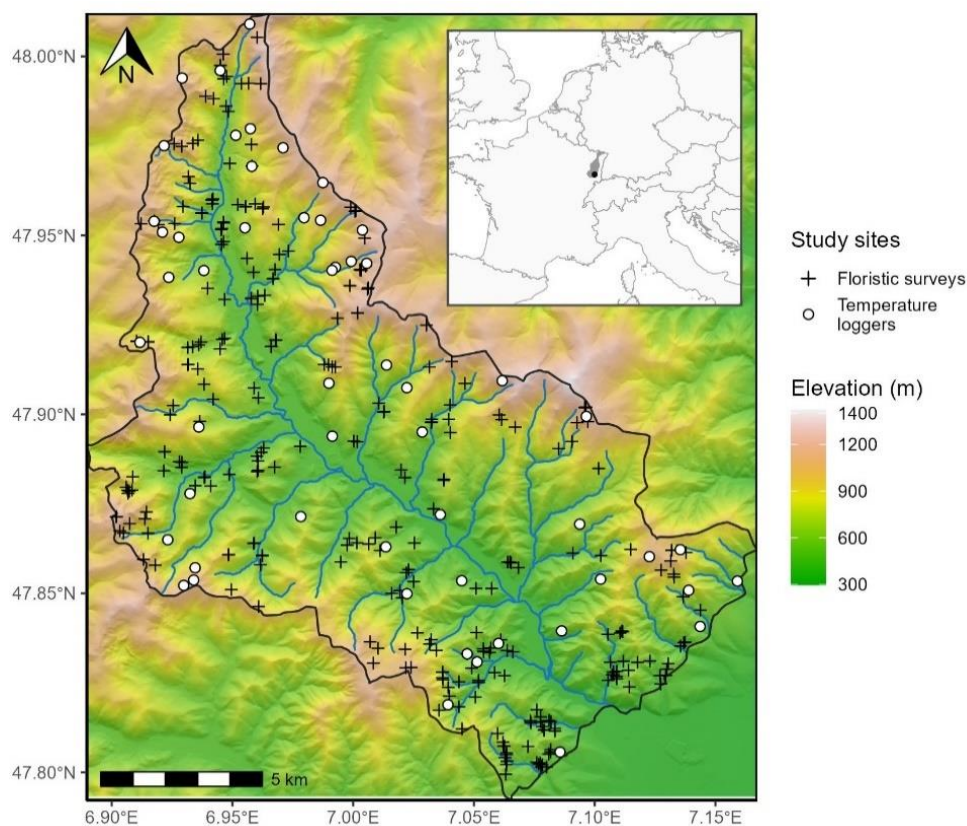
122 Here, we assessed the effects and relative importance of elevation, topography and  
123 canopy cover on *in situ* measured understory temperatures and plant community  
124 composition and richness. This partitioning will shed light on whether communities are more  
125 responsive to canopy or topographic variability, processes that have very different spatial  
126 and temporal patterns. This will allow conservation planning to efficiently target  
127 conservation areas. After accounting for the elevation gradient, we specifically asked: (1)  
128 Does topography (aspect and topographic position) outweigh canopy in explaining understory  
129 temperature? (2) does topography and canopy-induced variation in temperature determine  
130 community richness and mean species thermal optimum? (3) Are plant habitat preference  
131 and climatic affinity related to understory temperature?

## 132 2. Materials and Methods

### 133 2.1. Study Area

134 Our study region (221 km<sup>2</sup>) is delineated by the basin of the Thur River, located in  
135 one of the southmost valleys of the Vosges Mountain range in France (Figure 1). The Vosges  
136 are characterized by a continental climate with harsh winters and short and stormy summers.  
137 Its mean annual temperature ranges from 6 °C to 10 °C and precipitation ranges from 800 to  
138 2,000 mm year<sup>-1</sup> (period 1970-2000, Météo France weather stations IGN, 2013). The Thur  
139 River basin is on the warm and dry end gradient of the Vosges Mountains (IGN, 2013). Forests  
140 cover 76% of the Vosges, which transitions from mixed oak stands and monospecific *Picea*  
141 *abies* stands to mixtures of *Picea abies*, *Abies alba* and *Fagus sylvatica* as elevation increases  
142 (IGN, 2013). The soil of our study region is mostly shallow loam and sand with coarse  
143 elements. The most acidic soils are found at higher altitude because of the dominance of  
144 needles in the humus and the lower temperature at mountaintops (IGN, 2013; Piqué *et al.*,  
145 1994; Thomas *et al.*, 1999). The topography is highly variable, with an elevation ranging  
146 from 327 to 1424 m a.s.l. (but forest occurrence stops past 1250 m a.s.l.) with high  
147 topographic heterogeneity (Figure 1, Figure S1).

148



149  
150 *Figure 1: Study area (black outline) with the location of the temperature loggers (white*  
151 *circles) and the floristic surveys (black crosses). The colored scale represents elevation*  
152 *above sea level, in meters, obtained from a 25-m spatial resolution digital elevation model*

153 (IGN, 2017). Hillshade effects have been added to visualize the terrain. The blue line  
154 represents the Thur River and its tributaries. The inset shows the Vosges Mountain range  
155 (grey) and the location of the studied valley (black point) in western Europe.

## 156 2.2. Temperature Predictors

157 We used 25-meter resolution digital elevation model (IGN, 2017) to extract elevation  
158 (m a.s.l.), slope and aspect and to calculate topographical indices. Elevation was kept as is,  
159 as the lapse rate predictor, but does not fall under our definition of topography as we  
160 considered it a macroclimatic feature given how much control it has over temperature. This  
161 is evidenced by spatial autocorrelation (semivariance) of elevation saturating at a distance  
162 ten times greater than small scale topographic features (Figure S2). Accordingly, our  
163 definition of topoclimatic effect will be focused on smaller scale topographic features  
164 described hereafter. We specifically wanted to investigate the difference in radiation  
165 received between slopes of differences aspects, a well know driver of topoclimate  
166 temperatures, which its effect is less clear under canopy (Macek *et al.*, 2019). We did so by  
167 computing the Heat Load Index (HLI). HLI ranges from 0 to 1 (least to most incoming solar  
168 radiation) contingent on latitude, slope orientation and steepness. It is a measure of how  
169 daily mean temperature is warmed by topographic features most exposed to sunlight, and  
170 during the warmest period of the day (south and west slope in the northern hemisphere).

171 To investigate how cold air pooling, dictated by the topography of river basins,  
172 influences temperature, we computed a topographic position index (TPI). Cold air pooling  
173 ought to be a prominent explanatory factor of community persistence (Finocchiario *et al.*,  
174 2023; Pastore *et al.*, 2022). To do so, we normalized the Euclidian distance between the  
175 nearest ridge and nearest thalweg ( $TPI = D_{thalweg} / (D_{thalweg} + D_{ridge})$ ). TPI is the relative  
176 position of the cell in the shortest trajectory between a ridge and a drainage basin end,  
177 ranging from 0 (valley bottom) to 1 (ridge, Piedallu *et al.*, 2023).

178 We obtained the ‘tree cover density’ from the 2018 product of the Copernicus  
179 monitoring service as proxy for local canopy closure (Copernicus, 2018; Sannier *et al.*, 2023).  
180 This product consists of a 10-meter resolution percentage of canopy presence within the  
181 pixel (ranging from 0 to 100%) and was successfully used before to model microclimate  
182 buffering by canopy (Haesen *et al.*, 2021). To validate the assumption that this is a proxy of  
183 local canopy closure, and thus microclimatic variation induced by canopy, we correlated it  
184 with our field measurements of canopy closure (see below, 2.3 Temperature sampling). We  
185 rescaled this product to match the 25-m resolution of our other maps using bilinear  
186 interpolation (Hijmans, 2020). We rasterized (25-meter resolution) a 20-meter precision  
187 polygon map of French forest (IGN, 2019) to create a mask of the forested area of our study  
188 region to limit our analysis and temperature projection to forests, as we only investigate  
189 understory flora and temperatures in this study.

190 Our in our study region, within forested areas, our elevation ranges from 327 to 1362  
191 m a.s.l., HLI ranges from 0.16 to 1, TPI from 0 to 1, slope from 0.1 to 50° and canopy closure

192 from 0 (temporary deforested) to 1 (Figure S1). Variation in canopy closure was hover low,  
193 as 90% of the cells display a canopy closure higher than 72% (Figure S1), this indicates that  
194 the remote sensed product we use may not reflect finer scale gaps in canopy.

### 195 **2.3. Temperature Sampling**

196 We created a stratified sampling scheme to capture forest understory microclimate  
197 variability (Lembrechts *et al.*, 2021; Schweiger *et al.*, 2016). We created 8 elevation strata  
198 (spanning 20 m a.s.l. intervals) separated by 102 m. Those strata thus range from [468 - 488]  
199 to [1184 - 1204] m a.s.l. They are meant to control for the lapse rate (steady decrease in air  
200 temperature as pressure decreases with elevation, Lembrechts *et al.*, 2021), it is the main  
201 driver of temperature in the study area but we wanted to separate lapse rate from other  
202 topographic features effect.

203 Inside each of these strata, we defined 8 types of plots: 4 plots of below and above  
204 the median canopy closure of our study area (90% canopy closure) with a south or a north-  
205 facing slope (HLI > 0.70 and HLI < 0.60, respectively, value chosen to avoid flat terrains of  
206 HLI: 0.66). These 4 plots had moderate topographic position indices (between 0.2 and 0.8)  
207 and slope ( $10^\circ < \text{slope} < 25^\circ$ ), to avoid confounding their effects with the canopy closure  
208 and heat load effects. Additionally, we defined 2 plots with contrasting topographic position  
209 indices (lower than 0.2 and higher than 0.8) under high canopy closure and moderate slope.  
210 Lastly, we defined 2 plots with contrasting slopes: one on flat (slope <  $10^\circ$ ) and one steep  
211 (slope >  $25^\circ$ ) under high canopy closure and moderate topographic position (summary of the  
212 sampling scheme:

213

214 Table S1). These theoretical strata and plots were designed to systematically cover  
215 elevation, HLI, TPI and canopy closure variability, yielding similar results as the PCA-based  
216 approach proposed in Lembrechts *et al.*, 2021 as shown in Figure S3.

217 Of the initial 64 theoretical plots spanning the 8 strata, only 59 of the defined  
218 situations occurred, mostly because we lacked low topographic position indices (valley  
219 bottom) in high elevation classes. We randomly selected one cell for each plot and stratum  
220 located in public forests. We repeated this random drawing 10,000 times and kept the set  
221 of plots that maximized the mean minimum geographical distance between plots to reduce  
222 spatial autocorrelation.

223 We established the 59 temperature loggers in May 2021 and recorded their location  
224 with a GNSS receiver (Trimble TDC600, accuracy=  $\pm 2$  m undercover). We placed every logger  
225 in public forests to avoid legal constraints (public forest makes up 80% of the forested area  
226 in our study region), with no constraints regarding accessibility. We measured canopy closure  
227 (0-100%) by a visual observation in a 25-meter radius around the logger. We also estimated  
228 canopy closure (0-100%) with a planar picture of the canopy by means of a smartphone  
229 (Samsung A40, focal length: 25mm, sensor size: 1/2.8") placed on top of the logger and the

230 sky segmentation ‘*Glama*’ application (Tichý, 2016). Plots tagged as low canopy cover were  
231 placed accordingly by selecting sites with less than 50% canopy closure as computed by  
232 ‘*Glama*’. The visual estimation of canopy closure (25-meter radius) was significantly  
233 correlated with the remote sensed tree density ( $R^2$  of the linear relationship = 30.0%, Figure  
234 S4), but a weak and non-significant correlation was found with the picture analyzed by  
235 ‘*Glama*’ (Figure S4).

236 We recorded air and soil temperatures with TMS-4 loggers (resolution= 0.0625 °C,  
237 accuracy=  $\pm 0.5$  °C) protected with a radiation shield (Wild *et al.*, 2019). The loggers  
238 recorded temperature every 15 minutes until August 2022. We used air temperature 15 cm  
239 above the soil surface because it is likely the most representative temperature experienced  
240 by understory plants. We cleaned the time series with the ‘*myClim*’ R package (Man *et al.*,  
241 2023). More specifically, we removed any duplicates, checked for missing values, and  
242 resolved inconsistent time step to the closest 15 minutes default of our loggers. We  
243 calibrated the loggers beforehand for a range of -20 °C to +40 °C by placing them in a freezer  
244 and drying oven along with a T-type thermocouple (accuracy=  $\pm 0.2$  °C). From the recorded  
245 period, we focused on the growing season (GS hereafter), from 01/04/2023 to 15/08/2023,  
246 as it is the most critical period for plant growth. Out of the 59 loggers, 11 were either  
247 malfunctioning, stolen, destroyed by animals or displayed erroneous values and were  
248 discarded.

249 We checked the capacity of our final sample to cover the variability of our study  
250 region following the PCA-based approach of Lembrechts *et al.*, (2021). Our final sampling  
251 was able to cover the variability of the valley, except for extreme values of low canopy  
252 cover and the unusual valley bottoms of high elevations. The loss of loggers was evenly  
253 distributed over plot types, except for the low canopy cover that suffered the most losses  
254 (Figure S3).

#### 255 **2.4. Floristic and Species Characteristic Dataset**

256 To test how flora responded to understory temperature, we compiled floristic surveys  
257 performed (during the growing season) by students and professors covering soil and climatic  
258 transect of the region between 2009 and 2022 (average year= 2015.6). All plots were  
259 surveyed for all vascular plant species in the herb layer (smaller than 1 m) and their  
260 percentage ground cover was visually estimated. We had 306 floristics surveys in total across  
261 the study region. Floristic surveys were performed in 20 x 20 m squares (400 m<sup>2</sup>) with the  
262 GPS position (recorded with built-in tablet GPS; accuracy=  $\pm 10$  m) as the center. We used  
263 this position to extract elevation, heat load index, topographic position index and canopy  
264 cover for every survey. We harmonized taxonomy to the TaxRef V13 standard (Gargominy,  
265 2022). We focused on herbaceous species in the analysis to focus on community dynamics  
266 that may reflect shorter-term climate while not being directly targeted by forest  
267 management interventions.



268 One of the objectives of our study is to assess whether local variation of temperature  
269 due to topography and canopy benefits cold-adapted species, as they are projected to be  
270 the most threatened by climate warming (Thuiller *et al.*, 2005). For this purpose, we used  
271 the species' thermal optimum value from ClimPlant V.1.2 (Vangansbeke *et al.*, 2021). These  
272 thermal optima are computed from the mean annual temperature (°C) within the range of  
273 species obtained from Europe-extent distribution atlases and represent the median  
274 temperature of the realized niche. Out of the 348 unique recorded species, 309 were  
275 assigned a thermal optimum value, covering 90.0% of the occurrences of the whole floristic  
276 dataset. We averaged the thermal optimum of every species (without weighting for  
277 abundance) of a given survey to obtain the Community Thermal Index (hereafter CTI), which  
278 quantifies the thermal preference of the whole community (Borderieux *et al.*, 2023;  
279 Vangansbeke *et al.*, 2021). We did not weigh the calculation by species abundance, from a  
280 conservation standpoint rarer species may be the most interesting in CTI calculation but may  
281 be underrepresented when weighted by abundance. We calculated species richness of a plot  
282 as the number of recorded species whether they had an associated thermal optimum in the  
283 database or not. By doing so, we wanted to include rare species that were not included in  
284 ClimPlant so that our specific richness is representative of the species pool of our study  
285 region. The soil of our study region can greatly vary in acidity, we also assigned a pH optimum  
286 value obtained from a bioindication database to each species (Gégout *et al.*, 2005), and  
287 averaged (not weighted by abundance) it to obtain to control for soil conditions via a  
288 bioindicated pH per plot.

289 We used the EuForPlant regional list of forest plant species (Heinken *et al.*, 2022) to  
290 assess species habitat affinity. We assigned to each species one of the following affinities:  
291 (1.1) species of closed forest (1.2) species which occur in forest edges and openings (2.1)  
292 Species which primarily occur in forests but also found in cultural landscapes and forest  
293 remnants (2.2) species of open habitats that occurs in forest exclusively through opening  
294 and early succession. We excluded species of open vegetation (classified "O") because of  
295 their low number of occurrences (n= 42). In total, 274 species were assigned to an affinity  
296 class, covering 85.7% of the occurrences.

## 297 **2.5. Understory Temperature Modeling**

298 We aggregated the 15-minute frequency time series of the recorded temperature of  
299 the growing season 2022 (a warmer than average year, see 3.1) to daily mean and maximum  
300 temperature. This aggregation process first removed values outside of the 5<sup>th</sup> to 95<sup>th</sup> centile  
301 interval of daily values to avoid biasing results due to logger malfunction or a brief burst of  
302 sunshine on a logger (thus maximum temperature is the 95<sup>th</sup> centile). We then averaged the  
303 mean or maximum daily temperature to obtain one unique value per logger, the mean daily  
304 and maximum daily temperature of the growing season. Having a unique value facilitates  
305 the modeling process by removing the need to account for the lack of statistical dependence  
306 of temperature time series, and one summary value of the GS is enough as we aim to uncover  
307 spatial variation of community composition instead of temporal variation.

308 We wanted to disentangle the relative contribution of lapse rate, topography and  
309 canopy to understory temperature, and wanted to map estimates of understory over the  
310 study area. To this end, we used a linear model to predict mean and maximum daily  
311 temperature of the growing season with elevation, heat load index, topographic position  
312 index and remote sensed canopy density as explanatory variables. We preferred remote-  
313 sensed canopy cover over the *in-situ* measurements which allowed us to map the  
314 temperature models over the entire study area, and thus infer the understory temperature  
315 of floristic surveys (mostly without canopy closure records). The warming due to radiation  
316 can be tempered when there is canopy to intercept light, canopy buffering is most apparent  
317 during the warmest hour of the day (Davis *et al.*, 2019; De Frenne *et al.*, 2021). To account  
318 for this, we tested an interaction between heat load index and canopy closure and retained  
319 the interaction in the final model if found significant. We checked the assumption of linearity  
320 between temperature and its predictors by visually assessing the raw data (Figure S5) and  
321 the residuals (Zuur & Ieno, 2016). The Variance Inflation Factor never exceeded 1.2 in our  
322 understory temperature models, indicating no sign of correlation among predictors.

323 For each understory temperature model, we did an analytical partitioning of variance  
324 to assess which process influenced understory temperature most (Barbosa *et al.*, 2013). The  
325 contribution of the predictors was grouped into three groups: elevation, “topoclimate” (TPI  
326 and HLI) and “microclimate” (canopy closure). For simplicity and because shared effects had  
327 little contribution, we added to each group contribution half of their shared effect to  
328 summarize the contribution of the three groups in three numbers.

329 We additionally fitted two linear models with the field measured canopy closure (25  
330 m radius observation and planar photography) instead of the remotely sensed measurement  
331 to test different methods of canopy closure estimations (Table S2, Table S3).

332 We used the mean understory temperature model ( $R^2 = 92.2\%$ ) to map the  
333 contribution of elevation (i.e., lapse rate), of topoclimate (heat load index and topographic  
334 position) and of forest-induced microclimate (canopy closure) to the mean understory  
335 temperature separately. We mapped the lapse rate by using only the intercept and the  
336 elevation parameter. We mapped the topography effect on temperature compared to a  
337 reference situation (heat load index of a flat terrain = 0.66 and topographic position index  
338 equal to 0.5, prediction of + 1.34°C) and using the two topographic indices. We mapped the  
339 contribution of canopy cover by multiplying its parameter to the tree density product, this  
340 projection is however extrapolated for the 20% of pixels with a canopy closure lower than  
341 79%. This extrapolation was necessary to cover the whole study region and to predict  
342 temperature to floristic surveys within those areas. To assess the spatial autocorrelation of  
343 the resulting maps (Figure S2), we computed their variogram (scaled semivariance), with a  
344 lag of 25 m and a cutoff of 2000 m (Naimi *et al.*, 2014).

## 345      **2.6. Floristic Composition Analyses**

346           We used a linear model to predict CTI. Species richness being a positive discrete  
347 number, we used a negative binomial generalized linear model as overdispersion prevented  
348 the use of a Poisson model. The predictors of both models were the contribution to mean  
349 understory temperature of elevation, topoclimate and microclimate (the unit of every  
350 predictor is thus °C). The soil of our study region can display very different nutrition status  
351 and acidity, which can impact both the richness and composition of a community (Degen et  
352 al., 2005; Koerner et al., 1997; Zellweger et al., 2015). In addition, soil pH is also negatively  
353 correlated with elevation (Pearson coefficient: 0.40 ,Piqué *et al.*, 1994; Thomas *et al.*,  
354 1999). To account for this, bioindicated pH was also a predictor in the models. We tested  
355 that no collinearity between soil acidity and elevation arose when including both by  
356 computing a Variance Inflation Factor (VIF, Fox & Weisberg, 2019). For both models,  
357 elevation displayed the higher VIF (1.27, well below the threshold of 5, that indicates  
358 collinearity, James *et al.*, 2023).

359           We assessed the validity of our models (including temperature models) by testing the  
360 assumption of normality and homoscedasticity of the residuals model following (Zuur & Ieno,  
361 2016). All assumptions were met (Figure S6), all the P-values of the Kolmogorov-Smirnov  
362 test, dispersion test and outlier test of the normalized Dharma residuals were not significant  
363 (Hartig, 2024). We tested the significant difference from 0 of the estimated parameters with  
364 a Wald test.

365           As the 306 surveys uniformly covered the topography effect on temperature (Figure  
366 S7), we could split them into three classes of 102 surveys corresponding to a “cold”,  
367 “moderate” and “warm” topoclimate effect (a linear prediction of contribution to  
368 temperature by TPI and HLI as there was no interaction with canopy cover). The thresholds  
369 separating the three classes were determined so that classes have equal number of plots.  
370 This discretization allows to directly compare the total occurrence of species, as in Figure  
371 4, thanks to a fixed sampling intensity between classes. It also allows to compute more  
372 comprehensive effects of topoclimate over CTI and species richness (e.g. “cold” plots exhibit  
373 on average 5 more species than “warm” plots) than with linear estimates. We tested the  
374 difference in species richness and CTI between these classes with Wilcoxon rank-sum tests  
375 (Rey & Neuhäuser, 2011).

## 376      **2.7. Software**

377           We handled spatial data with the ‘*raster*’ and ‘*sf*’ package (Hijmans, 2020; Pebesma,  
378 2018), all the later analyses were carried on with R.4.2.2 (R Core Team, 2019). We computed  
379 HLI (McCune & Keon, 2002) using the ‘*spatialEco*’ R package (Evans & Murphy, 2021). We  
380 used the ‘*MASS*’ package to fit the negative binomial generalized model (Venables & Ripley,  
381 2002). We computed the VIF using the ‘*car*’ package (Fox & Weisberg, 2019). Microclimate  
382 temperatures were cleaned using the ‘*myClim*’ R package (Man *et al.*, 2023). We used  
383 ‘*ggplot2*’ and ‘*ggspatial*’ packages for data visualization (Dunnington & Thorne, 2020;

384 Wickham, 2011). We performed variance partitioning with the ‘*modEVA*’ package (Barbosa  
385 *et al.*, 2013).

## 386 **3. Results**

### 387 **3.1. Environmental Determinant of the Understory Temperature**

388 The growing season (GS) temperature of 2022 was above average (mean GS  
389 temperature of the period 2005-2020=11.6 °C, mean 2022 GS temperature=13.2 °C,  
390 Markestein weather station (1,184 m a.s.l), (Météo France, 2024)). As a result, the mean  
391 daily temperature of the understory (15 cm above the soil surface) was 14.6 °C and spanned  
392 between 11.9 °C to 17.5 °C for the higher (1203 m a.s.l) and lower (475 m a.s.l) elevation  
393 sensors, respectively. The mean daily maximum temperature of the GS was 19.3 °C and  
394 reached a maximum of 24.7 °C for the lowest elevation plots.

395 The lapse rate explained 87.4% of the variation in mean temperature, the topographic  
396 factors (heat load and topographic position index) 3.95%, and canopy cover accounted for  
397 0.82%. The  $R^2$  of the linear model was 92.2%. Elevation was the primary driver of mean  
398 temperature variation, with a lapse rate estimated at -0.68 °C by 100m (Table 1). The model  
399 revealed that HLI - contingent on aspect and slope - was the second driver of mean  
400 temperature, which can vary up to 1 °C between low and high radiation slopes. Topographic  
401 position also had a significant effect on temperature: the mean temperature was 0.56 °C  
402 lower in the bottom of a valley compared to ridges. Lastly, canopy closure (remotely sensed)  
403 cooled understory temperatures. An increase of 20% of total canopy cover resulted in a  
404 decrease of 0.57 °C. No significant interaction between topography features metric and  
405 canopy closure was found in the mean and maximum understory temperature model.

406 The same predictors except for topographic position were significant in the mean  
407 daily maximum temperature model, but the model explained overall less variation ( $R^2$  of  
408 81.2 %). The heat load index had a higher contribution (21.5%) in the maximum temperature  
409 compared to the mean temperature model, daily maxima varied for 3.3 °C between low and  
410 high heat load indices (Table S4). Canopy closure has a stronger effect (contribution to  $R^2$   
411 of 3.2%) on maximum temperature than on mean temperature.

412 Same models where remotely-sensed canopy closure was replaced with field-  
413 measured canopy closure showed overall similar trends, but with difference in estimates  
414 significance. Canopy cover visually estimated in a 25-meter radius was not significant in  
415 predicting mean temperature (Table S2). Immediate canopy cover (smartphone  
416 photography) above the logger explained significantly mean temperature with an interaction  
417 with heat load index, low immediate canopy cover in high radiation slopes displayed warmer  
418 mean temperature (Table S3).

419 *Table 1: Estimated parameters, their standard error and p-values of the predictors included*  
420 *in models of the daily mean growing season temperature. The range of the predictors in*

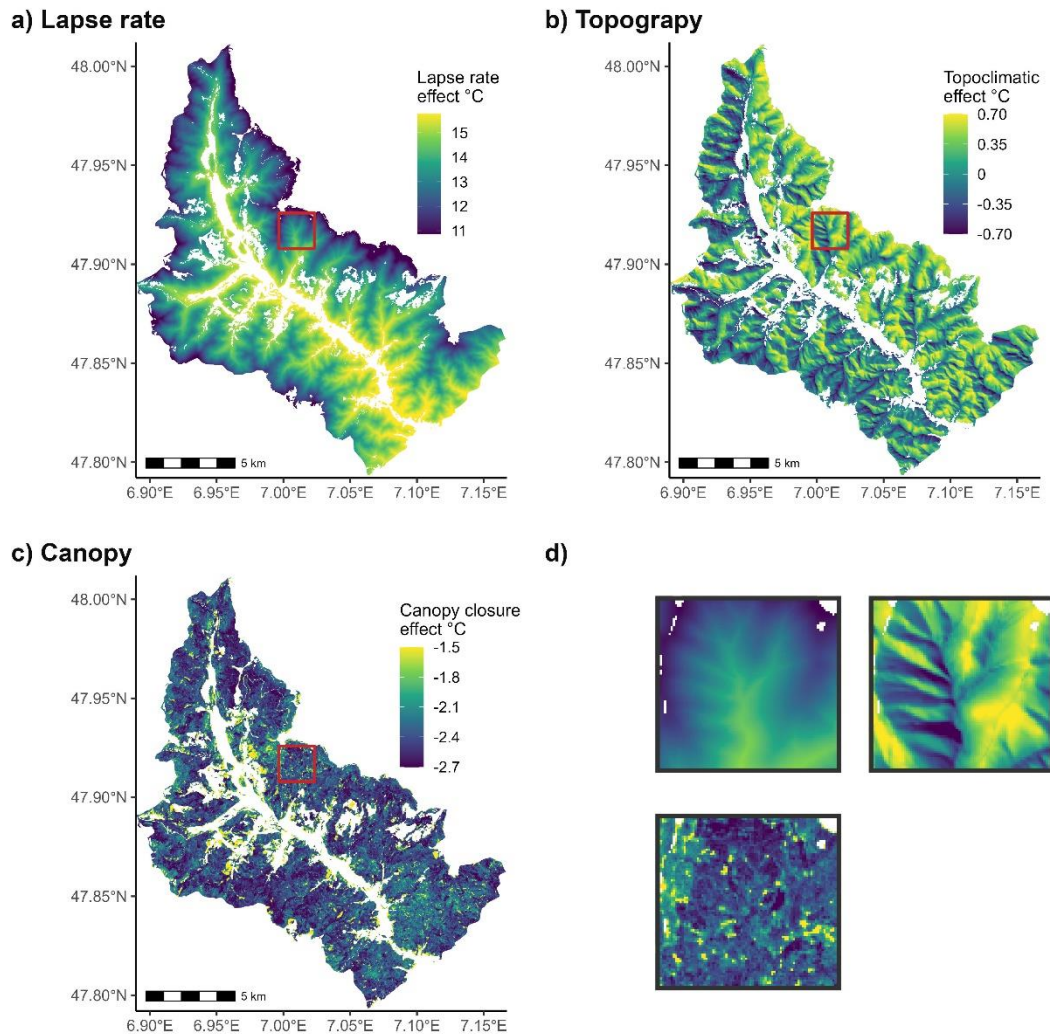
421 the calibration dataset and their standardized effect size on the temperature (standard  
 422 deviation \* estimate) are displayed. The percentage of explained variation per type of  
 423 predictor is included. P-values were obtained with a Wald test on parameters. Heat load  
 424 and topographic position have no units (n.u., refer to the methods for their calculation).

Predictor	Type of predictor	Estimate	Standard error	Range	Effect size (°C)	Explained variation (%)	P-value
Intercept (°C)		21,1	1,11				<10 <sup>-4</sup>
Elevation (m a.s.l.)	Elevation	-0.00684	0.000311	475 : 1203	-1.50	87.4	<10 <sup>-4</sup>
Heat load index (n.u)	Topoclimate	1.53	0.333	0.34 : 0.95	0.30	3.95	<10 <sup>-4</sup>
Topographic position (n.u)		0.656	0.276	0.15 : 1	0.16		0.0220
Canopy closure (%)	Microclimate	-0.0272	0.0115	79.0: 100	-0.16	0.817	0.0229

425

426 The spatial variation of elevation, topography and canopy closure reveals a complex  
 427 and fine-grained contribution of this factors to the forest understory climate (Figure 2). We  
 428 mapped the individual contributions of elevation (Figure 2.a), topoclimate (heat load index  
 429 and topographic position summed; Figure 2.b) and canopy cover (i.e., microclimate; Figure  
 430 2.c) in the study area. We observed strong effects on understory temperatures caused by  
 431 steep spatial difference of elevation, topography and fine-grained canopy cover (Figure 2.d).  
 432 Lapse rate autocorrelation peaked at 6000 m, while topography in was autocorrelated in a  
 433 moderate scale 750 m, canopy-induced variation in temperature autocorrelated in the  
 434 smallest scale and peaked at 450 m (Figure S2).

435



436  
 437 *Figure 2: a) Elevation induced change in mean growing season understory temperature of*  
 438 *the growing season (lapse rate of  $-0.68^{\circ}\text{C}\cdot 100\text{ m}^{-1}$ ), assuming a canopy closure of 90% and*  
 439 *no effect from topography. b) mean understory temperature effect induced by topography*  
 440 *(heat load and topographic position, i.e. topography) assuming an average canopy cover*  
 441 *(90%), compared to a moderate situation (flat terrain midslope). c) mean understory*  
 442 *temperature cooling induced by canopy closure assuming no effect from topography. For*  
 443 *visualization purposes only we restrained the minimal cooling to  $-1.5^{\circ}\text{C}$ , however some*  
 444 *pixels displayed lower values up to  $0^{\circ}\text{C}$  due to low canopy closure. d) 2 km per 2 km zoomed*  
 445 *inset of the red square of the other panels, their color gradient corresponds to the color*  
 446 *scale presented in the other panels a-c, respectively. Blank pixels represent land covers*  
 447 *other than forests or forests outside of the study region. Linear model  $R^2$ : 92.2%.*

### 448 **3.2. Microclimatic Determinants of the Floristic Composition**

449 Floristic surveys harbored on average 19 herbaceous species (s.d. 10.7), and a mean  
 450 community thermal index (CTI) of  $7.8^{\circ}\text{C}$  (s.d. 0.55). Bioindicated soil pH was the main  
 451 predictor of CTI and species richness (Table 2). More acidic soils had less diverse and cold-  
 452 adapted communities. The overall linear CTI model explained a moderate amount of  
 453 variability ( $R^2$ : 35.6%).

454           After soil pH, elevation-induced (lapse rate) and topoclimate were the main predictor  
455 of CTI, of comparable importance (effect size of 0.14 and 0.12 respectively). Topographic  
456 effect was also a significant predictor of species richness, of major importance (an increase  
457 of 1.5 species per plot per decrease, of one standard deviation of topographic effect on  
458 temperature, i.e., cooling, Table 2). The lapse rate was not significant in explaining species  
459 richness (Table 2). The forest-induced microclimate was not a significant predictor in any of  
460 the models (Table 2). We focused the subsequent community analysis around topoclimatic  
461 effects, as canopy cooling did not significantly explain the species richness nor CTI.

462           Mean and maximum temperature were highly correlated (Pearson coefficient: 0.86),  
463 as a result, a similar effect on flora is found when using predicted effect on max temperature  
464 instead of mean temperature, with a small decrease in fit quality (-1.4% in  $R^2$  for CTI model,  
465 -6 in log-likelihood for the species richness model, Table S5).

466

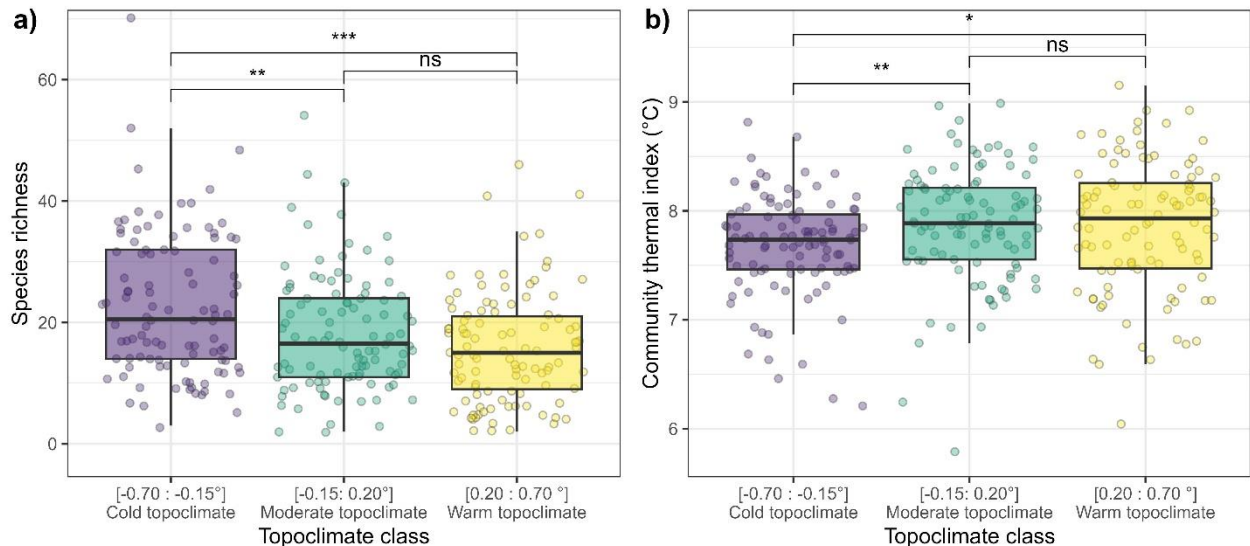
467 *Table 2: Estimated parameters, their standard error and p-values of the predictors of the*  
 468 *community thermal index (CTI) linear model, and the species richness negative binomial*  
 469 *generalized linear model. The range of the predictors and their standardized effect size*  
 470 *on the community predicted variable (standard deviation \* estimate) are displayed. The P-*  
 471 *value is obtained by a Wald test on the parameter.*

Model	Predictor	Estimate	Standard error	Range	Effect size	P-value
<b>Species richness</b>	Intercept (°C)	0.212	0.403			0.598
	Lapse rate (°C)	0.0218	0.0187	12.6 : 18.5	0.46	0.243
	Topography effect (°C)	-0.38	0.0795	-1.55 : -0.13	-1.50	<10 <sup>-4</sup>
	Canopy cooling (°C)	0.0439	0.121	-2.72 : -1.31	0.13	0.716
	Bioindicated pH	0.406	0.0315	3 : 7.15	5.2	<10 <sup>-4</sup>
<b>Community Thermal Index (°C)</b>	Intercept (°C)	5.18	0.406			<10 <sup>-4</sup>
	Lapse rate (°C)	0.0885	0.0188	12.6 : 18.5	0.14	<10 <sup>-4</sup>
	Topography effect (°C)	0.364	0.0804	-1.55 : -0.13	0.12	<10 <sup>-4</sup>
	Canopy cooling (°C)	-0.0236	0.123	-2.72 : -1.31	-0.049	0.848
	Bioindicated pH	0.272	0.0308	3 : 7.15	0.25	<10 <sup>-4</sup>

472

473 We divided the 306 floristic surveys into cold, moderate and warm topoclimatic  
 474 classes each comprised of 102 surveys based on topography-induced change in temperature.  
 475 The cold topoclimatic class displayed 23 species on average, while the two other classes  
 476 displayed 18.5 species on average (Figure 3.a). This difference of approximately 5 species  
 477 was significantly different (Figure 3.a). The mean CTI of the cold topoclimatic class was 7.7  
 478 °C, which is significantly lower by 0.19°C than the CTI of the two other classes (Figure 3.b).  
 479 No such differences were found when using microclimatic (canopy) cooling was used to  
 480 create the classes (Figure S8). This discretization of the dataset displayed results as those  
 481 observed using the continuous predictors of the linear model (Table 2, Figure S7).

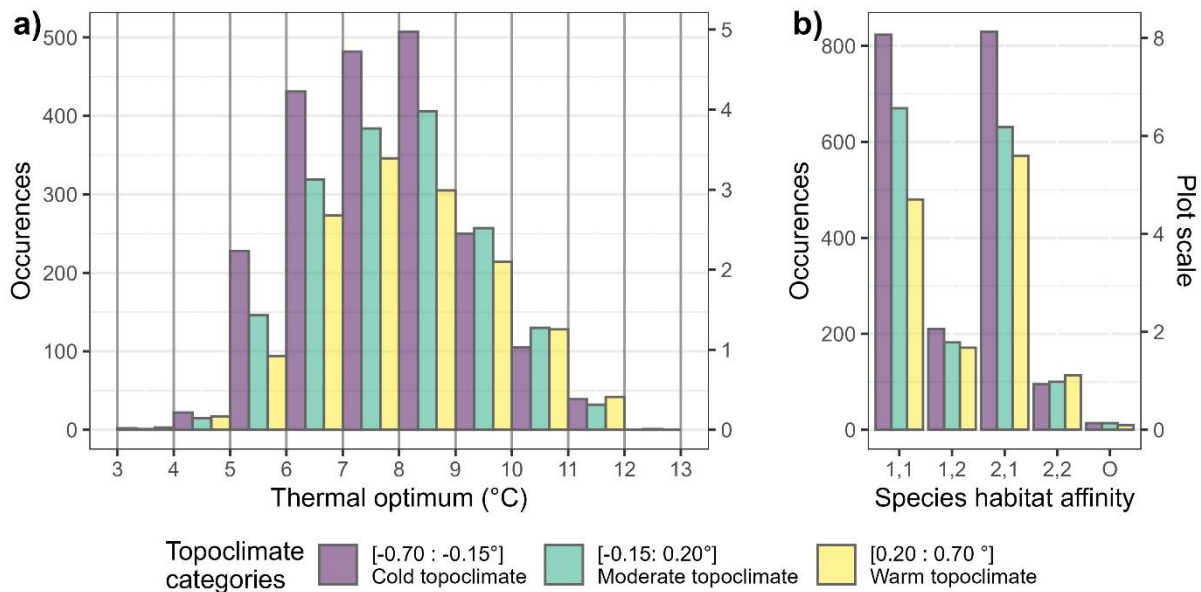




482  
 483 *Figure 3: Species richness (a) and community thermal index (b) of 306 floristic surveys*  
 484 *evenly spread into three topoclimate classes of even number of plots (n=102 species by*  
 485 *class). The p-value significance of a Wilcoxon test between two classes is displayed as*  
 486 *follows: (ns):  $p > 0.05$  (\*):  $p < 0.05$  (\*\*):  $p < 0.01$  (\*\*\*):  $P < 0.001$ .*

487 The decreases in CTI and the increase in species richness in the cold topoclimatic  
 488 class were explained by a surplus of relatively cold-adapted species (i.e. with a species  
 489 thermal optimum of 9 °C or less) (Figure 4.a). A two-sided Kolmogorov-Smirnov test  
 490 confirmed that the distribution of species thermal optimum in the cold topoclimate class is  
 491 significantly different from the other two (P-value against warm=  $< 10^{-6}$ , P-value against  
 492 moderate = 0.00282). No difference in distribution was found between the warm and  
 493 moderate class (P-value = 0.18). The plots (n=102 vegetation surveys) in cold topoclimates  
 494 displayed in total more than 50 to 100 more occurrences of relatively cold-adapted species  
 495 per thermal optimum classes (1°C) than the other two categories (Figure 4.a). The  
 496 intermediate topoclimatic class (n=102) also had a higher number of cold-adapted species  
 497 compared to the warm topoclimatic class (n=102, Figure 4.a). The cold topoclimatic class  
 498 displayed 300 more forest-specialist species occurrences (Heinken *et al.*, 2022) than the  
 499 other warmer topoclimatic classes, whereas the occurrences of generalist species increased  
 500 by 200 in total (Figure 4.b). We recorded a total of 246, 242 and 223 species (i.e., species  
 501 pool) in the cold, intermediate and warm topoclimatic classes, respectively. A total of 58,  
 502 41, and 33 species were unique to the cold, intermediate and warm topoclimatic classes,  
 503 respectively. This means that there are nestedness of species between communities, as  
 504 shown in Figure S9.

505



506  
 507 **Figure 4:** Occurrences of species in the three topoclimatic classes as a function of a) their  
 508 thermal optimum (°C) and b) their habitat affinity defined by the EuForPlant list as follows:  
 509 1,1: closed forest mainly 1,2: forest edges and opening 2,1: forest and open vegetation 2,2:  
 510 mainly in open vegetation (Heinken et al., 2022) The plot-scale occurrence of species is also  
 511 shown (e.g., 400 occurrences corresponds to approximately 4 species per plots).

## 512 4. Discussion

513 We found that both canopy cover and topographic factors strongly influenced  
 514 (without interacting) understory temperature during the growing season. We disentangled  
 515 the elevation gradient from the topoclimatic and canopy-induced factors by estimating the  
 516 lapse rate separately, which was expectably the main driver of understory temperature  
 517 (Figure 2). After controlling for the lapse and pH, the temperature cooling by topographic  
 518 factors (Heat load and topographic position) was the only significant driver of community  
 519 composition and richness. Our understory temperature model allowed us to separately  
 520 predict the lapse rate, topoclimatic effect and canopy cover cooling with mean temperature  
 521 as a unit. This allows inferring direct links between temperature variation and communities,  
 522 a necessary step to advance correlative studies.

### 523 4.1. Understory temperature determinants

524 The positive correlation found between temperature and heat load can be attributed  
 525 to the higher radiation an equator-facing slope receives, which increases both the mean and  
 526 daily maximum temperature of the growing season in closed forests. This contrasts with a  
 527 previous study which only found an effect of heat load on maximum temperature (Macek *et al.*,  
 528 2019). We measured temperature at 15 cm above the surface, which may explain the  
 529 higher sensitivity of mean GS temperature to aspect compared to Macek *et al.*, (2019), who  
 530 measured temperature at 2 m above the surface. Alongside heat load, we found that  
 531 topographic position influenced mean temperature so that ridges were warmer, and valley  
 532 bottoms were cooler (given equal elevation) but had no effect on maximum temperature.

533 We attribute this decrease in temperature to cold air pooling that occurs during nighttime,  
534 thus influencing mean daily temperature but with a minimal effect during the hottest hour  
535 of the day, when air temperature is homogeneously warm (Smith *et al.*, 2010; Vosper &  
536 Brown, 2008). The cooling effect of understory temperature by canopy cover was most  
537 apparent for maximum temperature but was also significant for mean temperature, although  
538 with a small effect size of  $-0.16$  °C. These observations concur with studies with comparable  
539 sampling (Davis *et al.*, 2019; Macek *et al.*, 2019).

540 We found that topoclimatic factors outweighed canopy closure in explaining  
541 understory temperature in our study area. This finding adds to the current divergent results  
542 from Macek *et al.*, (2019) who found no effect of canopy and Vandewiele *et al.*, (2023) who  
543 found a predominance of canopy control on temperature in mountain forests. These  
544 apparent contrasting results illustrate the complexity of factors in mountain forest  
545 microclimates, potentially depending on site-specific variations in topography and canopy  
546 cover, alongside with synoptic conditions leading to difference in transmittance. Our  
547 sampling design and subsequent loss of loggers hampered our ability to capture the canopy  
548 closure gradient effect on temperature. In our effort of representativeness, our “low  
549 canopy” plots displayed a remotely sensed canopy closure of 75%, as there was a dramatic  
550 decrease of pixels with values lower than that (Figure S9). However, Zellweger *et al.*, (2019)  
551 showed that temperature canopy cooling is more apparent at low canopy cover levels, and  
552 saturates past 80% canopy cover. Our limited number of loggers below that threshold could  
553 also be the reason why we did not observe a strong effect of canopy on temperature. We  
554 argue that our results are interpretable as a comparison of topographic and canopy effects  
555 within already forested stands, but not as a comparison of open and closed forests. In  
556 previous iterations of the temperature models, we tried to account for the ration of  
557 broadleaved and evergreen canopy trees (Díaz-Calafat *et al.*, 2023) but found no significant  
558 effect. This could be due to the study period of the growing season, representing leaf-on  
559 conditions and thus reducing the difference in canopy buffering induced by lack of leaves in  
560 leaf-off conditions.

561 Part of the challenge to determine canopy cover controls in mountain forests stems  
562 from the myriads of methods that are used to estimate canopy cover, ranging from  
563 hemispheric photographs, terrestrial lidar derived metrics to remotely sensed canopy cover  
564 estimations (Ma *et al.*, 2017; Zellweger, De Frenne, *et al.*, 2019). We used Copernicus tree  
565 density 2018 satellite images to calibrate the microclimatic model and predict its buffering  
566 effect on communities. Remote sensed tree closure density does not account for the vertical  
567 profile of trees, which have profound influence on sunlight interception and consequently  
568 on understory temperatures (Gril *et al.*, 2023; Zellweger, Coomes, *et al.*, 2019). Remotely  
569 sensed canopy cover was significantly but poorly correlated with our field measures (visual  
570 estimation and photography). This poor correlation could increase uncertainty in subsequent  
571 prediction of canopy-induced change in temperature, making more difficult to study  
572 community composition and richness. Consistent hemispheric photography of loggers and

573 vegetation plots, or remote sensed lidar offers appealing alternatives to better capture  
574 canopy closure variation independent of the topography context.

575 We fitted additional understory temperature models with in-situ measurements of canopy  
576 cover to conservatively reject canopy cover as prominent driver of microclimate and  
577 consequently community composition. These models showed no correlation between  
578 understory temperatures and canopy closure except from the interaction between  
579 immediate canopy closure (photography) and Heat Load Index (Table S2,

580 Table S3). Previous studies have shown that a localized lack of canopy has stronger warming  
581 effect when being located in equator-facing slopes (Davis et al., 2019; Rita et al., 2021).  
582 This explains why our most local measure of canopy closure only shows a significant  
583 interaction. This demonstrates the need to simultaneously study multiple microclimatic  
584 drivers and their interactions in mountain ranges (Davis et al., 2019; Greiser et al., 2020).

#### 585 **4.2. Understory temperature effect on communities**

586 We found that temperature variation owing to topography was equally important in  
587 shaping a community's affinity to climate compared to that of the elevational gradient  
588 (Table 2, after soil pH has been controlled for). This is likely a consequence of environmental  
589 selection pressure on community assembly. Lower temperature at higher altitudes or in  
590 topographically shaded slopes can exert a selection pressure on species not adapted to cold  
591 whereas lower elevation and high radiation slopes select species not sensitive to late  
592 freezing and adapted to warmer temperature (Figure 3, Rita et al., 2021; Wei et al., 2024).  
593 Our prediction of both elevation and topography control on mean temperature are quantified  
594 the same unit, Celsius degrees °C, but topography-induced temperature effect on  
595 community composition is fourfold compared to that of elevation (Table 2). This implies that  
596 temperature alone cannot drive the difference in community composition, and other  
597 biophysical factors correlated with topography-induced temperature should be at play.  
598 Maximum temperature could be a better predictor of the crossing of physiological thresholds  
599 dictating species selection (Macek et al., 2019; Pérez-Navarro et al., 2021). However, this  
600 hypothesis could not be tested with our dataset as mean and maximum understory  
601 temperature were highly correlated. Soil moisture and vapor pressure deficit can also  
602 explain the important contribution of topography to communities (Davis et al., 2019).

603 Our topographic position metric relies on hydrography, demonstrating that cold air  
604 pooling could occur alongside wetter soils and synergistically favor cold-adapted species not  
605 tolerant to drought (Bénichou & Le Breton, 1987; Finocchiaro et al., 2023; Raduła et al.,  
606 2018). Conversely, ridges and south facing slopes exacerbate the effect of warmer  
607 temperature by desiccation, via stronger winds and evaporation, respectively (Davis et al.,  
608 2019; Piedallu et al., 2023; Rita et al., 2021). These underlying factors altogether can also  
609 explain the differences we found in contribution to community composition. They  
610 underscore the potential in using several microclimate variables (e.g., mean temperature,  
611 vapor pressure deficit) to predict community patterns and species distribution, explicitly

612 considering other microscale biophysical factors in a multivariate fashion (Pérez-Navarro *et*  
613 *al.*, 2021). The improvement of mechanistic modeling of microclimate (Maclean, 2020) could  
614 also improve predictions of present and future community composition.

615 The cold-adapted communities we observed in cold topoclimates are the result of an  
616 increase in relatively cold-adapted species occurrences rather than of a decrease in  
617 relatively warm-adapted species (Figure 3). This hints that the constraints on community  
618 assembly, in our study region, are a result of temperature becoming too warm for cold-  
619 adapted species, rather than otherwise. This increase in occurrences explains the higher  
620 specific richness in cold topoclimates (Figure 3). Further to an understory cooling, colder  
621 topoclimates could also increase moisture, thus alleviating competition for water during  
622 summer and allowing more species to co-occur (Raduła *et al.*, 2018; Sanceruk *et al.*, 2022).  
623 Canopy cover has been identified as the driver of the diversity of many taxa in lowland  
624 forests due to its buffering of microclimate and light interception (Tinya *et al.*, 2021;  
625 Zellweger *et al.*, 2015). Its lower contribution to microclimate variation in mountain forests  
626 and the limitation in its measurement mentioned earlier may explain why we do not detect  
627 this pattern.

628 Aside from the technical limitations in estimating canopy control on temperature we  
629 discussed above, other factors may be at play in explaining the lack of flora response to  
630 canopy-induced microclimate. It was outside of the scope of our analysis but explicitly  
631 unveiling seasonal microclimatic differences from leaf out timing can help uncover fine  
632 community differences such as presence of species vulnerable to cold winter, late freezing  
633 and spring ephemeral species. We also showed that after the lapse rate and topoclimate,  
634 canopy-induced microclimate is the most variable in space (i.e., spatially autocorrelated in  
635 smaller scale, Figure S2). A recent study has shown that plant's thermal preference  
636 computed with macroclimate are not responsive to microscale variation in temperature, but  
637 rather reflect macroclimatic provenance differences (Gril *et al.*, 2024). Surprisingly,  
638 topography, a moderate spatial scale contributor of temperature, had an important effect  
639 on these macroscales estimate of plant thermal preference. This demonstrates that  
640 topoclimate, being more stable in space and time, can promote cold-adapted species  
641 comparably to a macroclimate gradient.

### 642 **4.3. Implications**

643 How local cooler and wetter conditions are decoupled from the climate warming  
644 trend is of utmost importance as they allow for the persistence of cold-adapted species  
645 (Greiser *et al.*, 2020; Lenoir *et al.*, 2017), or provide opportunities to facilitate colonization  
646 and facilitates range shifts (Serra-Diaz *et al.*, 2015). The thermal heterogeneity topoclimate  
647 produced in mountain ranges (Figure 2) should also be considered as a driver of landscape-  
648 scale diversity (Stein *et al.*, 2014) and a potential source of community adaptation because  
649 species of diverging climatic adaptation coexist in a relatively small area (Hylander *et al.*,  
650 2022; Lenoir *et al.*, 2013, 2013). More specifically, our results support the “identifying and

651 protecting microrefugia” section highlighted by Hylander *et al.*, (2022), as north-facing  
652 slopes and topographic depressions are easily identifiable from maps, and their cooling  
653 capacities and cold-adapted communities can be confirmed by visits in the field.

654 The predominance of topoclimate as a driving force of community composition and  
655 richness allows for potential stable refugia to occur. Indeed, buffering of community by  
656 canopy alone is prone to disturbances (e.g., increased mortality of trees triggered by climate  
657 change) and the magnitude of the buffering effect on community is still under scrutiny  
658 (Bertrand *et al.*, 2020). Still, a continuity of tree cover in cold topoclimate is recommended,  
659 as it ultimately creates the understory microclimate that benefits from such topographic  
660 effects. This could be achieved through selective logging and continuous cover silviculture  
661 and the reduction of edge effects thanks to buffer zones around the microrefugia.  
662 Topography displaying higher control over communities shows that targeting cold  
663 topoclimates is an efficient conservation strategy than increasing canopy density in already  
664 closed forests. Conservation targeting cold topoclimates is more robust because of the  
665 increase in redundancy and biodiversity those locations provide (Figure S9). Additionally,  
666 maintaining a connected forest will foster the benefits of the thermal heterogeneity created  
667 by topography (Hylander *et al.*, 2022). Indeed, warm topoclimates ought to serve as source  
668 populations of species adapted to the current climate, and cold topoclimates have the  
669 potential to maintain cold-adapted populations (given sufficient buffering and areas wide  
670 enough to sustain a population), resulting in a landscape with heterogenous communities.

671 In summary, we show that elevation, topography, and to a lesser extent, canopy  
672 closure determines growing season understory temperature in the Vosges mountains in  
673 France. Besides elevation, the contribution of topoclimate was the main predictor of  
674 community composition and diversity. Understory plant communities of cold topoclimates  
675 (north facing slopes and valley bottoms) harbored a higher number of generalist and forest  
676 specialist cold-adapted species. Our results place topography as a prominent driver of forest  
677 temperature and a key factor to consider for protecting forest cold-adapted species in the  
678 context of accelerated global warming.

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693 with the content of this article.

## 694 **6. Data availability**

695 The spatial, microclimatic, and floristic data used for this analysis can be found in  
696 the repository: [https://github.com/Jeremy-borderieux/Article\\_microclim\\_vosges.git](https://github.com/Jeremy-borderieux/Article_microclim_vosges.git), and  
697 in the archive: <https://zenodo.org/records/12626861> along with the R script that can be  
698 used to reproduce the analyses and the figures.

## 699 **7. References**

- 700 Ashcroft, M. B. (2010). Identifying refugia from climate change : Identifying refugia from  
701 climate change. *Journal of Biogeography*. [https://doi.org/10.1111/j.1365-  
702 2699.2010.02300.x](https://doi.org/10.1111/j.1365-2699.2010.02300.x)
- 703 Ashcroft, M., Chisholm, L., & French, K. (2008). The effect of exposure on landscape scale  
704 soil surface temperatures and species distribution models. *Faculty of Science - Papers  
705 (Archive)*, 211-225. <https://doi.org/10.1007/s10980-007-9181-8>
- 706 Barbosa, A. M., Real, R., Munoz, A. R., & Brown, J. A. (2013). New measures for assessing  
707 model equilibrium and prediction mismatch in species distribution models. *Diversity  
708 and Distributions*, 19(10), 1333-1338. <https://doi.org/10.1111/ddi.12100>
- 709 Bénichou, P., & Le Breton, O. (1987). Prise en compte de la topographie pour la cartographie  
710 de champs pluviométriques statistiques : La méthode Aurelhy. *Colloques de l'INRA*,  
711 39(51-69).
- 712 Bertrand, R., Aubret, F., Grenouillet, G., Ribéron, A., & Blanchet, S. (2020). Comment on  
713 "Forest microclimate dynamics drive plant responses to warming". *Science*,  
714 370(6520). <https://doi.org/10.1126/science.abd3850>
- 715 Borderieux, J., Gégout, J.-C., & Serra-Diaz, J. M. (2023). High landscape-scale forest cover  
716 favours cold-adapted plant communities in agriculture-forest mosaics. *Global Ecology  
717 and Biogeography*, 32(6), 893-903. <https://doi.org/10.1111/geb.13676>
- 718 Bramer, I., Anderson, B. J., Bennie, J., Bladon, A. J., De Frenne, P., Hemming, D., Hill, R.  
719 A., Kearney, M. R., Körner, C., Korstjens, A. H., Lenoir, J., Maclean, I. M. D., Marsh,  
720 C. D., Morecroft, M. D., Ohlemüller, R., Slater, H. D., Suggitt, A. J., Zellweger, F.,  
721 & Gillingham, P. K. (2018). Chapter Three—Advances in Monitoring and Modelling  
722 Climate at Ecologically Relevant Scales. In D. A. Bohan, A. J. Dumbrell, G. Woodward,  
723 & M. Jackson (Éds.), *Advances in Ecological Research* (Vol. 58, p. 101-161). Academic  
724 Press. <https://doi.org/10.1016/bs.aecr.2017.12.005>
- 725 Copernicus. (2018). *High Resolution Layer Tree Cover Density* [Data set].  
726 <https://land.copernicus.eu/en/products/high-resolution-layer-tree-cover-density>
- 727 Davis, F. W., Synes, N. W., Fricker, G. A., McCullough, I. M., Serra-Diaz, J. M., Franklin, J.,  
728 & Flint, A. L. (2019). LiDAR-derived topography and forest structure predict fine-  
729 scale variation in daily surface temperatures in oak savanna and conifer forest  
730 landscapes. *Agricultural and Forest Meteorology*, 269-270, 192-202.  
731 <https://doi.org/10.1016/j.agrformet.2019.02.015>
- 732 De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B. R., Zellweger, F., Aalto, J., Ashcroft, M.  
733 B., Christiansen, D. M., Decocq, G., De Pauw, K., Govaert, S., Greiser, C., Gril, E.,

734 Hampe, A., Jucker, T., Klinges, D. H., Koelemeijer, I. A., Lembrechts, J. J., Marrec,  
735 R., ... Hylander, K. (2021). Forest microclimates and climate change : Importance,  
736 drivers and future research agenda. *Global Change Biology*.  
737 <https://doi.org/10.1111/gcb.15569>

738 De Frenne, P., Rodriguez-Sanchez, F., Coomes, D. A., Baeten, L., Verstraeten, G., Vellend,  
739 M., Bernhardt-Romermann, M., Brown, C. D., Brunet, J., Cornelis, J., Decocq, G. M.,  
740 Dierschke, H., Eriksson, O., Gilliam, F. S., Hedl, R., Heinken, T., Hermy, M., Hommel,  
741 P., Jenkins, M. A., ... Verheyen, K. (2013). Microclimate moderates plant responses  
742 to macroclimate warming. *Proceedings of the National Academy of Sciences*, 110(46),  
743 18561-18565. <https://doi.org/10.1073/pnas.1311190110>

744 Degen, T., Devillez, F., & Jacquemart, A.-L. (2005). Gaps promote plant diversity in beech  
745 forests (Luzulo-Fagetum), North Vosges, France. *Annals of Forest Science*, 62(5),  
746 429-440. <https://doi.org/10.1051/forest:2005039>

747 Díaz-Calafat, J., Uria-Diez, J., Brunet, J., De Frenne, P., Vangansbeke, P., Felton, A.,  
748 Öckinger, E., Cousins, S. A. O., Bauhus, J., Ponette, Q., & Hedwall, P.-O. (2023).  
749 From broadleaves to conifers: The effect of tree composition and density on  
750 understory microclimate across latitudes. *Agricultural and Forest Meteorology*, 341,  
751 109684. <https://doi.org/10.1016/j.agrformet.2023.109684>

752 Dietz, L., Collet, C., Dupouey, J.-L., Lacombe, E., Laurent, L., & Gégout, J.-C. (2020).  
753 Windstorm-induced canopy openings accelerate temperate forest adaptation to  
754 global warming. *Global Ecology and Biogeography*.  
755 <https://doi.org/10.1111/geb.13177>

756 Dobrowski, S. Z. (2011). A climatic basis for microrefugia : The influence of terrain on  
757 climate. *Global Change Biology*, 17(2), 1022-1035. <https://doi.org/10.1111/j.1365-2486.2010.02263.x>

759 Dunnington, D., & Thorne, B. (2020). ggspatial: Spatial Data Framework for ggplot2. *R*  
760 *package version1*, 1.

761 Ellis, C. J., & Eaton, S. (2021). Climate change refugia : Landscape, stand and tree-scale  
762 microclimates in epiphyte community composition. *The Lichenologist*, 53(1),  
763 135-148. <https://doi.org/10.1017/S0024282920000523>

764 Evans, J. S., & Murphy, M. A. (2021). *spatialEco*.  
765 <https://github.com/jeffrejevans/spatialEco>

766 Finocchiaro, M., Médail, F., Saatkamp, A., Diadema, K., Pavon, D., & Meineri, E. (2023).  
767 Bridging the gap between microclimate and microrefugia : A bottom-up approach  
768 reveals strong climatic and biological offsets. *Global Change Biology*, 29(4),  
769 1024-1036. <https://doi.org/10.1111/gcb.16526>

770 Fox, J., & Weisberg, S. (2019). *An R Companion to Applied Regression* (Third). Sage.  
771 <https://www.john-fox.ca/Companion/>

772 Franklin, J., Davis, F. W., Ikegami, M., Syphard, A. D., Flint, L. E., Flint, A. L., & Hannah,  
773 L. (2013). Modeling plant species distributions under future climates : How fine scale  
774 do climate projections need to be? *Global Change Biology*, 19(2), 473-483.  
775 <https://doi.org/10.1111/gcb.12051>

776 Franklin, J., Serra-Diaz, J. M., Syphard, A. D., & Regan, H. M. (2016). Global change and  
777 terrestrial plant community dynamics. *Proceedings of the National Academy of*  
778 *Sciences*, 113(14), 3725-3734. <https://doi.org/10.1073/pnas.1519911113>

779 Gargominy, O. (2022). *TAXREF v13.0, référentiel taxonomique pour la France*. [Data set].  
780 UMS PatriNat (OFB-CNRS-MNHN), Paris. <https://doi.org/10.15468/VQUEAM>

781 Gégout, J.-C., Coudun, C., Bailly, G., & Jabiol, B. (2005). EcoPlant : A forest site database  
782 linking floristic data with soil and climate variables. *Journal of Vegetation Science*,  
783 16(2), 257-260. <https://doi.org/10.1111/j.1654-1103.2005.tb02363.x>

784 Greiser, C., Ehrlén, J., Meineri, E., & Hylander, K. (2020). Hiding from the climate :  
785 Characterizing microrefugia for boreal forest understory species. *Global Change*  
786 *Biology*, 26(2), 471-483. <https://doi.org/10.1111/gcb.14874>



- 787 Gril, E., Laslier, M., Gallet-Moron, E., Durrieu, S., Spicher, F., Le Roux, V., Brasseur, B.,  
788 Haesen, S., Van Meerbeek, K., Decocq, G., Marrec, R., & Lenoir, J. (2023). Using  
789 airborne LiDAR to map forest microclimate temperature buffering or amplification.  
790 *Remote Sensing of Environment*, 298, 113820.  
791 <https://doi.org/10.1016/j.rse.2023.113820>
- 792 Gril, E., Spicher, F., Vanderpoorten, A., Vital, G., Brasseur, B., Gallet-Moron, E., Le Roux,  
793 V., Decocq, G., Lenoir, J., & Marrec, R. (2024). Ecological indicator values of  
794 understorey plants perform poorly to infer forest microclimate temperature. *Journal*  
795 *of Vegetation Science*, 35(2), e13241. <https://doi.org/10.1111/jvs.13241>
- 796 Gudiksen, P. H., Leone, J. M., King, C. W., Ruffieux, D., & Neff, W. D. (1992). Measurements  
797 and Modeling of the Effects of Ambient Meteorology on Nocturnal Drainage Flows.  
798 *Journal of Applied Meteorology and Climatology*, 31(9), 1023-1032.  
799 [https://doi.org/10.1175/1520-0450\(1992\)031<1023:MAMOTE>2.0.CO;2](https://doi.org/10.1175/1520-0450(1992)031<1023:MAMOTE>2.0.CO;2)
- 800 Haesen, S., Lembrechts, J. J., De Frenne, P., Lenoir, J., Aalto, J., Ashcroft, M. B., Kopecký,  
801 M., Luoto, M., Maclean, I., Nijs, I., Niittynen, P., van den Hoogen, J., Arriga, N.,  
802 Brúna, J., Buchmann, N., Čiliak, M., Collalti, A., De Lombaerde, E., Descombes, P.,  
803 ... Van Meerbeek, K. (2021). ForestTemp - Sub-canopy microclimate temperatures of  
804 European forests. *Global Change Biology*, 27(23), 6307-6319.  
805 <https://doi.org/10.1111/gcb.15892>
- 806 Haesen, S., Lenoir, J., Gril, E., De Frenne, P., Lembrechts, J. J., Kopecký, M., Macek, M.,  
807 Man, M., Wild, J., & Van Meerbeek, K. (2023). Microclimate reveals the true thermal  
808 niche of forest plant species. *Ecology Letters*, 26(12).  
809 <https://doi.org/10.1111/ele.14312>
- 810 Hannah, L., Flint, L., Syphard, A. D., Moritz, M. A., Buckley, L. B., & McCullough, I. M.  
811 (2014). Fine-grain modeling of species' response to climate change: Holdouts,  
812 stepping-stones, and microrefugia. *Trends in Ecology & Evolution*, 29(7), 390-397.  
813 <https://doi.org/10.1016/j.tree.2014.04.006>
- 814 Hartig, F. (2024). *DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed)*  
815 *Regression Models*. <https://CRAN.R-project.org/package=DHARMA>
- 816 Heinken, T., Diekmann, M., Liira, J., Orczewska, A., Schmidt, M., Brunet, J., Chytrý, M.,  
817 Chabrierie, O., Decocq, G., De Frenne, P., Dřevojan, P., Dzwonko, Z., Ewald, J.,  
818 Feilberg, J., Graae, B. J., Grytnes, J.-A., Hermy, M., Kriebitzsch, W.-U., Laiviņš, M.,  
819 ... Vanneste, T. (2022). The European Forest Plant Species List (EuForPlant): Concept  
820 and applications. *Journal of Vegetation Science*, 33(3), e13132.  
821 <https://doi.org/10.1111/jvs.13132>
- 822 Hijmans, R. J. (2020). *raster: Geographic Data Analysis and Modeling*. [https://CRAN.R-](https://CRAN.R-project.org/package=raster)  
823 [project.org/package=raster](https://CRAN.R-project.org/package=raster)
- 824 Hylander, K., Greiser, C., Christiansen, D. M., & Koelemeijer, I. A. (2022). Climate  
825 adaptation of biodiversity conservation in managed forest landscapes. *Conservation*  
826 *Biology*, 36(3), e13847. <https://doi.org/10.1111/cobi.13847>
- 827 IGN. (2013). *Fiches descriptives des grandes régions écologiques (GRECO) et des*  
828 *sylvoécorégions (SER)*. <https://inventaire-forestier.ign.fr/spip.php?article773>
- 829 IGN. (2017). *BD ALTI Le modèle numérique de terrain (MNT) maillé qui décrit le relief du*  
830 *territoire français à moyenne échelle* [Data set].  
831 <https://geoservices.ign.fr/documentation/donnees/alti/bdalti>
- 832 IGN. (2019). *BD Forêt version 2*. Institut National de l'Information Géographique et  
833 Forestière. <https://inventaire-forestier.ign.fr/spip.php?article646>
- 834 IPCC. (2021). Summary for Policymakers. In V. Masson-Delmotte, P. Zhai, A. Pirani, S. L.  
835 Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang,  
836 K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi,  
837 R. Yu, & B. Zhou (Éds.), *Climate Change 2021: The Physical Science Basis.*  
838 *Contribution of Working Group I to the Sixth Assessment Report of the*  
839 *Intergovernmental Panel on Climate Change* (p. 3–32). Cambridge University Press.  
840 <https://doi.org/10.1017/9781009157896.001>

841 James, G., Witten, D., Hastie, T., Tibshirani, R., & Taylor, J. (2023). *An Introduction to*  
842 *Statistical Learning : With Applications in Python*. Springer International Publishing.  
843 <https://doi.org/10.1007/978-3-031-38747-0>

844 Johnston, A. K., Brewster, D., & Berghaus, H. K. W. (1848). *The physical atlas : A series of*  
845 *maps & notes illustrating the geographical distribution of natural phenomena* [Map].  
846 William Blackwood & Sons.

847 Kempainen, J., Lembrechts, J. J., Van Meerbeek, K., Carnicer, J., Chardon, N. I., Kardol,  
848 P., Lenoir, J., Liu, D., Maclean, I., Pergl, J., Saccone, P., Senior, R. A., Shen, T.,  
849 Słowińska, S., Vandvik, V., von Oppen, J., Aalto, J., Ayalew, B., Bates, O., ... De  
850 Frenne, P. (2023). *Microclimate, an inseparable part of ecology and biogeography*.  
851 Zenodo. <https://doi.org/10.5281/zenodo.7973314>

852 Koerner, W., Dupouey, J. L., Dambrine, E., & Benoit, M. (1997). Influence of Past Land Use  
853 on the Vegetation and Soils of Present Day Forest in the Vosges Mountains, France.  
854 *Journal of Ecology*, 85(3), 351-358. <https://doi.org/10.2307/2960507>

855 Lembrechts, J. J., Lenoir, J., Scheffers, B., & De Frenne, P. (2021). Designing countrywide  
856 and regional microclimate networks. *Global Ecology and Biogeography*.  
857 <https://doi.org/10.1111/geb.13290>

858 Lenoir, J., Graae, B. J., Aarrestad, P. A., Alsos, I. G., Armbruster, W. S., Austrheim, G.,  
859 Bergendorff, C., Birks, H. J. B., Bråthen, K. A., Brunet, J., Bruun, H. H., Dahlberg,  
860 C. J., Decocq, G., Diekmann, M., Dynesius, M., Ejrnæs, R., Grytnes, J.-A., Hylander,  
861 K., Klanderud, K., ... Svenning, J.-C. (2013). Local temperatures inferred from plant  
862 communities suggest strong spatial buffering of climate warming across Northern  
863 Europe. *Global Change Biology*, 19(5), 1470-1481.  
864 <https://doi.org/10.1111/gcb.12129>

865 Lenoir, J., Hattab, T., & Pierre, G. (2017). Climatic microrefugia under anthropogenic  
866 climate change: Implications for species redistribution. *Ecography*, 40(2), 253-266.  
867 <https://doi.org/10.1111/ecog.02788>

868 Ma, Q., Su, Y., & Guo, Q. (2017). Comparison of Canopy Cover Estimations From Airborne  
869 LiDAR, Aerial Imagery, and Satellite Imagery. *IEEE Journal of Selected Topics in*  
870 *Applied Earth Observations and Remote Sensing*, 10(9), 4225-4236.  
871 <https://doi.org/10.1109/JSTARS.2017.2711482>

872 Macek, M., Kopecký, M., & Wild, J. (2019). Maximum air temperature controlled by  
873 landscape topography affects plant species composition in temperate forests.  
874 *Landscape Ecology*, 34(11), 2541-2556. <https://doi.org/10.1007/s10980-019-00903-x>

875 Maclean, I. M. D. (2020). Predicting future climate at high spatial and temporal resolution.  
876 *Global Change Biology*, 26(2), 1003-1011. <https://doi.org/10.1111/gcb.14876>

877 Man, M., Kalčík, V., Macek, M., Brůna, J., Hederová, L., Wild, J., & Kopecký, M. (2023).  
878 myClim: Microclimate data handling and standardised analyses in R. *Methods in*  
879 *Ecology and Evolution*, 14(9). <https://doi.org/10.1111/2041-210X.14192>

880 McCune, B., & Keon, D. (2002). Equations for potential annual direct incident radiation and  
881 heat load. *Journal of Vegetation Science*, 13(4), 603-606.  
882 <https://doi.org/10.1111/j.1654-1103.2002.tb02087.x>

883 McLaughlin, B. C., Ackerly, D. D., Klos, P. Z., Natali, J., Dawson, T. E., & Thompson, S. E.  
884 (2017). Hydrologic refugia, plants, and climate change. *Global Change Biology*, 23(8),  
885 2941-2961. <https://doi.org/10.1111/gcb.13629>

886 Météo France. (2024). *Meteo.data.gouv.fr*. <https://meteo.data.gouv.fr/datasets>

887 Naimi, B., Hamm, N. a s, Groen, T. A., Skidmore, A. K., & Toxopeus, A. G. (2014). Where is  
888 positional uncertainty a problem for species distribution modelling. *Ecography*, 37,  
889 191-203. <https://doi.org/10.1111/j.1600-0587.2013.00205.x>

890 Pastore, M. A., Classen, A. T., D'Amato, A. W., Foster, J. R., & Adair, E. C. (2022). Cold-air  
891 pools as microrefugia for ecosystem functions in the face of climate change. *Ecology*,  
892 103(8), e3717. <https://doi.org/10.1002/ecy.3717>

893 Pebesma, E. (2018). Simple Features for R: Standardized Support for Spatial Vector Data.  
894 *The R Journal*, 10(1), 439-446. <https://doi.org/10.32614/RJ-2018-009>

- 895 Pérez-Navarro, M. Á., Serra-Diaz, J. M., Svenning, J., Esteve-Selma, M. Á., Hernández-  
896 Bastida, J., & Lloret, F. (2021). Extreme drought reduces climatic disequilibrium in  
897 dryland plant communities. *Oikos*. <https://doi.org/10.1111/oik.07882>
- 898 Piedallu, C., Dallery, D., Bresson, C., Legay, M., Gégout, J.-C., & Pierrat, R. (2023). Spatial  
899 vulnerability assessment of silver fir and Norway spruce dieback driven by climate  
900 warming. *Landscape Ecology*, 38(2), 341-361. <https://doi.org/10.1007/s10980-022-01570-1>
- 901
- 902 Piqué, A., Pluck, P., Schneider, J.-L., & Whitechurch, H. (1994). The Vosges Massif. In J.  
903 Chantraine, J. Rolet, D. S. Santallier, A. Piqué, & J. D. Keppie (Éds.), *Pre-Mesozoic*  
904 *Geology in France and Related Areas* (p. 416-425). Springer.  
905 [https://doi.org/10.1007/978-3-642-84915-2\\_32](https://doi.org/10.1007/978-3-642-84915-2_32)
- 906 R Core Team. (2019). *R: A Language and Environment for Statistical Computing*. R  
907 Foundation for Statistical Computing. <https://www.R-project.org/>
- 908 Raduła, M. W., Szymura, T. H., & Szymura, M. (2018). Topographic wetness index explains  
909 soil moisture better than bioindication with Ellenberg's indicator values. *Ecological*  
910 *Indicators*, 85, 172-179. <https://doi.org/10.1016/j.ecolind.2017.10.011>
- 911 Rey, D., & Neuhauser, M. (2011). Wilcoxon-Signed-Rank Test. In M. Lovric (Éd.),  
912 *International Encyclopedia of Statistical Science* (p. 1658-1659). Springer.  
913 [https://doi.org/10.1007/978-3-642-04898-2\\_616](https://doi.org/10.1007/978-3-642-04898-2_616)
- 914 Richard, B., Dupouey, J.-L., Corcket, E., Alard, D., Archaux, F., Aubert, M., Boulanger, V.,  
915 Gillet, F., Langlois, E., Macé, S., Montpied, P., Beaufils, T., Begeot, C., Behr, P.,  
916 Boissier, J.-M., Camaret, S., Chevalier, R., Decocq, G., Dumas, Y., ... Lenoir, J.  
917 (2021). The climatic debt is growing in the understorey of temperate forests : Stand  
918 characteristics matter. *Global Ecology and Biogeography*, 30(7).  
919 <https://doi.org/10.1111/geb.13312>
- 920 Rita, A., Bonanomi, G., Allevato, E., Borghetti, M., Cesarano, G., Mogavero, V., Rossi, S.,  
921 Saulino, L., Zotti, M., & Saracino, A. (2021). Topography modulates near-ground  
922 microclimate in the Mediterranean *Fagus sylvatica* treeline. *Scientific Reports*, 11(1),  
923 8122. <https://doi.org/10.1038/s41598-021-87661-6>
- 924 Rolland, C. (2003). Spatial and Seasonal Variations of Air Temperature Lapse Rates in Alpine  
925 Regions. *Journal of Climate*, 16(7), 1032-1046. [https://doi.org/10.1175/1520-0442\(2003\)016<1032:SASVOA>2.0.CO;2](https://doi.org/10.1175/1520-0442(2003)016<1032:SASVOA>2.0.CO;2)
- 926
- 927 Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-  
928 Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M.,  
929 Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M.,  
930 & Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. *Science (New*  
931 *York, N.Y.)*, 287(5459), 1770-1774. <https://doi.org/10.1126/science.287.5459.1770>
- 932 Sanczuk, P., De Lombaerde, E., Haesen, S., Van Meerbeek, K., Luoto, M., Van der Veken,  
933 B., Van Beek, E., Hermy, M., Verheyen, K., Vangansbeke, P., & De Frenne, P. (2022).  
934 Competition mediates understorey species range shifts under climate change.  
935 *Journal of Ecology*, 110(8), 1813-1825. <https://doi.org/10.1111/1365-2745.13907>
- 936 Sannier, C., Gallego, J., Langanke, T., Donezar, U., & Pennec, A. (2023). Tree cover area  
937 estimation in europe based on the combination of in situ reference data and the  
938 copernicus high resolution layer on tree cover density. *The International Archives of*  
939 *the Photogrammetry, Remote Sensing and Spatial Information Sciences*, XLVIII-M-  
940 1-2023, 277-284. <https://doi.org/10.5194/isprs-archives-XLVIII-M-1-2023-277-2023>
- 941 Schweiger, A. H., Irl, S. D. H., Steinbauer, M. J., Dengler, J., & Beierkuhnlein, C. (2016).  
942 Optimizing sampling approaches along ecological gradients. *Methods in Ecology and*  
943 *Evolution*, 7(4), 463-471. <https://doi.org/10.1111/2041-210X.12495>
- 944 Serra-Diaz, J. M., Scheller, R. M., Syphard, A. D., & Franklin, J. (2015). Disturbance and  
945 climate microrefugia mediate tree range shifts during climate change. *Landscape*  
946 *Ecology*, 30(6), 1039-1053. <https://doi.org/10.1007/s10980-015-0173-9>

- 947 Smith, S. A., Brown, A. R., Vosper, S. B., Murkin, P. A., & Veal, A. T. (2010). Observations  
948 and Simulations of Cold Air Pooling in Valleys. *Boundary-Layer Meteorology*, 134(1),  
949 85-108. <https://doi.org/10.1007/s10546-009-9436-9>
- 950 Stein, A., Gerstner, K., & Kreft, H. (2014). Environmental heterogeneity as a universal driver  
951 of species richness across taxa, biomes and spatial scales. *Ecology Letters*, 17(7),  
952 866-880. <https://doi.org/10.1111/ele.12277>
- 953 Thomas, A. L., Dambrine, E., King, D., Party, J. P., & Probst, A. (1999). A spatial study of  
954 the relationships between streamwater acidity and geology, soils and relief (Vosges,  
955 northeastern France). *Journal of Hydrology*, 217(1), 35-45.  
956 [https://doi.org/10.1016/S0022-1694\(99\)00014-1](https://doi.org/10.1016/S0022-1694(99)00014-1)
- 957 Thuiller, W., Lavorel, S., Araújo, M. B., Sykes, M. T., & Prentice, I. C. (2005). Climate change  
958 threats to plant diversity in Europe. *Proceedings of the National Academy of  
959 Sciences*, 102(23), 8245-8250. <https://doi.org/10.1073/pnas.0409902102>
- 960 Tichý, L. (2016). Field test of canopy cover estimation by hemispherical photographs taken  
961 with a smartphone. *Journal of Vegetation Science*, 27(2), 427-435.  
962 <https://doi.org/10.1111/jvs.12350>
- 963 Tinya, F., Kovács, B., Bidló, A., Dima, B., Király, I., Kutszegi, G., Lakatos, F., Mag, Z.,  
964 Márialigeti, S., Nascimbene, J., Samu, F., Siller, I., Szél, G., & Ódor, P. (2021).  
965 Environmental drivers of forest biodiversity in temperate mixed forests - A multi-  
966 taxon approach. *Science of The Total Environment*, 795, 148720.  
967 <https://doi.org/10.1016/j.scitotenv.2021.148720>
- 968 Vandewiele, M., Geres, L., Lotz, A., Mandl, L., Richter, T., Seibold, S., Seidl, R., & Senf, C.  
969 (2023). Mapping spatial microclimate patterns in mountain forests from LiDAR.  
970 *Agricultural and Forest Meteorology*, 341, 109662.  
971 <https://doi.org/10.1016/j.agrformet.2023.109662>
- 972 Vangansbeke, P., Máliš, F., Hédl, R., Chudomelová, M., Vild, O., Wulf, M., Jahn, U., Welk,  
973 E., Rodríguez-Sánchez, F., & Frenne, P. D. (2021). ClimPlant: Realized climatic  
974 niches of vascular plants in European forest understoreys. *Global Ecology and  
975 Biogeography*, 30(6), 1183-1190. <https://doi.org/10.1111/geb.13303>
- 976 Venables, W. N., & Ripley, B. D. (2002). *Modern Applied Statistics with S* (Fourth). Springer.  
977 <https://www.stats.ox.ac.uk/pub/MASS4/>
- 978 Vosper, S. B., & Brown, A. R. (2008). Numerical Simulations of Sheltering in Valleys: The  
979 Formation of Nighttime Cold-Air Pools. *Boundary-Layer Meteorology*, 127(3),  
980 429-448. <https://doi.org/10.1007/s10546-008-9272-3>
- 981 Wei, L., Sanczuk, P., De Pauw, K., Caron, M. M., Selvi, F., Hedwall, P., Brunet, J., Cousins,  
982 S. A. O., Plue, J., Spicher, F., Gasperini, C., Iacopetti, G., Orczewska, A., Uria-Diez,  
983 J., Lenoir, J., Vangansbeke, P., & De Frenne, P. (2024). Using warming tolerances to  
984 predict understory plant responses to climate change. *Global Change Biology*, 30(1),  
985 e17064. <https://doi.org/10.1111/gcb.17064>
- 986 Wickham, H. (2011). Ggplot2. *WIREs Computational Statistics*, 3(2), 180-185.  
987 <https://doi.org/10.1002/wics.147>
- 988 Wiens, J. J. (2016). Climate-Related Local Extinctions Are Already Widespread among Plant  
989 and Animal Species. *PLOS Biology*, 14(12), e2001104.  
990 <https://doi.org/10.1371/journal.pbio.2001104>
- 991 Wild, J., Kopecký, M., Macek, M., Šanda, M., Jankovec, J., & Haase, T. (2019). Climate at  
992 ecologically relevant scales: A new temperature and soil moisture logger for long-  
993 term microclimate measurement. *Agricultural and Forest Meteorology*.  
994 <https://doi.org/10.1016/j.agrformet.2018.12.018>
- 995 Zellweger, F., Braunisch, V., Morsdorf, F., Baltensweiler, A., Abegg, M., Roth, T., Bugmann,  
996 H., & Bollmann, K. (2015). Disentangling the effects of climate, topography, soil and  
997 vegetation on stand-scale species richness in temperate forests. *Forest Ecology and  
998 Management*, 349, 36-44. <https://doi.org/10.1016/j.foreco.2015.04.008>
- 999 Zellweger, F., Coomes, D., Lenoir, J., Depauw, L., Maes, S. L., Wulf, M., Kirby, K. J., Brunet,  
1000 J., Kopecký, M., Máliš, F., Schmidt, W., Heinrichs, S., den Ouden, J., Jaroszewicz,

1001 B., Buyse, G., Spicher, F., Verheyen, K., & De Frenne, P. (2019). Seasonal drivers of  
1002 understory temperature buffering in temperate deciduous forests across Europe.  
1003 *Global Ecology and Biogeography*, 28(12), 1774-1786.  
1004 <https://doi.org/10.1111/geb.12991>

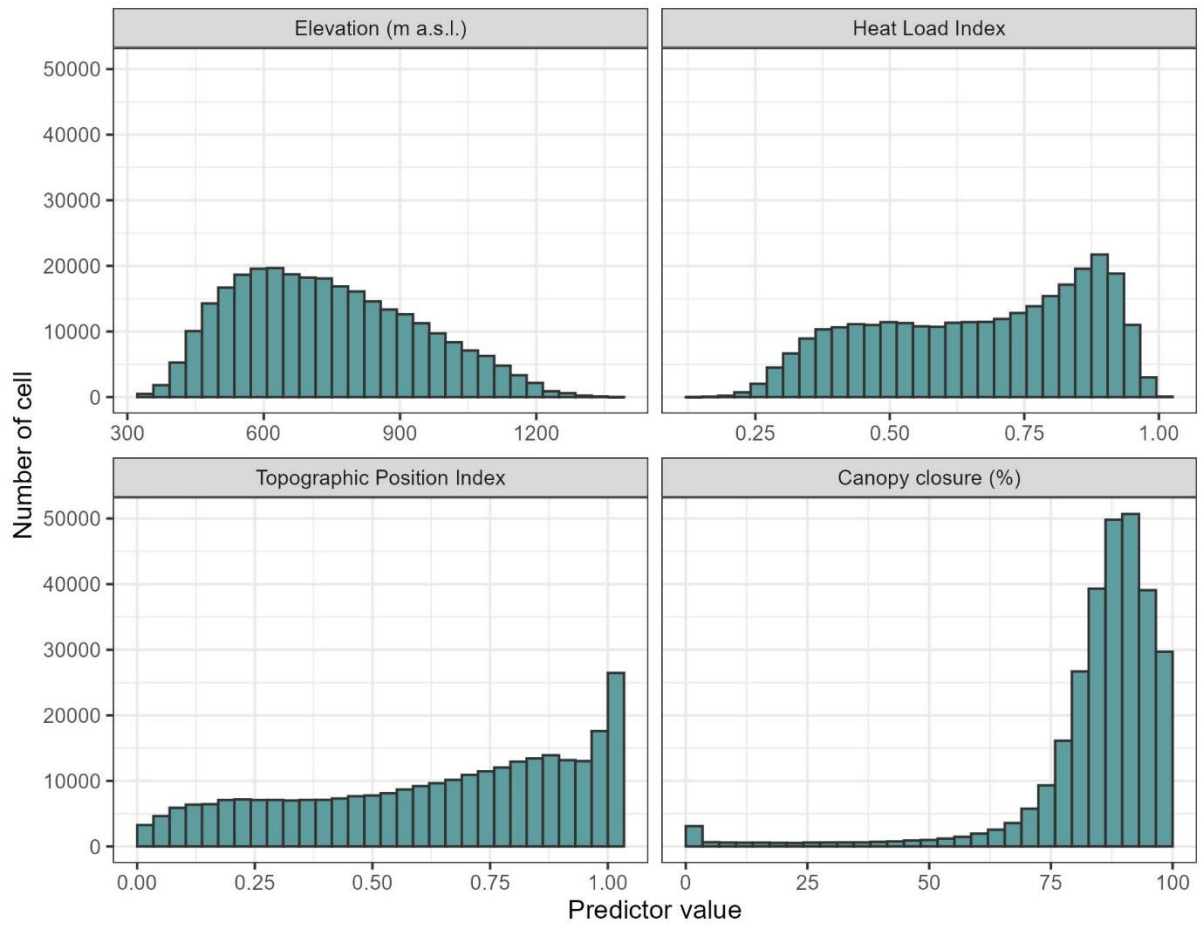
1005 Zellweger, F., De Frenne, P., Lenoir, J., Rocchini, D., & Coomes, D. (2019). Advances in  
1006 Microclimate Ecology Arising from Remote Sensing. *Trends in Ecology & Evolution*,  
1007 34(4), 327-341. <https://doi.org/10.1016/j.tree.2018.12.012>

1008 Zellweger, F., De Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-  
1009 Römermann, M., Baeten, L., Hédler, R., Berki, I., Brunet, J., Van Calster, H.,  
1010 Chudomelová, M., Decocq, G., Dirnböck, T., Durak, T., Heinken, T., Jaroszewicz, B.,  
1011 Kopecký, M., Máliš, F., ... Coomes, D. (2020). Forest microclimate dynamics drive  
1012 plant responses to warming. *Science*, 368(6492), 772-775.  
1013 <https://doi.org/10.1126/science.aba6880>

1014 Zuur, A. F., & Ieno, E. N. (2016). A protocol for conducting and presenting results of  
1015 regression-type analyses. *Methods in Ecology and Evolution*, 7(6), 636-645.  
1016 <https://doi.org/10.1111/2041-210X.12577>

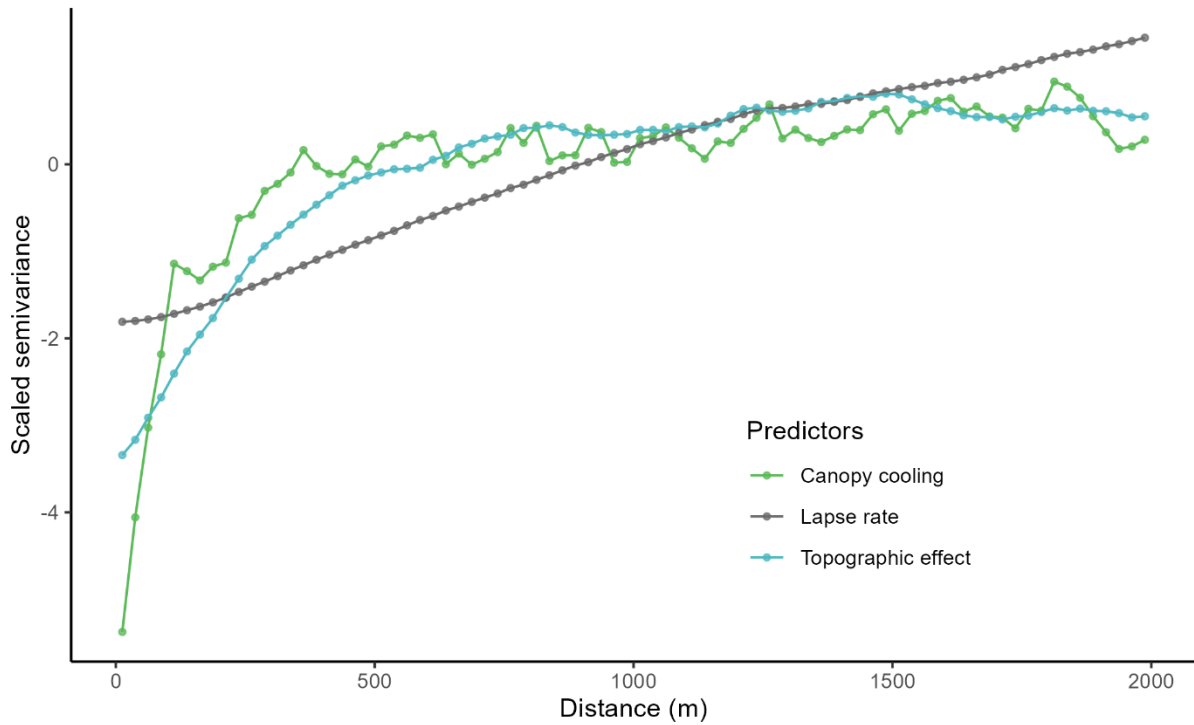
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1019 **8. Supplementary materials**



1020

1021 *Figure S1: Distribution of the value of the four tested predictor of understory temperature*  
1022 *through all the cells of the study region (forested cells of the Thur valley).*



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1024 *Figure S2: Variogram of the 3 maps of flora predictors (Figure 2), with a lag of 25m.*  
 1025 *Canopy cooling scale semivariance saturates first, followed by topographic effect and the*  
 1026 *lapse rate. The saturation of the lapse rate is not shown but is estimated at 6000 m.*

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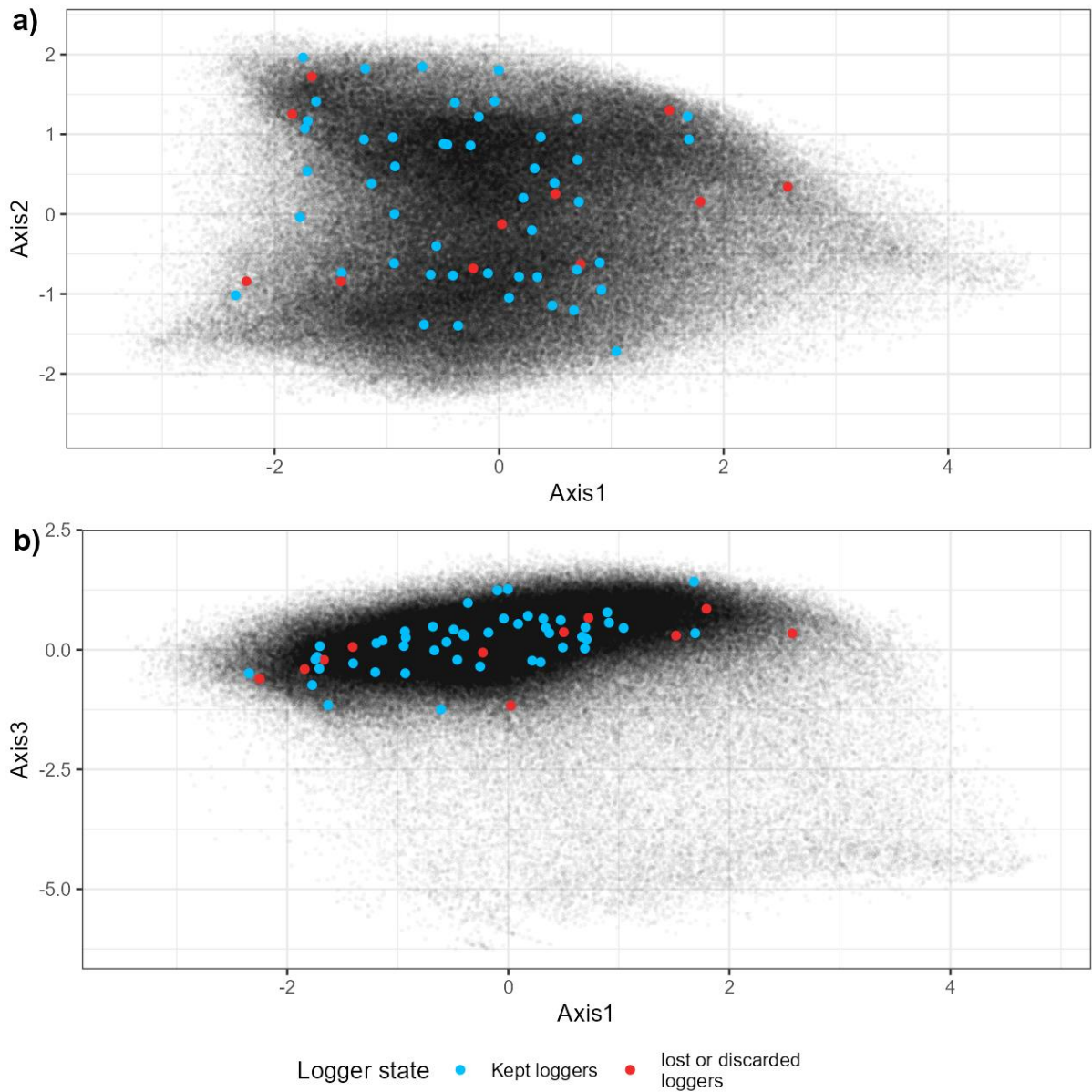
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1029 *Table S1: Summary of the sampling scheme. The left number represents the theoretical*  
 1030 *number of plots for the combination of targeted topographic feature and canopy closure*  
 1031 *(there were in total 8 strata), the right number represents the number of plots that had*  
 1032 *usable temperature data (logger found functioning). All other topographic feature aside*  
 1033 *from the targeted one were set to an intermediate value (nor high or low), read M&M 2.3*  
 1034 *for more information on the sampling scheme.*

		Canopy closure	
		Low (< 80%)	High (> 80%)
Heat Load Index	Low (< 0.6)	8 - 5	8 - 8
	High (> 0.7)	8 - 5	8 - 8
Topographic Position Index	Low (< 0.2)		8 - 7
	High (> 0.8)		8 - 6
Slope	Low (< 10°)		8 - 4
	High (> 25°)		8 - 5

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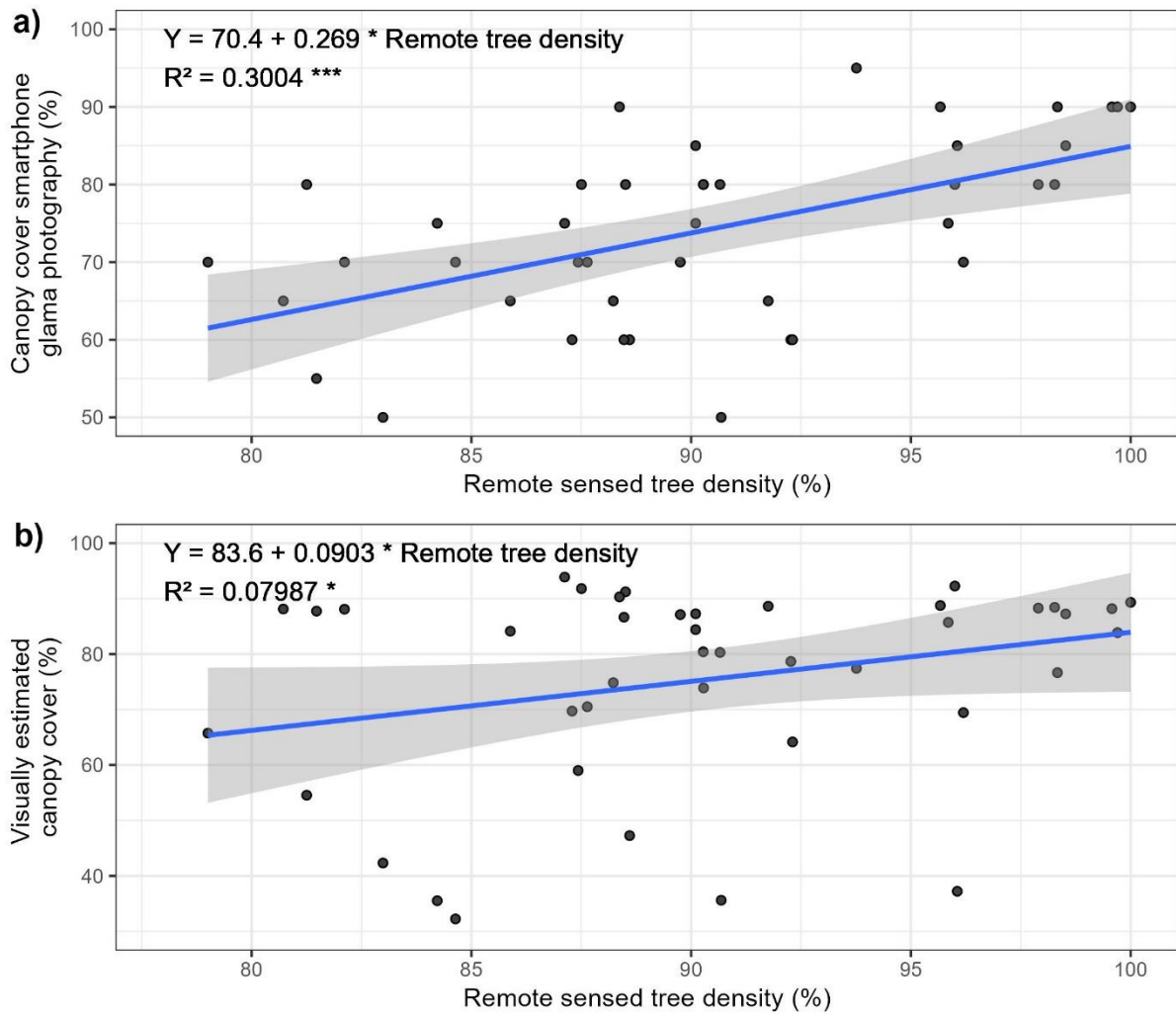
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1038 *Figure S3; Principal component analysis of the spatial factor (Elevation, HLI, TPI, slope,*  
 1039 *canopy closure) ought to influence microclimate. Each point represents a forested cell (25m*  
 1040 *per 25 m, 289,733 cells) of the Thur Valley. Axis 1 is explained by elevation and topographic*  
 1041 *position (low values mean high elevation and TPI), Axis 2 represents mostly head load index*  
 1042 *(low values mean high HLI), Axis 3 represents mostly canopy cove (low values mean low*  
 1043 *canopy closure). The position in the PCA projection of the initial sampling and the final*  
 1044 *selection of loggers is shown (Lembrechts et al., 2021).*

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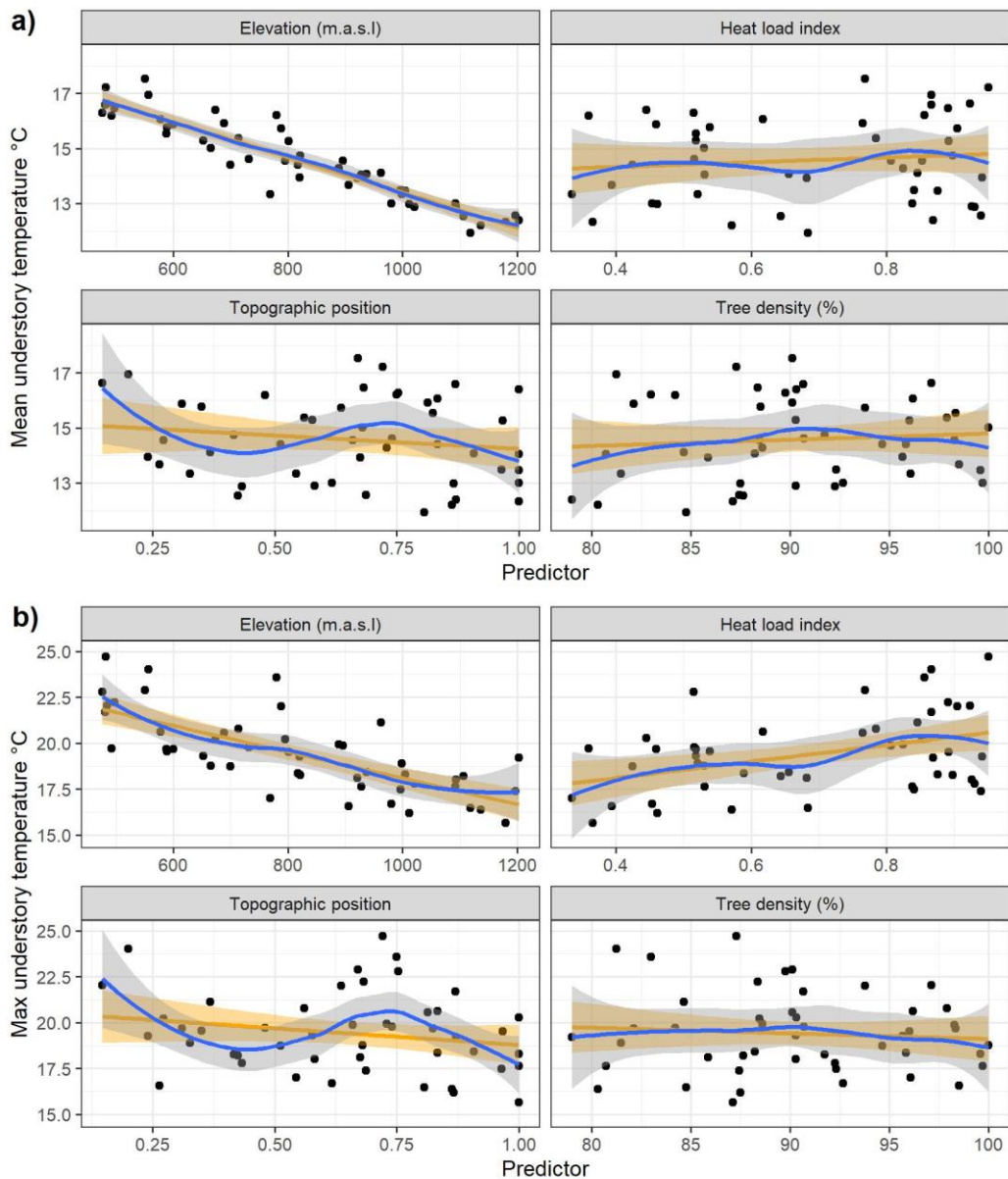
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1048 *Figure S4: Relationship between Copernicus remote sensed tree density and canopy closure*  
 1049 *estimated in a 25-meter radius circle (a) and canopy cover estimated by a smartphone*  
 1050 *photography and segmented by the ‘Glama’ application (b). The blue line corresponds to a*  
 1051 *fitted linear model which equation, Person  $R^2$ , and its statistical significance are displayed*  
 1052 *(\*\*\*):  $P < 0.001$ , (\*)  $P < 0.1$ . The ribbons are the confidence interval of the model.*



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1054 *Figure S5: Relationship between mean (a) and maximum (b) understory temperature of*  
 1055 *the growing season with the 4 predictors of the linear temperature model. A loess*  
 1056 *smoother (blue) and an univariate linear model (orange) and their confidence interval are*  
 1057 *also displayed.*

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1065 *Table S2: Estimated parameters, their standard error and p-values of the predictors*  
 1066 *included in models of the field canopy closure daily mean growing season temperature. The*  
 1067 *range of the predictors in the calibration dataset and their standardized effect size on the*  
 1068 *temperature (standard deviation \* estimate) are displayed. The percentage of explained*  
 1069 *variation per type of predictor is included. P-values were obtained with a Wald test on*  
 1070 *parameters.*

Predictor	Type of predictor	Estimate	Standard error	Range	Effect size (°C)	Explained variation (%)	P-value
<b>Intercept (°C)</b>		19.2	0.605				<10 <sup>-4</sup>
<b>Elevation (m a.s.l.)</b>	Elevation	-0.00656	0.000333	475 : 1203	-1.49	56.5	<10 <sup>-4</sup>
<b>Heat load index (n.u)</b>	Topography	1.52	0.359	0.335 : 0.951	0.29	21.5	<10 <sup>-4</sup>
<b>Topographic index (n.u)</b>		0.42	0.295	0.201 : 1	0.15		0.163
<b>Canopy closure 25 radius (%)</b>	Canopy	-0.00767	0.00599	50 : 95	-0.092	3.17	0.208

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1073 *Table S3: Estimated parameters, their standard error and p-values of the predictors*  
 1074 *included in models of the immediate canopy closure (i.e. 'Glama' application) daily mean*  
 1075 *growing season temperature. The range of the predictors in the calibration dataset and*  
 1076 *their standardized effect size on the temperature (standard deviation \* estimate) are*  
 1077 *displayed. The percentage of explained variation per type of predictor is included. P-values*  
 1078 *were obtained with a Wald test on parameters. The canopy cover was estimated visually in*  
 1079 *a 25-meter radius circle around the loggers. Immediate canopy cover was measured used a*  
 1080 *hemispherical photography above the logger and a sky segmentation application.*

Predictor	Type of predictor	Estimate	Standard error	Range	Effect size (°C)	P-value
<b>Intercept (°C)</b>		16.2	0.812			<10 <sup>-4</sup>
<b>Elevation (m a.s.l.)</b>	Elevation	-0.00672	0.000299	475 : 1203	-1.52	<10 <sup>-4</sup>
<b>Heat load index (n.u)</b>	Topography	5.47	1.22	0.335 : 0.951		<10 <sup>-4</sup>
<b>Topographic index (n.u)</b>	Topography	0.481	0.256	0.147 : 1	0.15	0.0682
<b>Immediate canopy closure (%)</b>	Canopy	0.0346	0.0109	32.23 : 93.88		0.00311
<b>Topography index X Immediate canopy closure</b>	Interaction	-0.0547	0.0162			0.00171

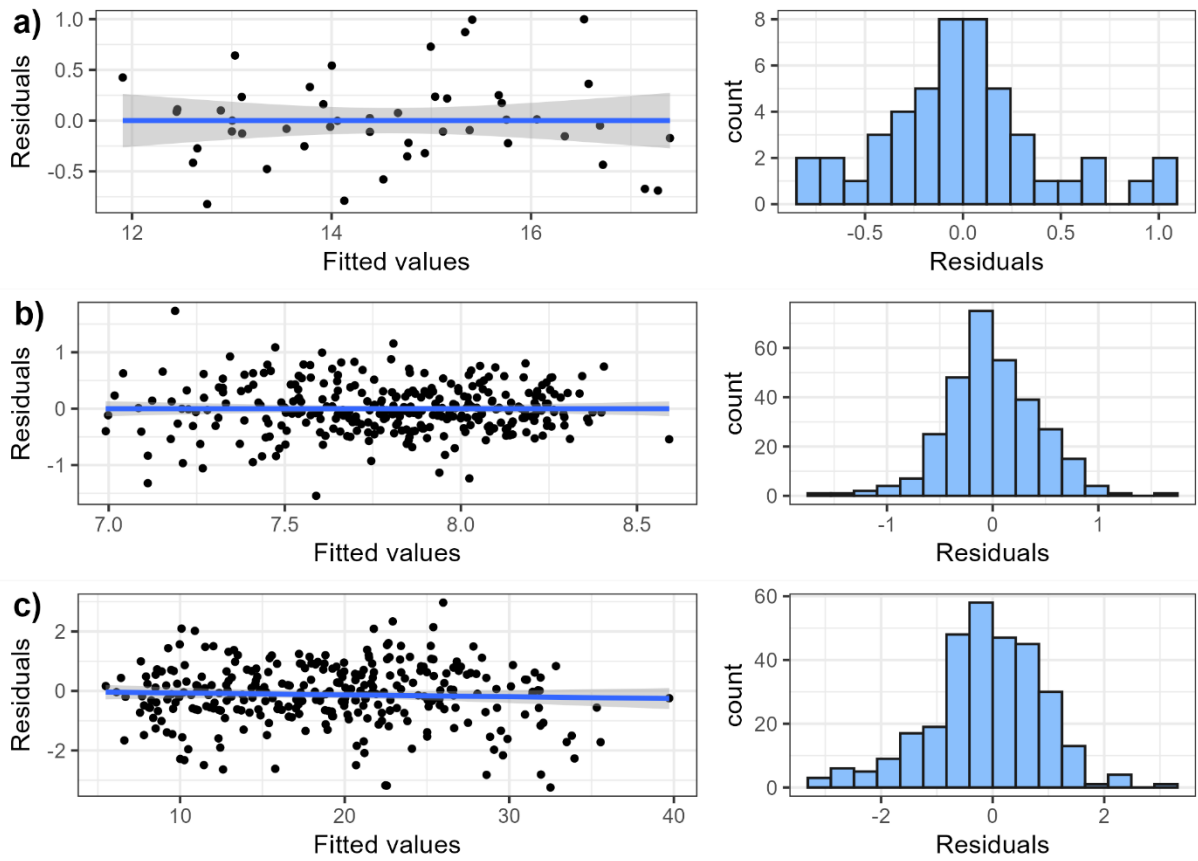
1081 *Table S4: Estimated parameters, their standard error and p-values of the predictors*  
 1082 *included in models of the daily maximum growing season temperature. The range of the*  
 1083 *predictors in the calibration dataset and their standardized effect size on the temperature*  
 1084 *(standard deviation \* estimate) are displayed. The percentage of explained variation per*  
 1085 *type of predictor is included. P-values were obtained with a Wald test on parameters. Heat*  
 1086 *load and topographic indices have no units, refer to the methods for their calculation.*

Predictor	Type of predictor	Estimate	Standard error	Range	Effect size (°C)	Explained variation (%)	P-value
<b>Intercept (°C)</b>		30.6	2.45				<10 <sup>-4</sup>
<b>Elevation (m a.s.l.)</b>	Elevation	-0.00803	0.000685	475.69 : 1203.17	-1.77	56.5	<10 <sup>-4</sup>
<b>Heat load index (n.u)</b>	Topography	5.35	0.732	0.335 : 0.951	1.05	21.5	<10 <sup>-4</sup>
<b>Topographic index (n.u)</b>		0.333	0.607	0.147 : 1	0.081		0.587
<b>Canopy closure (%)</b>	Canopy	-0.0947	0.0253	79.004 : 100	-0.54	3.17	<10 <sup>-4</sup>

1087 *Table S5: Estimated parameters, their standard error and p-values of the max temperature*  
 1088 *predictors of the community thermal index (CTI) linear model, and the species richness*  
 1089 *negative binomial generalized linear model. The range of the predictors and their*  
 1090 *standardized effect size on the community predicted variable (standard deviation \* estimate)*  
 1091 *are displayed. The P-value is obtained by a Wald test on the parameter. (R<sup>2</sup> of*  
 1092 *the CTI model: 34.0%)*

Model	Predictor	Estimate	Standard error	Range	Effect size	P-value
<b>Species richness</b>	Intercept (°C)	0.307	0.478	NA	NA	0.522
	Lapse rate (°C)	0.0351	0.0156	20.6 : 27.5	1.15	0.024
	Topography effect (°C)	-0.112	0.0271	1.79 : 5.36	-1.76	<10 <sup>-4</sup>
	Canopy cooling (°C)	0.00365	0.035	-9.47 : -4.58	0.0464	0.917
	Bioindicator pH	0.413	0.032	3 : 7.15	7.97	<10 <sup>-4</sup>
<b>Community Thermal Index (°C)</b>	Intercept (°C)	4.57	0.484	NA	NA	<10 <sup>-4</sup>
	Lapse rate (°C)	0.0589	0.0156	20.6 : 27.5	0.106	<10 <sup>-4</sup>
	Topography effect (°C)	0.0965	0.0273	1.79 : 5.36	0.0912	<10 <sup>-4</sup>
	Canopy cooling (°C)	-0.00128	0.0356	-9.47 : -4.58	-0.00093	0.971
	Bioindicator pH	0.268	0.0313	3 : 7.15	0.243	<10 <sup>-4</sup>

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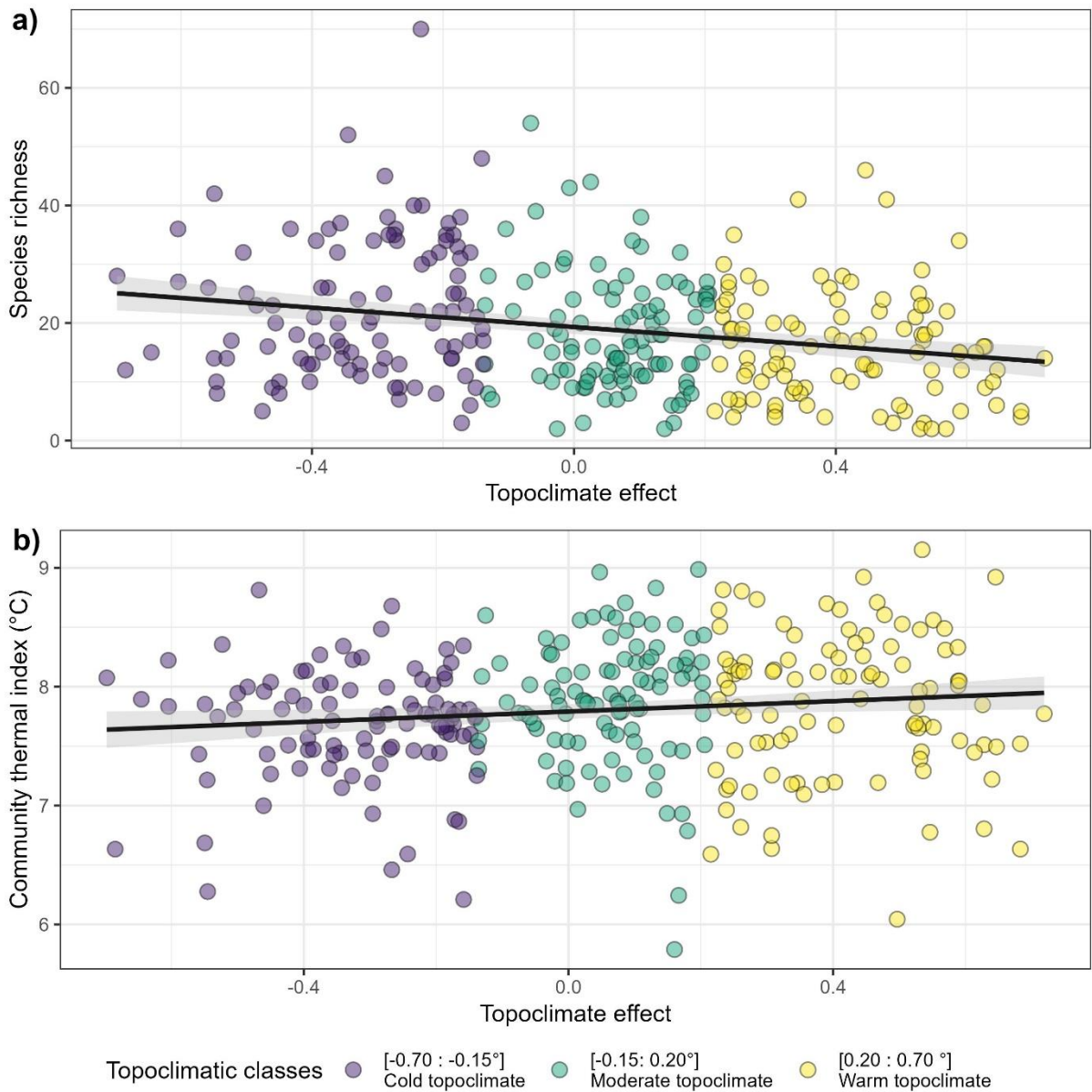


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1095 *Figure S6: Relationship between residuals and fitted values, and histogram of residuals of*  
 1096 *the linear mean temperature model (a), the CTI linear model (b) and the species richness*  
 1097 *negative model (c).*

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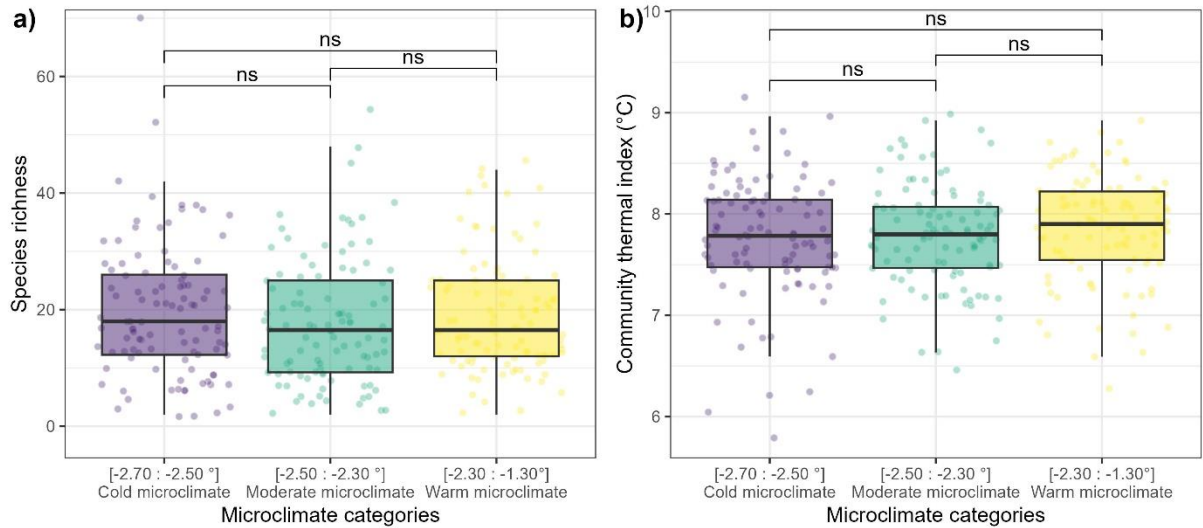


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1101 *Figure S7 Species richness (a) and community thermal index (b) of 306 floristic surveys*  
 1102 *evenly spread into three topoclimatic buffering classes, as function of predicted*  
 1103 *topoclimatic effect on temperature (°C, compared to a moderate topographic situation).*

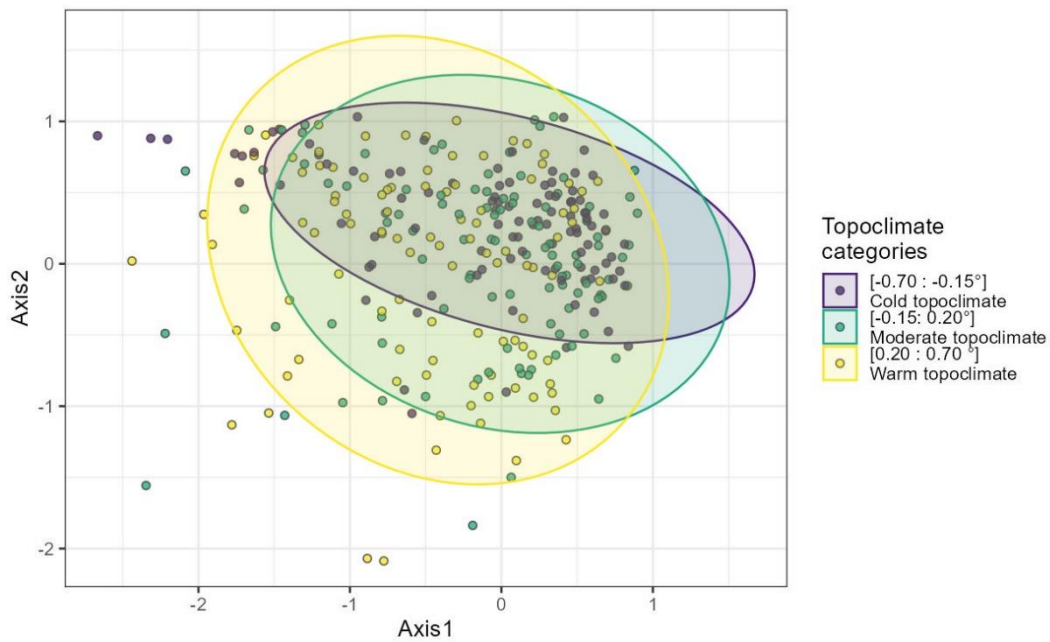
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1107 *Figure S8: Species richness (a) and community thermal index (b) of 306 floristic surveys*  
 1108 *evenly spread into three microclimatic cooling classes. The p-value significance of a*  
 1109 *Wilcoxon test between two classes is displayed as follows: (ns):  $p > 0.05$ .*



1110

1111 *Figure S9: The first two axes of a correspondence analysis of the 306 floristic surveys spread*  
 1112 *among the three topoclimatic cooling class.*

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1114