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## Thermal differences between juveniles and adults increased over time in European forest trees

Maria Mercedes Caron, Florian Zellweger, Kris Verheyen, Lander Baeten, Radim Hédli, Markus Bernhardt-römermann, Imre Berki, Jörg Brunet, Guillaume Decocq, Sandra Díaz, et al.

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1 **Title: Thermal differences between juveniles and adults increased over time in European forest**  
2 **trees**

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68

70 **Abstract**

- 71 1. Woody species' requirements and environmental sensitivity change from seedlings to adults,  
72 a process referred to as ontogenetic shift. Such shifts can be increased by climate change. To  
73 assess the changes in the difference of temperature experienced by seedlings and adults in  
74 the context of climate change, it is essential to have reliable climatic data over long periods  
75 that capture the thermal conditions experienced by the individuals throughout their life cycle.
- 76 2. Here we used a unique cross-European database of 2195 pairs of resurveyed forest plots  
77 with a mean intercensus time interval of 37 years. We inferred macroclimatic temperature  
78 (free-air conditions above tree canopies – representative of the conditions experienced by  
79 adult trees) and microclimatic temperature (representative of the juvenile stage at the forest  
80 floor, inferred from the relationship between canopy cover, distance to the coast, and below-  
81 canopy temperature) at both surveys. We then address the long-term, large-scale, and  
82 multitaxa dynamics of the difference between the temperatures experienced by adults and  
83 juveniles of 25 temperate tree species.
- 84 3. We found significant, but species-specific, variations in the perceived temperature (calculated  
85 from presence/absence data) between life stages during both surveys. Additionally, the  
86 difference of the temperature experienced by the adult *versus* juveniles significantly increased  
87 between surveys for eight of 25 species. We found evidence of a relationship between the  
88 difference of temperature experienced by juveniles and adults over time and one key  
89 functional trait (i.e. leaf area). Together, these results suggest that the temperatures  
90 experienced by adults *vs* juveniles became more decoupled over time for a subset of species,  
91 probably due to the combination of climate change and a recorded increase of canopy cover  
92 between the surveys resulting in higher rates of macroclimate than microclimate warming.
- 93 4. *Synthesis.* We document warming and canopy-cover induced changes in the difference of the  
94 temperature experienced by juveniles and adults. These findings have implications for forest  
95 management adaptation to climate change such as the promotion of tree regeneration by  
96 creating suitable species-specific microclimatic conditions. Such adaptive management will  
97 help to mitigate the macroclimate change in the understory layer.

98 **Key words:** climate change, forestREplot, microclimate, plant functional traits, resurvey, temperate  
99 tree species, ontogenetic shift  
100

101           **1. Introduction**

102 Accelerated climate change (Smith, Edmonds, Hartin, Mundra, & Calvin, 2015) is impacting global  
103 biodiversity (Díaz et al., 2019; Petr, Boerboom, Van der Veen, & Ray, 2014; Segan, Murray, &  
104 Watson, 2016; Shepherd et al., 2016; Urban, 2015). Documented impacts of climate change on plants  
105 include changes in community composition, species richness, population dynamics, physiology,  
106 phenology, and species distribution (e.g. Lenoir et al. 2008; Steinbauer et al. 2018; Dusenge et al.  
107 2019; Kuhn & Gegout 2019; Piao et al. 2019). Macro-scale redistributions of organisms, including  
108 trees, in response to climate change depend on dispersal and establishment in previously  
109 uncolonized areas (Monleon & Lintz, 2015). However, the species' environmental requirements and  
110 tolerances (in terms of e.g. temperature, humidity and light requirements) can change from seedlings  
111 to adult life stages (Grubb, 1977; Parrish & Bazzaz, 1985a), a process referred to as ontogenetic shift  
112 (Bertrand, Gegout, & Bontemps, 2011; Eriksson, 2002; Miriti, 2006; Parrish & Bazzaz, 1985b; Werner  
113 & Gilliam, 1984). Therefore, sites with environmental conditions suitable for adults might be less  
114 suitable for their offspring, and vice versa.

115 In general, early stages of plant's life cycle (i.e. seedlings and juveniles) are considered more  
116 sensitive than adults of the same species to environmental factors such as heat, frost and drought  
117 (Bennett, Mcdowell, Allen, & Anderson-Teixeira, 2015; Lloret, Peñuelas, Prieto, Llorens, & Estiarte,  
118 2009; Mérian & Lebourgeois, 2011). Hence, it is likely that climate change will differently impact adults  
119 and juveniles of the same species. Therefore, it is essential to further our understanding of how  
120 environmental change affects plants along their entire life cycle. The capacity to disperse, colonize  
121 and successfully persist in new suitable areas and therefore the species' capacity to change their  
122 distribution tracking novel climatic conditions is influenced by (i) the speed at which an individual can  
123 produce offspring and regenerate, (ii) morphological (e.g. leaf-height-seed) and physiological traits  
124 (e.g. maximum photosynthesis capacity, leaf nitrogen content) and (iii) species properties (e.g. shade  
125 tolerance, grazing tolerance) (Burke & Grime, 1996; Bussotti, Pollastrini, Holland, & Brüggemann,  
126 2015; Díaz et al., 2016; Dobrowski et al., 2015; Sádlo, Chytrý, Pergl, & Pyšek, 2018). It is expected  
127 that species resistance and resilience to climatic variability is affected by the presence of certain  
128 functional traits (e.g. leaf mass per area is linked to the responses of plants to drought, high light and  
129 scarcity of nutrients; Bussotti et al., 2015; Lohbeck et al., 2015). The environment, including  
130 temperature, can strongly affect all the phases of plant species' regeneration from dormancy break

131 until seedling establishment and survival (Carón et al., 2014, 2015; De Frenne et al., 2011; Fay &  
132 Schultz, 2009; González-Rodríguez, Villar, & Navarro-Cerrillo, 2011; Shevtosova et al., 2009; Walck,  
133 Hidayati, Dixon, Thompson, & Poschlod, 2011). Therefore, regeneration responses to climate change  
134 vary among species with contrasting functional traits.

135 Differences in the distribution range along elevational and latitudinal gradients between life stages  
136 (i.e. adults and juveniles of the same species) are frequently linked to the associated environmental  
137 conditions and climate change (e.g. Lenoir et al. 2009; Woodall et al. 2009; Rabasa et al. 2013; Zhu  
138 et al. 2014; Monleon & Lintz 2015). However, despite that many studies link these differences to  
139 climate change there is a disparity in the direction of the reported shifts. For example, Monleon &  
140 Lintz (2015) showed that, across 46 temperate forest tree species in the United States of America, the  
141 mean annual temperature of the range of seedlings was 0.120°C colder than that of the range of  
142 adults. This difference was attributed to climate change because most species' seedlings'  
143 distributional ranges showed a consistent shift towards colder environments than mature trees.  
144 Conversely, Zhu et al. (2014) showed that most (77%) of the juveniles of 65 tree species in the  
145 eastern United States have higher optimal temperature (in relation to the species abundance), than  
146 the adults. Across species, they detected relatively more abundant juveniles than adults of the same  
147 species in warmer climates, again relating this pattern to climate change. However, other studies  
148 attributed the differences between seedling and adult distributions to ontogenetic shifts. For instance,  
149 seedlings were growing in warmer and drier conditions than adults of the same species, in 12 tree  
150 species in Slovakia (Central Europe) (Máliš et al., 2016). Hence, there is evidence suggesting that the  
151 differences in the environmental conditions experienced by seedlings vs adults from a given species  
152 can be due to ontogenetic shifts, climate change or both acting together (ontogenetic shifts enhanced  
153 by climate change).

154 To accurately study thermal ontogenetic shifts in the context of climate change, and to better  
155 understand the relative importance of ontogenetic shifts and climate change on the contrasting  
156 thermal conditions experienced by adults and juveniles, it is essential to have precise and accurate  
157 data on the actual temperatures experienced by the individuals throughout their different life stages:  
158 from tree seedlings to adult trees and over long time periods. Temperature conditions in forest  
159 systems can vary substantially near the ground surface (understory conditions where juveniles grow)  
160 compared to the conditions at the canopy to which the leaves of adult trees are exposed (De Frenne,

161 Zellweger, Rodríguez-Sánchez, Scheffers, Hylander, Luoto, Vellend, Verheyen, & Lenoir, 2019;  
162 Zellweger et al., 2020).

163 Forest canopy cover, structure and composition strongly influence the microclimatic conditions at the  
164 forest floor including light, humidity and temperature, thereby impacting seedling regeneration, early  
165 survival and growth (George & Bazzaz, 1999) with long-term effects in forest composition, structure  
166 and functioning (Royo & Carson, 2006). Across biomes, the temperature difference between free-air  
167 conditions (macroclimate) and the understory (microclimate) can vary between 1 – 4 °C resulting in  
168 less extreme and less variable conditions below the canopy (De Frenne, Zellweger, Rodríguez-  
169 Sánchez, Scheffers, Hylander, Luoto, Vellend, Verheyen, & Lenoir, 2019). Therefore, the combined  
170 influence of climate change and forest management on forest canopy cover can strongly alter the  
171 microclimatic temperature as perceived by seedlings and juveniles on the forest floor. In some  
172 temperate European forests, an increase in tree growth and forest densities has been reported as a  
173 consequence of decreasing sulphur pollution at the end of the 1980s, an increase in soil nitrogen  
174 availability since the 1950s and changes in forest management practices over the past decades  
175 including a decrease in management intensity. As a matter of fact, many forest sites in Europe have  
176 become either unmanaged or experienced lower management intensities (Baeten et al., 2014;  
177 Depauw et al., 2020; Gold, Korotkov, & Sasse, 2006; Luysaert et al., 2010; McGrath et al., 2015;  
178 Norby et al., 2005; Pretzsch, Biber, Schu, Uhl, & Ro, 2014; Rautiainen, Wernick, Waggoner, Ausubel,  
179 & Kauppi, 2011). In many parts of Europe, logging and natural losses of tree biomass have been  
180 significantly lower than annual increments, resulting in approximately doubled standing stocks of trees  
181 per hectare in 2000 compared to the stocks recorded in 1950 (Gold et al., 2006). This increase in  
182 canopy density produced cooler and darker conditions in the understory. These changes have the  
183 potential to mitigate or even reverse the effects of recent warming in the understory (De Frenne et al.  
184 2013; De Frenne et al. 2019; Zellweger et al. 2020). Therefore, it is likely that adults and juveniles of  
185 tree species have experienced different levels of climate warming: macroclimate warming vs.  
186 microclimate warming (*sensu* Zellweger et al. 2020).

187 Despite the importance of considering the differences between overstory and understory  
188 temperatures, many ecological studies focusing on forest systems still rely on gridded macroclimate  
189 data (Worldclim: Fick & Hijmans 2017; CHELSA; Karger et al. 2017; and TerraClimate; Abatzoglou et  
190 al. 2018) based on weather stations located outside forests above short grass. Such weather stations



191 only reflect macroclimatic conditions misrepresenting the sub-canopy climatic conditions (i.e.  
192 microclimatic conditions). However, a correct representation of the temperature at the understory is  
193 key, especially for forest regeneration studies. Indeed, the mismatch between the environmental  
194 requirements of tall adults vs. juveniles on the forest floor is extremely important in that respect  
195 (Geiger, Aron, & Todhunter, 2003; Lenoir, Hattab, & Pierre, 2017; Uvarov, 1931; Zellweger et al.,  
196 2020). Fortunately, recent advances have made it possible to use local forest microclimatic data  
197 obtained from a network of microclimate sensors located in forest understories across Europe. Based  
198 on that information, a relationship between macroclimate, forest cover and microclimate was  
199 established (see Zellweger et al. 2019). To correctly evaluate the impacts of climate change on the  
200 adult and juvenile life stages (i.e. ontogenetic shifts in the context of climate change), it is necessary  
201 to have repeated records (resurveys) of both layers (canopy and understory) in undisturbed forest and  
202 with sufficient time between records (several decades) in order to capture the effects of climate  
203 warming on species occurrences. Moreover, if resurveys with long intervals between surveys are  
204 combined, with accurate records of temperature over multiple regions, it is possible to increase the  
205 representativeness, and thus generality, of the results (Verheyen et al., 2017).

206 Here we specifically address the long-term, large-scale, multitaxa dynamics of the difference between  
207 the temperatures perceived by adults and juveniles, for 25 of the most common European temperate  
208 forest tree species. To this end, we took advantage of a unique database containing 2195 pairs of  
209 resurveyed plots in 48 regions (12 countries) across Europe. Our database contains species  
210 presence and cover data (visual estimates of percentage ground cover by each species) of adults and  
211 juveniles <1.3 m) with a mean time interval between the baseline survey and the resurvey of 37 years.  
212 For both surveys, we extracted macroclimatic temperatures from global climate grids and calculated  
213 microclimate temperatures in the forest understory (representative of the juvenile layer) across the  
214 continent using, for the first time at such scale, the established relationship between macroclimatic  
215 temperature, tree canopy cover and the temperature offset inside the forest (see Zellweger *et al.*  
216 2019). This relationship was fitted by calculating the difference of temperature outside and inside the  
217 forest by combining microclimate data obtained from a sensor network with weather station records  
218 across Europe. We determined: (i) the degree of warming as perceived by the canopy of the adult  
219 (macroclimate temperature) and juvenile (microclimate temperature) layers between the baseline and  
220 resurvey period (thermal shift over time for each life stage); (ii) the difference in the perceived

221 temperature between the adult and juvenile layers during each survey (ontogenetic shift); (iii) whether  
222 the difference in temperature as experienced by adults and juveniles changed over time (ontogenetic  
223 shift over time) and (iv) whether any difference in ontogenetic shift over time was correlated with  
224 species properties and key morphological and physiological traits important for dispersal and  
225 establishment and for coping with environmental conditions (i.e. LHS - leaf-height-seed traits and  
226 species' shade tolerance).

227 Our overarching hypothesis is that both life stages (adults and juveniles) experienced warming  
228 between surveys due to climate change. However, we expect lower sub-canopy than above-canopy  
229 warming, caused by a canopy-induced offset of maximum daytime temperatures. Therefore, we  
230 expect that a climate change-induced increase in canopy cover increased the thermal decoupling  
231 between both layers. Additionally, we expect that if there are changes over time in the differences  
232 between the perceived temperature of the adults and juveniles such changes will be species-specific  
233 and linked to key functional traits and to species' shade tolerance. Traits are known to influence  
234 species' migration rates and therefore the species' capacity to track suitable environmental conditions  
235 but also the species' capacity to successfully establish and develop under changing environmental  
236 conditions such as warming, drought and shading (Burke & Grime, 1996; Bussotti et al., 2015;  
237 Dobrowski et al., 2015). Hence, traits affect the range of environmental conditions that both phases  
238 (adults and juveniles) are able to tolerate. We expect that species with small seeds, large leaves and  
239 high shade tolerances will exhibit higher thermal differences between adults and juveniles. We expect  
240 this to be linked to (i) changes in distribution of the juveniles due to the higher dispersal capacity and  
241 (ii) to higher tolerances to shadier and cooler environments at the forest floor caused by denser  
242 canopies.

## 243 **2. Materials and methods**

### 244 *Database characterization and plots selection*

245 We used data from the forestREplot database (Verheyen et al., 2017). This database contains  
246 species presence and cover data (percentage of ground cover by the canopy of each species  
247 estimated consistently, in both surveys, in the same plots) from forest resurveys in permanent or  
248 quasi-permanent plots (no pseudoreplicates) with variable plot sizes (between 1 m<sup>2</sup> and 1000 m<sup>2</sup> but  
249 in most cases the plots were either a 10×10 m or a 9m radius plot) located in natural or semi-natural  
250 forests in temperate deciduous forests across Europe (see details of the database at

251 [www.forestreplot.ugent.be](http://www.forestreplot.ugent.be)). The vast majority of the plots in this database are in ancient and mainly  
252 undisturbed or very low-managed forests (between surveys).

253 We selected 2195 pairs of non-overlapping (in space) plots contained in 48 resurveyed datasets  
254 (hereafter regions). These plots have a broad spatial distribution across Europe (Fig. 1a) and were  
255 selected because they have accurate records of the adult layer (>7 m height) and the juvenile layer  
256 (seedlings and saplings < 1m or <1.3 m height depending on the region considered) during either the  
257 baseline survey or resurvey (see Perring et al. 2018) (Fig. 1b, Fig.1c and Table S1).

258 The first surveys (hereafter referred to as “baseline survey”) were carried out between 1933 and 1994  
259 while the resurveys of the same plots (hereafter referred to as “resurvey”) were carried out between  
260 1987 and 2017. The time intervals between the two surveys ranged between 12 and 66 years (with a  
261 mean of 37 years; Fig. 1b and Table S1).

262 For this study, we selected the 25 most common forest tree species spread across this plot network.  
263 All the selected species were present in at least 2.5 % of the plots available in the forestREplot  
264 database.

#### 265 *Temperature data*

266 Recorded and estimated macroclimate and microclimate temperatures, respectively, during both  
267 surveys (baseline and resurvey) were used for the analysis. The macroclimate above-canopy  
268 temperature used was the mean daily maximum summer temperature (June, July and August)  
269 extracted for each plot mainly from TERRACLIMATE (<http://www.climatologylab.org/terraclimate.html>)  
270 while the Climate Research Unit - CRU (<https://crudata.uea.ac.uk/cru/data/hrg/>) was used for 224  
271 plots of the baseline survey plots for which TERRACLIMATE information was not available. The  
272 TERRACLIMATE database was complemented when needed with the CRU database because they  
273 correlated strongly (in the baseline survey  $R=0.69$ ,  $p<0.001$  and in the resurvey  $R=0.81$ ,  $p<0.001$  for  
274 overlapping data points). The extracted maximum summer temperatures were averaged per plot for  
275 the five years preceding each survey (baseline surveys and resurveys) (Fig. 1c).

276 The microclimate temperature within the understory layer (where juveniles grow) at the baseline  
277 survey and resurvey were calculated at the plot level for plots where each species was present in  
278 either the baseline or the resurvey. To compute microclimate temperatures near the forest floor at  
279 both time periods, we used the information of canopy cover at each plot (visual estimates of  
280 percentage ground cover by each species) recorded *in situ* when each survey (baseline and resurvey)

281 took place (reflecting all the conditions that influenced the canopy cover e.g. management, soil  
282 nutrient, rainfall variability, CO<sub>2</sub> and Nitrogen deposition) and the empirical relationship established by  
283 Zellweger et al. (2019) between macroclimate temperature, canopy cover, distance to the coast and  
284 sub-canopy temperature. The microclimatic information used by Zellweger et al. (2019) was obtained  
285 from a network of sensors installed in ten plots representing a regional gradient of canopy cover  
286 distributed in ten regions across Europe (all included in this study). The air temperature at 1m above  
287 the ground was recorded hourly from February 2017 to February 2018, then, aggregated to minimum  
288 (T<sub>min</sub>), mean (T<sub>mean</sub>) and maximum (T<sub>max</sub>) daily temperature. Next, the temperature offset values  
289 were calculated as the difference between the daily temperature statistics (T<sub>min</sub>, T<sub>mean</sub>, T<sub>max</sub>)  
290 recorded inside the forest and the respective temperature statistic recorded by the closest weather  
291 station (macroclimate above-canopy temperature). Finally, the daily temperature offsets were  
292 aggregated to calculate monthly means (Zellweger et al. 2019).

293 The data obtained was used to build a set of models that analysed the temperature offset as function  
294 of two groups of explanatory variables i) local canopy structure and composition and ii) landscape  
295 structure and topography. Next, the best performing model (R<sup>2</sup>=0.33, RMSE gamm 0.92) with local  
296 canopy cover and distance to the coast as predictors was selected after evaluation using the cross-  
297 validation approach such that a model was calibrated based on data from nine out of 10 regions and  
298 validated based on the remaining one ('leave one out' approach). This model developed by Zellweger  
299 et al., (2019) was used to calculate the below-canopy (juvenile layer) maximum temperature during  
300 summer of the five years precedent to the year of each survey (to iron out any extremes that happen  
301 during the year of the survey) as it was proven to correctly predict the temperature offset in summer.  
302 Additionally, this model reflects principal physical mechanisms for driving the radiation regime below  
303 the canopy, which is a key determinant of the below canopy temperature offsets. During warm and  
304 clear days, a large part of the incoming short- wave radiation is absorbed and reflected by the canopy,  
305 while increasing evapotranspirative cooling, resulting in a cooling of the understory maximum  
306 temperature (De Frenne et al., 2021; De Frenne, Zellweger, Rodríguez-Sánchez, Scheffers,  
307 Hylander, Luoto, Vellend, Verheyen, Lenoir, et al., 2019). Moreover, as the variables used to fit the  
308 model are the plot-specific distance to the coast (invariable), the canopy cover (*in situ* recorded at the  
309 moment of each survey, in 100 plots included in this study) and the macro maximum summer  
310 temperatures extracted from TERRACLIMATE or CRU (extracted for each survey), and the model

311 relies on the physics of radiative transfers through vegetation canopies, the model despite its  
312 limitations, can be used to estimate the temperature at the juvenile layer during both surveys.

313 These analyses resulted in a database that contained mean daily maximum above-canopy  
314 temperatures during the summer extracted from weather stations close to the forests and mean daily  
315 maximum sub-canopy temperatures during the summer for each plot and averaged for the five years  
316 preceding each survey (baseline surveys and resurveys) (Fig. 1c).

317 The maximum summer macroclimate and microclimate temperatures were selected for the analysis  
318 because (i) canopy structure and composition play a key role in regulating the offset of maximum  
319 summer temperatures (Zellweger et al., 2019) and (ii) local maximum temperatures are of paramount  
320 importance for the response of organisms to climate warming due to its relationship with species-  
321 specific heat tolerances and fitness (Macek, Kopecký, & Wild, 2019). We do not interpret our results  
322 in terms of optimal niche locations since the distribution of our plots is not indicative of the species full  
323 distribution range or species performance.

#### 324 *Data analyses*

325 Plots where juveniles and adults of the selected species were recorded (presence/absence data) in  
326 either the baseline survey or the resurvey were used to extract the estimated maximum temperature  
327 data for juveniles (maximum microclimate temperature) and maximum temperature data for adults  
328 (maximum macroclimate temperature). These data were used to calculate: (i) temperature changes  
329 between surveys (thermal shifts over time for each life stage); (ii) temperature variations between life  
330 stages (thermal ontogenetic shifts during both the baseline survey and the resurvey); and (iii) the  
331 change between surveys of the difference in the temperature as perceived by adults and juveniles  
332 (temperature at the adult layer minus the temperature at the juvenile layer; thermal ontogenetic shift  
333 over time) (Fig 1d).

334 We analysed:

335 i) changes in temperature between surveys for the adult and juvenile layers separately using  
336 the temperature at each layer (adult temperature and juvenile temperature) as a response variable  
337 and the survey (baseline vs. resurvey) as explanatory fixed variable.

338 ii) variations of temperature between layers for each survey separately (baseline and  
339 resurvey) using the temperature at both layers (adult and juvenile temperatures) as a response  
340 variable and the layer as explanatory fixed variable (adult vs. juveniles).

341           iii) changes between surveys of the difference between the temperature experienced by the  
342 adult layer and the juvenile layer using the difference between the temperature experienced by the  
343 adults minus the temperature experienced by the juveniles as response variable while the survey was  
344 used as explanatory variable.

345 Generalized mixed-effect models for all the species together included species nested in region as  
346 random intercept, and models for each species separately (species-specific models) included only the  
347 region as random intercept to account for the nested nature and spread of the data within regions  
348 (Table 1). Additionally, to test that there was not pseudo-replication linked to the plot where the  
349 species were recorded i.e. more than one species could be recorded in the same plot, the same  
350 analysis was done with species nested in region and plot (see results in Table S6). Finally, to test that  
351 the results were not biased due to the presence of an adult individual adjoining but not inside the plot  
352 and therefore that plot was recorded as only containing juveniles, the same analyses were repeated  
353 assuming that all the plots where seedlings were present also had an adult individual (see results in  
354 Table S7). All the models were fitted using the lme4 package in R version 3.5.2 (R Core Team, 2018)  
355 and in all cases the significance of the explanatory variable was assessed based on likelihood ratio  
356 tests (Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

357 Next, to be able to understand and link the temperature responses to changes in forest canopy,  
358 changes in cover and frequency (number of times a plant species occurs) over time were analysed for  
359 all the species together and for each species separately using cover and frequency as a response  
360 variable, respectively, and survey as explanatory variable (see results in Tables S3 and S4). The  
361 models for all the species together included species nested in region as random intercept and the  
362 species-specific models included only the region as random intercept. The contribution of the  
363 explanatory variable was assessed based on the likelihood ratio tests (Zuur, Ieno, Walker, Saveliev, &  
364 Smith, 2009).

365 Finally, for all 25 species and then also for the 8 species that showed significant changes in thermal  
366 ontogenetic shifts between surveys (i.e. analysis iii), we correlated this difference (one value per  
367 species) with a shade tolerance index, and the mean and the standard deviation of key functional  
368 traits (leaf mass area, leaf area, plant height and seed mass, Table S2) (Westoby 1998, Díaz et al.  
369 2016). Pearson correlation was used for height while Spearman correlations were used for leaf mass  
370 area, leaf area and seed mass due to the non-normality of those data. The values of the key

371 functional traits were extracted from Díaz et al. (2016). The functional trait values provided by Díaz et  
372 al. (2016) are the geometric mean extracted from the Plant Trait Database TRY ([https:// www.try-  
374 db.org](https://www.try-<br/>373 db.org)) supplemented by published data not included in TRY and a small number of original  
375 unpublished data (Díaz et al., 2016). All data were standardized and subjected to error detection and  
376 quality control (see details in Díaz et al. 2016). The standard deviation values were calculated from  
377 the individual records of traits values available in the TRY database. The number of observations per  
378 trait and species range from a single one (in the case of rare, geographically restricted species) to  
379 hundreds (in the case of common species with broad ranges; Díaz et al. 2016). The shade tolerance  
index for each species was extracted from Niinemets & Valladares (2006).

### 380 **3. Results**

381 Across all species, the adult layer temperature increased by  $1.56\text{ }^{\circ}\text{C} \pm \text{SD } 0.53$  ( $0.38\text{ }^{\circ}\text{C}/\text{decade}$ )  
382 between the baseline and the resurvey while the juvenile layer temperature increased by  $1.34\text{ }^{\circ}\text{C} \pm \text{SD}$   
383  $0.42$  ( $0.35\text{ }^{\circ}\text{C}/\text{decade}$ ) between surveys (Table S3 and Table S12). However, the rate of temperature  
384 change in both layers was species-specific (Table S3, Fig. 2 and Table S12). In the adult layer,  
385 *Quercus rubra* experienced the highest degree of warming ( $3.59\text{ }^{\circ}\text{C}$ , i.e.  $0.78\text{ }^{\circ}\text{C}/\text{decade}$ ) while *Tilia*  
386 *cordata* exhibited the strongest warming in the juvenile layer ( $2.19\text{ }^{\circ}\text{C}$ , i.e.  $0.67\text{ }^{\circ}\text{C}/\text{decade}$ ) (Table S3,  
387 Fig. 2 and Table S12).

388 The adult layer experienced significantly higher temperatures than the juvenile layer in both the  
389 baseline survey ( $+2.19\text{ }^{\circ}\text{C} \pm \text{SD } 0.74$ ) and the resurvey ( $+2.41\text{ }^{\circ}\text{C} \pm \text{SD } 0.73$ ) across species (Table  
390 S3). However, the difference between the temperature experienced by the adults and juveniles was  
391 again species-specific (Table S3, Fig. 2 and Table S12). In the baseline survey, the highest difference  
392 between the temperature experienced by the adults and the juveniles was recorded in *Populus*  
393 *tremula* ( $+3.84\text{ }^{\circ}\text{C}$ ) and in the resurvey in *Tilia platyphyllos* ( $+3.92\text{ }^{\circ}\text{C}$ ) (Table S3, Fig. 2 and Table  
394 S12).

395 Temperature differences between adults and juveniles changed significantly between surveys when  
396 all the species are considered together (Table S3). We found that the temperature difference  
397 experienced by adults vs juveniles increased over time for 17 (68%) of the 25 analysed European tree  
398 species. However, this difference was significant for eight out of 25 species only (Table S3 and Fig.  
399 3). These eight species exhibited an average increase of  $0.18\text{ }^{\circ}\text{C}$  in the temperature difference  
400 between adult and juvenile layers when comparing the baseline survey to the resurvey (Fig. 3). In

401 other words, the thermal ontogenetic shift between putative “mothers” and “daughters” significantly  
402 increased over time for eight tree species. The only species in which this temperature difference  
403 significantly decreased, by 0.14 °C, was *Acer campestre* (Fig. 3).

404 Finally, we tested for relationships between thermal ontogenetic shifts and tree species traits. The  
405 evidence for the relationship between thermal ontogenetic shifts over time and traits was weak; when  
406 all 25 species were analysed together, there were no significant correlations between any analysed  
407 trait or their standard deviation and temporal temperature differences between adult and juvenile  
408 layers (correlation ranged from -0.38 to 0.36; Table S11). The difference between the temperature  
409 experienced by adult and juvenile layers over time slightly increased (non-significantly) with the shade  
410 tolerance index (correlation= 0.24, p-value= 0.239; Table S11). A significant positive correlation  
411 (correlation= 0.83, p-value=0.015) was detected between the leaf area, and the difference between  
412 surveys of the variation in the temperature experienced by adults and juveniles, but only for those  
413 eight species exhibiting a significant positive thermal ontogenetic shift over time (Fig. 4 and Table  
414 S10). However, significant positive thermal ontogenetic shifts were not related to leaf mass area, seed  
415 mass, shade tolerance, nor height or their standard deviation (correlations ranged from -0.64 to 0.41;  
416 Table S10).

#### 417 **4. Discussion**

418 The temperature experienced by the studied tree species of temperate European forests, in both the  
419 adult and juvenile layers, changed significantly between surveys. In other words, we detect a shift in  
420 the thermal conditions experienced by both life stages over time. The observed unequal warming of  
421 both layers over time is in line with our expectations of lower sub-canopy than above-canopy  
422 warming, due to a canopy-induced offset of maximum daytime temperatures (Davis, Dobrowski,  
423 Holden, Higuera, & Abatzoglou, 2019; De Frenne, Zellweger, Rodríguez-Sánchez, Scheffers,  
424 Hylander, Luoto, Vellend, Verheyen, & Lenoir, 2019; Zellweger et al., 2019). Considering that the  
425 juvenile layer might express current conditions while the distribution of adults rather expresses past  
426 conditions (Lenoir et al., 2009; Urbieto, Zavala, & Marañón, 2011; Woodall et al., 2009), the  
427 divergence in temperatures might also be influenced by the colonization of new areas (this in turn, is  
428 affected by species’ dispersal capacity). However, due to the warming recorded in the juvenile layer,  
429 our results suggest that species did not manage to shift their distributions to maintain the same  
430 thermal conditions in the resurvey as recorded in the baseline, and likely adapted to the new warmer



431 conditions. The higher difference in thermal conditions between surveys in adults than juveniles  
432 suggest that adult trees are lagging more behind macroclimate change than their conspecific  
433 juveniles.

434 We trust that our estimates of the juvenile layer temperatures are reliable because the model  
435 incorporates canopy cover (*in situ* recorded by experienced forest ecologists at the moment of each  
436 survey) and macroclimate which are the major drivers of below-canopy temperature offsets (De  
437 Frenne et al., 2021; De Frenne, Zellweger, Rodríguez-Sánchez, Scheffers, Hylander, Luoto, Vellend,  
438 Verheyen, Lenoir, et al., 2019) and relies on the physics of radiative transfers through vegetation  
439 canopies. Nonetheless, there are no old forest microclimate measurements in our plots so our  
440 estimates of the baseline temperature at the juvenile layer remain uncertain but are, to the best of our  
441 knowledge, the only ones available. Additionally, although this is carefully avoided in resurvey studies  
442 (Verheyen et al., 2018), possible differences in the way canopy cover was recorded in the baseline  
443 and the resurvey and the methods used by Zellweger et al. (2019) could affect the estimated  
444 temperatures at the juvenile layer. Moreover, there is a part of variability that remains unexplained by  
445 the model used here and it is possible that the variability of the estimated below canopy temperatures  
446 might be lower than the variation of the real observed data.

447 The warming recorded here in both layers is in line, but slightly higher than, the global mean land  
448 surface air temperature increase of 1.29 °C measured between 1940 and 2016 (the time period  
449 considered in this study) (IPCC, 2019). The higher degree of warming recorded in this work is likely  
450 due to the fact that we analysed maximum summer temperatures. The detected temperature increase  
451 was species-specific and, considering the close relationship between latitude and observed and  
452 projected temperatures (De Frenne, Graae, et al., 2013; Monleon & Lintz, 2015), it is likely that  
453 recorded species-specific warming is also linked to the spatial distribution of a species and its  
454 dispersal and establishment capacity (Table S8) despite the fact that our database did not cover the  
455 complete distribution of the species. This species-specific response, might also be linked to the  
456 species-specific crown architecture (e.g. *Betula* species transmit more light to the forest floor than for  
457 example *Abies alba*). However, the influence of crown architecture on the change in the temperature  
458 over time is beyond the scope of this work but should be considered in future studies. The observed  
459 species-specific pattern of temperature increase between surveys should be considered with caution  
460 because the estimates are based on temperature datasets that have a relatively coarse resolution

461 (~4x4 km for TERRACLIMATE). In our study focused on thermal shifts, we only consider one of the  
462 multiple factors that influence the presence of an individual, i.e. temperature, while other factors and  
463 processes could also influence the establishment of new individuals including masting, herbivory, the  
464 past legacy of human interventions and forest management (Lombaerde et al., 2020).

465 Among both surveys, thermal ontogenetic shifts were detected: in the baseline survey the adult layer  
466 experienced 2.19 °C warmer temperatures than the juveniles and in the resurvey this difference  
467 increased by 0.22 °C, reaching 2.41 °C. Differences in the temperatures experienced by adults and  
468 the juveniles were recorded in other forest types and regions including in the USA (Monleon & Lintz,  
469 2015; Zhu et al., 2014) and the Mediterranean (Urbieto et al., 2011). In some cases, these thermal  
470 differences between life stages have been linked to shifts in distribution as a response to climate  
471 change, namely younger life stages shifting towards currently cooler conditions compared to adults'  
472 distribution mirroring past climatic conditions (e.g. Lenoir et al. 2009; Woodall et al. 2009; Monleon &  
473 Lintz 2015). Others found that the range shifts among tree life stages were more consistent with  
474 ontogenetic differences in environmental requirements than with responses to climate change (Máliš  
475 et al., 2016). The latter conclusion was supported by the fact that the authors used recent and  
476 historical data reflecting conditions before current warmer period and identified similar differences  
477 between adults and juveniles in both time periods, driven by warmer growing conditions of seedlings  
478 than adults. Máliš et al. (2016) analysed changes in distribution and linked these distributional  
479 changes with mean macroclimatic conditions calculated for each plot using a network of local  
480 meteorological stations while we used maximum summer macro- and microclimatic temperatures  
481 estimated for each plot using global databases and the relationship between the canopy cover and  
482 the understory temperature. The model used here despite its limitations (see above) correctly predict  
483 the temperature offset in summer (Zellweger et al., 2019). Additionally, the use of the average of the  
484 five years presiding each survey avoids the bias linked to possible abnormal warm or cold summers.  
485 Other authors (e.g. Lenoir et al. 2009; Woodall et al. 2009; Monleon & Lintz 2015) reported results in  
486 the same direction as our findings (i.e. seedlings growing in colder conditions than adults) but linked  
487 these observations to climate warming-induced distributional shifts with seedlings or juveniles  
488 colonizing cooler locations and not to ontogenetic shifts. Using the macroclimatic (adult layer) and  
489 microclimatic (juvenile layer) temperatures, we detected thermal ontogenetic shifts in the studied tree  
490 species independently of the origin of the species and the time period considered (baseline survey

491 and resurvey). Indeed, non-native species such as *Prunus serotina* and *Quercus rubra* (introduced  
492 from the North America) had similar thermal ontogenetic shifts as native European species of the  
493 same genera.

494 The thermal difference experienced by the adults and juveniles (i.e. ontogenetic shift) increased over  
495 time for 17 (68%) of the 25 analysed European tree species. However, this shift was only significant  
496 for eight out of 25 species. Thus, the temperature experienced by the individuals at the two layers  
497 became increasingly decoupled over time for a subset of the studied species. This increased  
498 decoupling is likely caused by the higher warming rates at the canopy layer compared to the forest  
499 floor due to canopy-induced temperature offset. Indeed, the mean canopy cover increased between  
500 surveys in six out of the eight species where we observed increased decoupling between the  
501 temperature experienced by the adults and the juveniles (Table S4, Table S5 and Table S13). The  
502 significant decrease in the difference of the temperature experienced by adults and juveniles over  
503 time reported for one species (*Acer campestre*) might be linked to a decrease in cover in certain plots  
504 caused by mortality of adults of this species, potentially due to an exceedance of physiological  
505 tolerances due to macroclimate warming. Nevertheless, it is possible that the decoupling might also  
506 be linked to species making small local shifts in their ranges and differences in the ability of the  
507 juvenile stages to keep up with the velocity of climate change. It is even likely that these mechanisms  
508 are occurring simultaneously. The increased difference of temperature between the adult and juvenile  
509 layers between surveys partially compensated (0.18°C) macroclimate warming (De Frenne,  
510 Zellweger, Rodríguez-Sánchez, Scheffers, Hylander, Luoto, Vellend, Verheyen, & Lenoir, 2019). This  
511 means that for species that experienced an increase of the difference of temperature between the  
512 adult and juvenile layer between the baseline and recent surveys, the warming was less strong than  
513 for the other species.

514 Our trait-based analyses shed light on the causes of the divergent responses in the difference of the  
515 temperature experienced by adults vs. juveniles between surveys. Large-leafed species exhibited an  
516 increase of the difference between the temperature experienced by adults vs. juveniles over time,  
517 likely because large leaves provide competitive advantages in dealing with the darker conditions of  
518 the understory (Bequet et al., 2011; Li, Liu, & Berninger, 2004). Seedlings with larger leaves can  
519 overtop neighbouring vegetation and get better access to light at the forest floor (Leishman, Wright,  
520 Moles, & Westoby, 2000; Poorter & Rose, 2005). Additionally, larger leaves have usually a thicker

521 boundary layer that slows sensible heat exchange with the surrounding air, developing larger leaf-to-  
522 air temperature differences than smaller leaves. The wider leaf-to-air temperature differences of larger  
523 leaves may allow them to more quickly heat up during cool mornings to favourable temperatures for  
524 photosynthesis, what might allow for higher photosynthetic returns (Wright et al., 2017). The  
525 intraspecific variability of leaf area, included in our analysis as the traits' standard deviation,  
526 apparently, does not affect the difference between the temperature experienced by adults vs.  
527 juveniles over time (no significant correlation). Leaf traits as well as other species traits and properties  
528 (e.g., shade tolerance) can vary not only intraspecifically but also along the species life cycle (i.e.,  
529 ontogenetic shift in traits values). This variation of traits along the species life cycle is somehow  
530 present in our standard deviation analysis as the traits' database used here combines adult and  
531 juveniles' traits values as well as data collected in controlled experiments and in nature. However, a  
532 detail analysis of how ontogenetic changes in functional traits affect the difference between the  
533 temperature experienced by juveniles vs. adults is beyond the scope of this work. Finally, we did not  
534 find a significant relationship between the shade tolerance of the species and the changes in the  
535 adults vs. juveniles thermal differences among surveys. We had, however, a relatively small species  
536 sample size ( $n= 25$  or  $n= 8$ ) (Wasserstein & Lazar, 2016) and further analysis should be done with  
537 larger sample size to confirm these results.

### 538 **Conclusions**

539 In sum, the significant differences between the temperature experienced by adults vs. juveniles  
540 indicate that the different phases of the life cycle can differ in their thermal requirements and/or  
541 tolerances, in line with the ontogenetic shift theory (Bertrand et al., 2011; Eriksson, 2002; Máliš et al.,  
542 2016; Miriti, 2006; Parrish & Bazzaz, 1985b). These findings highlight the importance of studying the  
543 impacts of climate change on different phases of the plant life cycle using reliable climatic information  
544 for each phase and layer. Moreover, our findings suggest that the capacity to deal with climate  
545 change varies with the trees' life stages and with species identity. Adults are more likely to cope with  
546 warming by persisting locally for a long time while juveniles are less likely to do so and thus more  
547 likely to track the shifting isotherms thereby increasing the thermal ontogenetic shifts.

548 By disentangling the impacts of climate change on different phases of plants' life cycle, our work  
549 sheds light onto the ontogenetic changes across large geographical and temporal scales in the  
550 context of climate change. This information is key to advance our understanding of the ecology and

551 dynamics of temperate forests in the face of climate warming. Our findings could also assist forest  
552 managers in predicting future species composition based on climatic projections, and in promoting  
553 tree regeneration by creating suitable tree species-specific microclimatic conditions, helping to  
554 mitigate, at least partially, the change at the understory level driven by changes in macroclimate.

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570 FZ provided the climatic database. KV, LB, RH, MB-R, IB, JB, GD, TD, TD, TH, BJ, MK, JL, MM, MM,  
571 MF, NTA, PP, KR, RP, WS, KS, BT, MW and PDF collected the vegetation information available in  
572 the ForestREplot database. FZ, LB, SD, JL, MPP and PDF contributed to the initial discussion of the  
573 paper design. All the authors provided comments.

574 **Data Availability statement:** All vegetation data used in this paper is available in the forestREplot  
575 database ([www.forestreplot.ugent.be](http://www.forestreplot.ugent.be)). Macro and micro temperature data available from the Dryad  
576 Digital Repository <https://doi.org/10.5061/dryad.rfj6q57bh> (Caron, M. M., et al., 2021). The rest of the  
577 data is available in the cited references or presented in the tables or figures.

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Table 1: Mixed-effect models used for the analysis of thermal shift between surveys and layers and the change in the difference between the temperature experienced by adults (macroclimate) and juveniles (microclimate) over time across and within species

| <b>Models across species</b>   |  |                      |                       |
|--|--|----------------------|-----------------------|
|  | <b>Response variable</b>   | <b>Fixed effects</b> | <b>Random effects</b> |
| For the adult layer  | Macroclimate temperature   | Survey               | Region x sp + sp      |
| For the juvenile layer   | Microclimate temperature   | Survey               | Region x sp + sp      |
| For the baseline survey  | Temperature (macroclimate temperature & microclimate temperature)          | Layer                | Region x sp + sp      |
| For the resurvey   | Temperature (macroclimate temperature & microclimate temperature)          | Layer                | Region x sp + sp      |
| For the complete database (baseline and resurvey including adults and juveniles) | $\Delta$ Temperature (macroclimate temperature – microclimate temperature) | Survey               | Region x sp + sp      |
| <b>Species-specific models</b>   |  |                      |                       |
|  | <b>Response variable</b>   | <b>Fixed effects</b> | <b>Random effects</b> |
| For the adult layer  | Macroclimate temperature   | Survey               | Region                |
| For the juvenile layer   | Microclimate temperature   | Survey               | Region                |
| For the baseline survey  | Temperature (macroclimate temperature & microclimate temperature)          | Layer                | Region                |
| For the resurvey   | Temperature (macroclimate temperature & microclimate temperature)          | Layer                | Region                |
| For the complete database (baseline and resurvey including adults and juveniles) | $\Delta$ Temperature (macroclimate temperature – microclimate temperature) | Survey               | Region                |

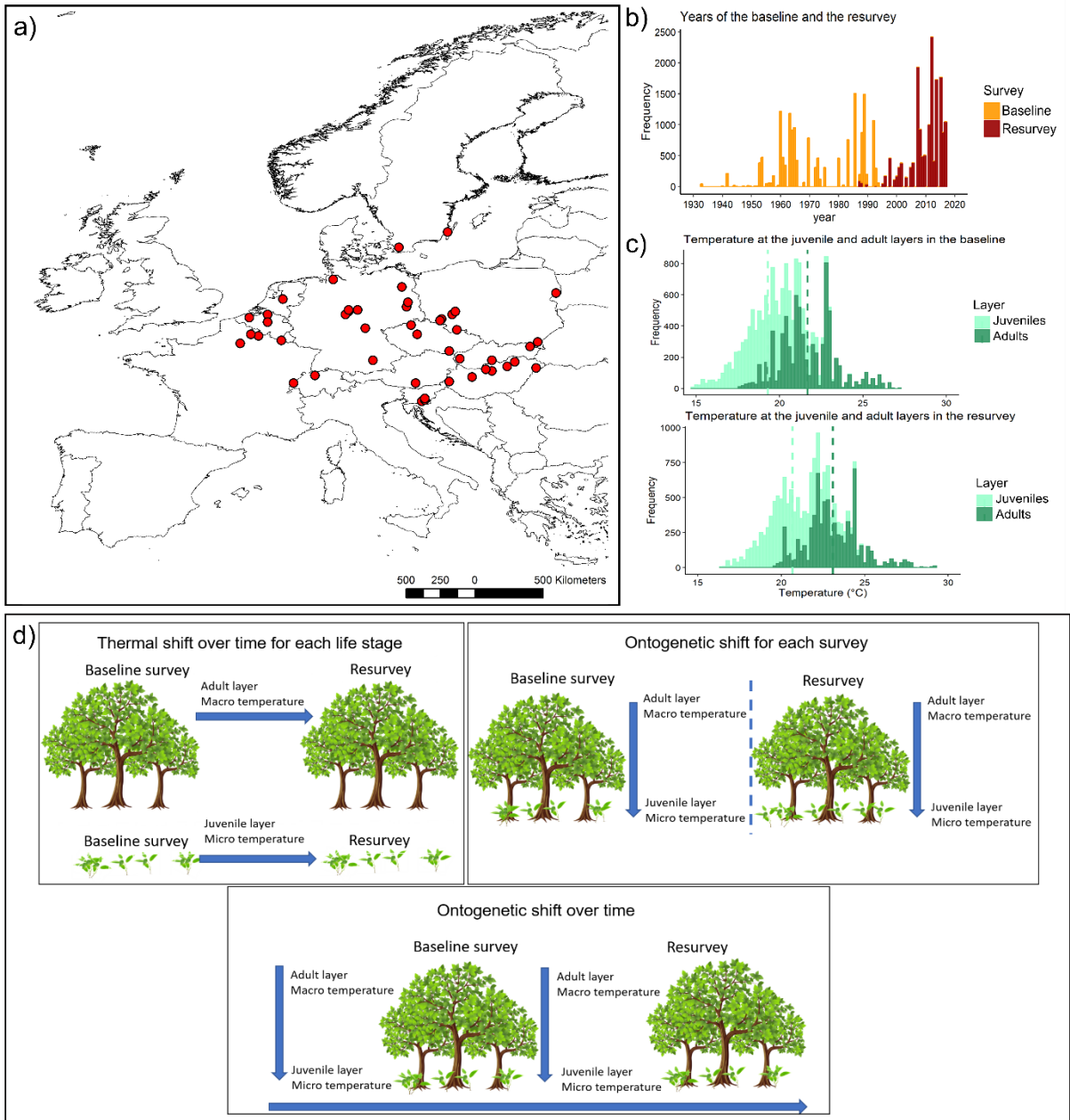


Fig. 1: a) Locations of the datasets used for the analysis, b) Histogram of number of plots with years of the baseline survey and resurvey and c) Histogram showing number of plots with given maximum summer temperature in the adult (i.e. macroclimate) and juvenile (i.e. microclimate) layer at the time of the baseline (top) and resurvey (bottom), vertical lines represent the means of each layer d) Scheme of the study design: we first calculate the thermal shift over time for each life stage as the difference in temperatures between resurvey and baseline survey. Second, we calculated ontogenetic thermal shift as the temperature of the canopy (adult layer) vs forest floor (juvenile layer). Finally, we merged both approaches and calculated the ontogenetic thermal shift difference over time integrating the first and second calculation.

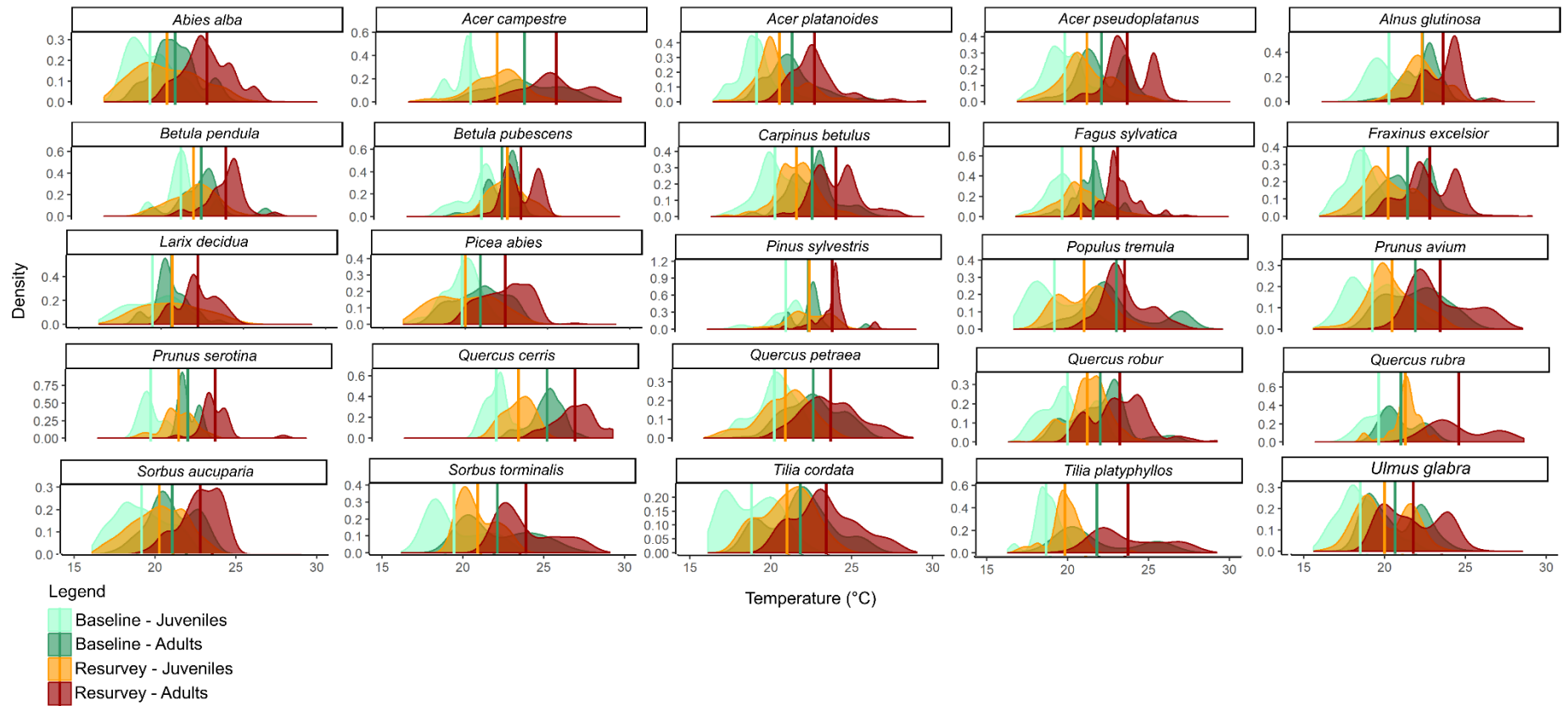


Fig. 2: Juvenile layer temperature (subcanopy microclimate temperature) and adult layer temperature (above-canopy macroclimate temperature) for the 25 most common tree species in the baseline survey and resurvey. Vertical lines represent the species means of each layer and survey.



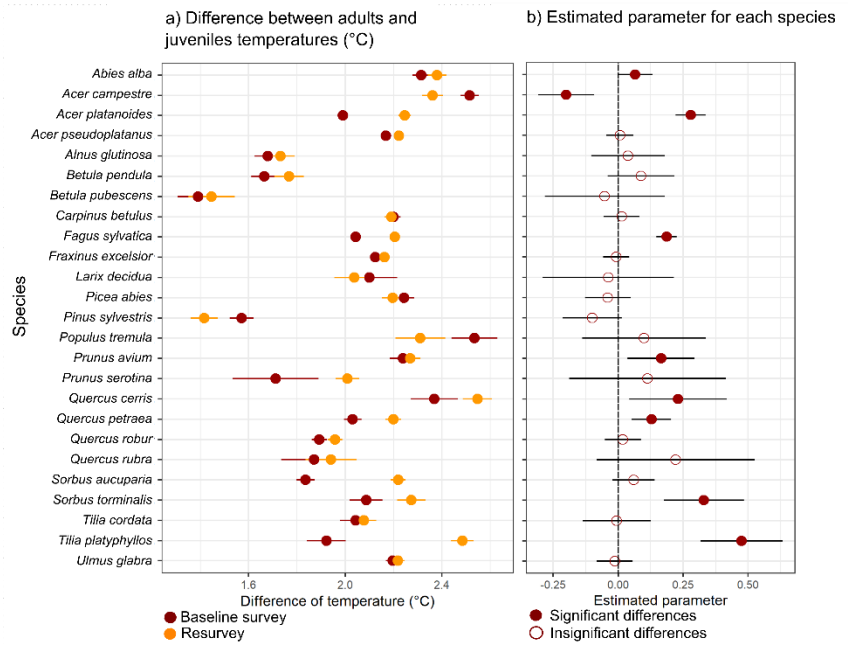


Fig. 3: a) Difference between the adult layer temperature and the juvenile layer temperature (calculated as adult layer minus juvenile layer such that positive values reflect warmer temperatures for the overstory trees) in the baseline survey (red) and the resurvey (yellow); error bars denote standard errors. b) Model estimates of the difference between the adult and juvenile layers temperatures over time. Full circles indicate significant differences and open circles insignificant differences, error bars denote two standard errors.

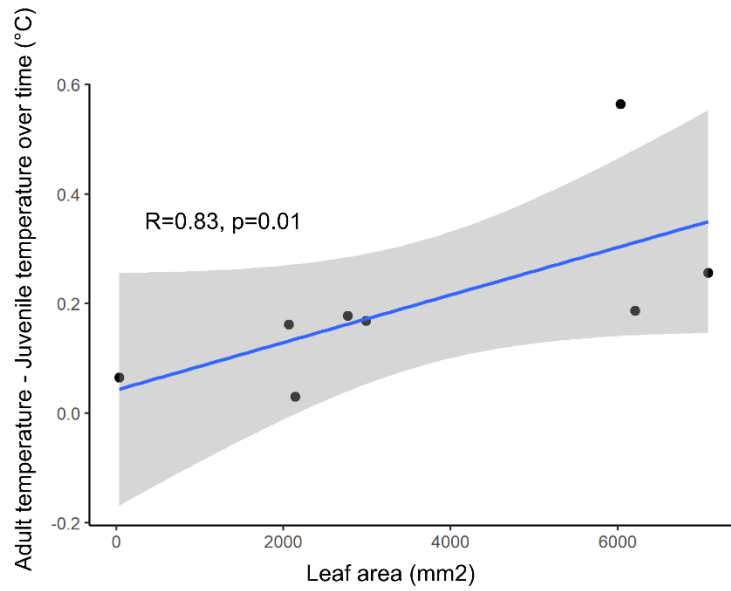


Fig. 4: Positive relationship between the temperature difference of adults minus juvenile trees over time (resurvey minus baseline survey) and leaf area (mm<sup>2</sup>). Shown here only for the eight species with a significant change in the ontogenetic thermal niche over time (n = 8).