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

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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 m² and 1000 m² 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). 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, CO₂ 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 (Tmin), mean (Tmean) and maximum (Tmax) daily temperature. Next, the temperature offset values
289 were calculated as the difference between the daily temperature statistics (Tmin, Tmean, Tmax)
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 ($R^2=0.33$, 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-
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, 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). 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
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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

Models across species			
	Response variable	Fixed effects	Random effects
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)	Δ Temperature (macroclimate temperature – microclimate temperature)	Survey	Region x sp + sp
Species-specific models			
	Response variable	Fixed effects	Random effects
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)	Δ Temperature (macroclimate temperature – microclimate temperature)	Survey	Region

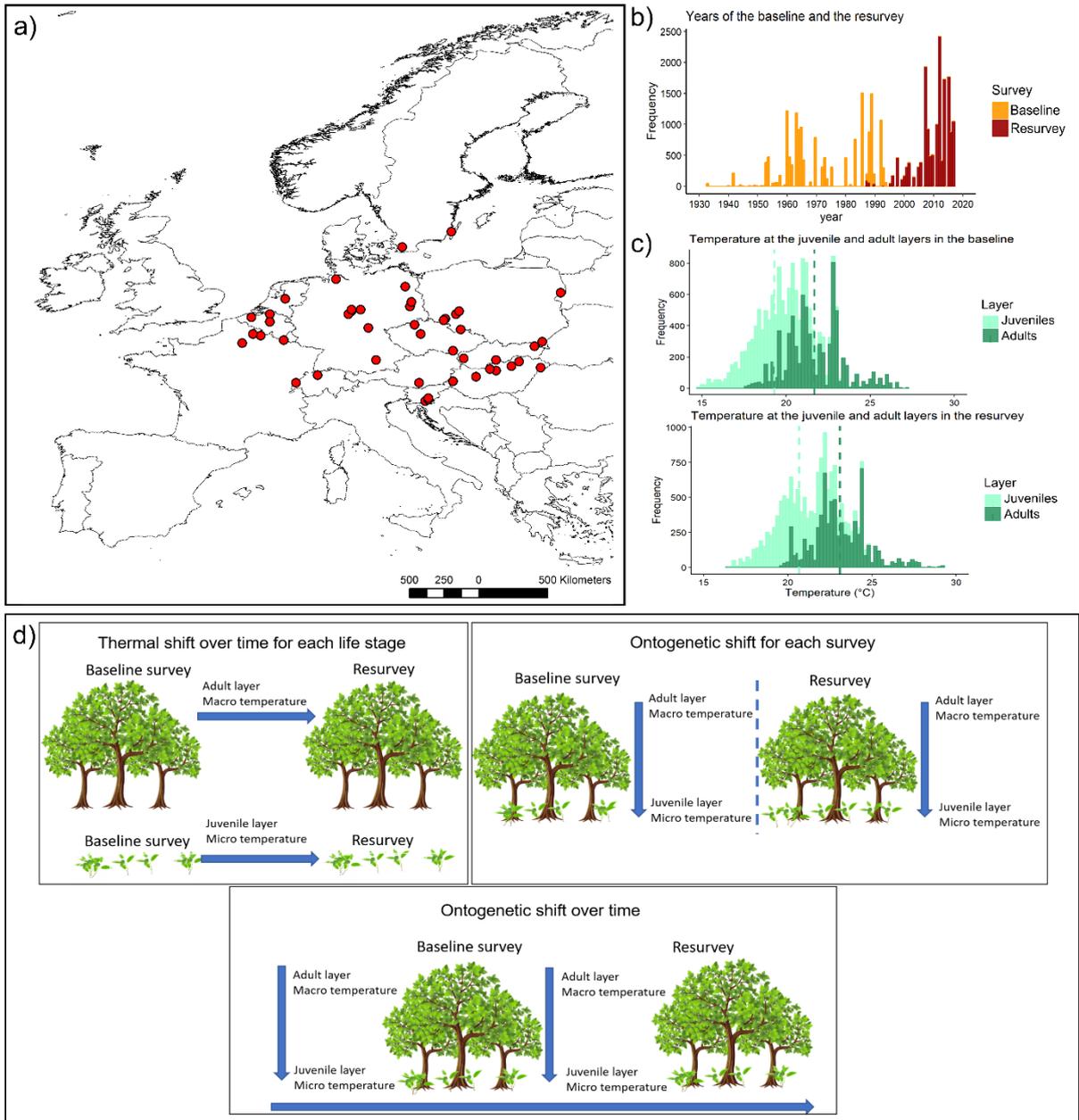


Fig. 1: a) Locations of the datasets used for the analysis, b) Histogram of number of plots with years of the baseline survey and resurvey and c) Histogram showing number of plots with given maximum summer temperature in the adult (i.e. macroclimate) and juvenile (i.e. microclimate) layer at the time 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.

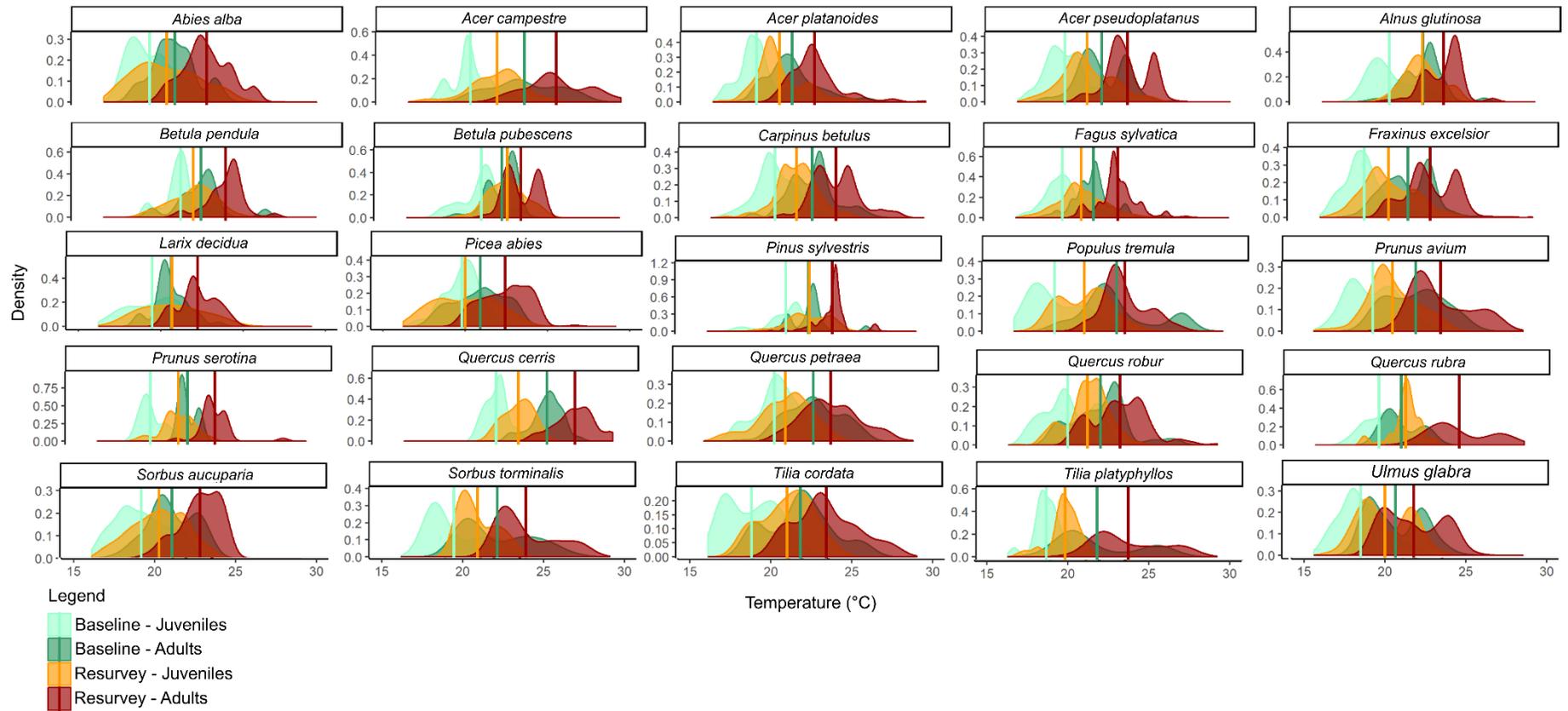


Fig. 2: Juvenile layer temperature (subcanopy microclimate temperature) and adult layer temperature (above-canopy macroclimate temperature) for the 25 most common tree species in the baseline survey and resurvey. Vertical lines represent the species means of each layer and survey.

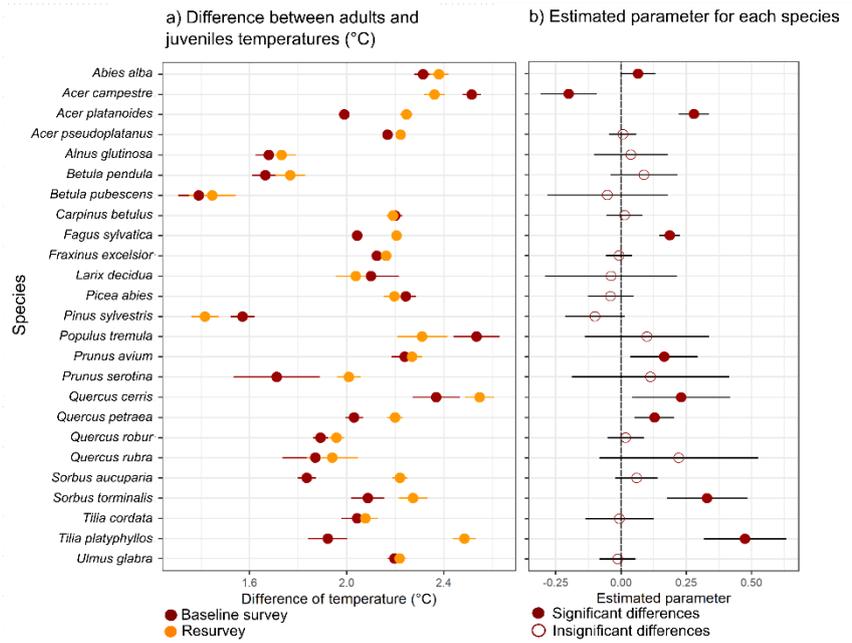


Fig. 3: a) Difference between the adult layer temperature and the juvenile layer temperature (calculated as adult layer minus juvenile layer such that positive values reflect warmer temperatures for the overstory trees) in the baseline survey (red) and the resurvey (yellow); error bars denote standard 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.

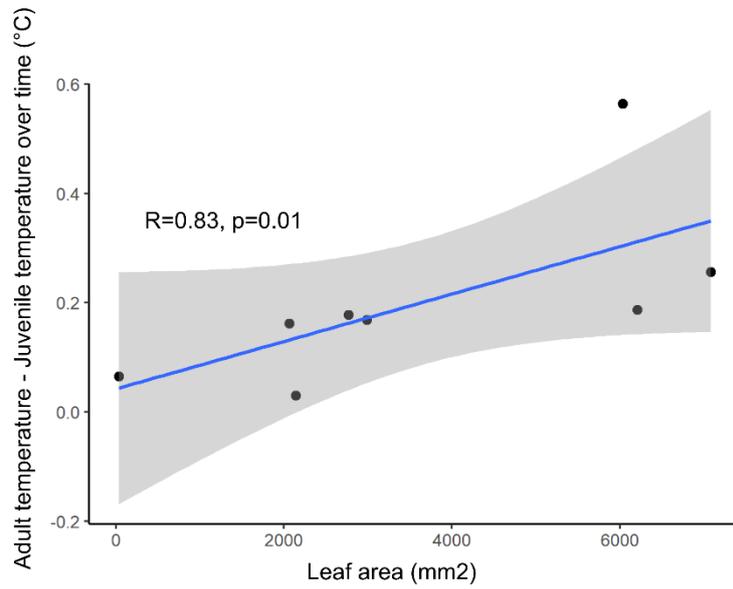


Fig. 4: Positive relationship between the temperature difference of adults minus juvenile trees over time (resurvey minus baseline survey) and leaf area (mm²). Shown here only for the eight species with a significant change in the ontogenetic thermal niche over time (n = 8).