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

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## Abstract

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

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

## 1. Introduction

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

In general, early stages of plant's life cycle (i.e. seedlings and juveniles) are considered more sensitive than adults of the same species to environmental factors such as heat, frost and drought (Bennett, Mcdowell, Allen, & Anderson-Teixeira, 2015; Lloret, Peñuelas, Prieto, Llorens, & Estiarte, 2009; Mérian & Lebourgeois, 2011). Hence, it is likely that climate change will differently impact adults and juveniles of the same species. Therefore, it is essential to further our understanding of how environmental change affects plants along their entire life cycle. The capacity to disperse, colonize and successfully persist in new suitable areas and therefore the species' capacity to change their distribution tracking novel climatic conditions is influenced by (i) the speed at which an individual can produce offspring and regenerate, (ii) morphological (e.g. leaf-height-seed) and physiological traits (e.g. maximum photosynthesis capacity, leaf nitrogen content) and (iii) species properties (e.g. shade tolerance, grazing tolerance) (Burke & Grime, 1996; Bussotti, Pollastrini, Holland, & Brüggemann, 2015; Díaz et al., 2016; Dobrowski et al., 2015; Sádlo, Chytrý, Pergl, & Pyšek, 2018). It is expected that species resistance and resilience to climatic variability is affected by the presence of certain functional traits (e.g. leaf mass per area is linked to the responses of plants to drought, high light and scarcity of nutrients; Bussotti et al., 2015; Lohbeck et al., 2015). The environment, including temperature, can strongly affect all the phases of plant species' regeneration from dormancy break until seedling establishment and survival (Carón et al., 2014, 2015; De Frenne et al., 2011; Fay & Schultz, 2009; González-Rodríguez, Villar, & Navarro-Cerrillo, 2011; Shevtosova et al., 2009; Walck, Hidayati, Dixon, Thompson, & Poschlod, 2011). Therefore, regeneration responses to climate change vary among species with contrasting functional traits.

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

To accurately study thermal ontogenetic shifts in the context of climate change, and to better understand the relative importance of ontogenetic shifts and climate change on the contrasting thermal conditions experienced by adults and juveniles, it is essential to have precise and accurate data on the actual temperatures experienced by the individuals throughout their different life stages: from tree seedlings to adult trees and over long time periods. Temperature conditions in forest systems can vary substantially near the ground surface (understory conditions where juveniles grow) compared to the conditions at the canopy to which the leaves of adult trees are exposed (De Frenne, Zellweger, Rodríguez-Sánchez, Scheffers, Hylander, Luoto, Vellend, Verheyen, & Lenoir, 2019; Zellweger et al., 2020).

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

Despite the importance of considering the differences between overstory and understory temperatures, many ecological studies focusing on forest systems still rely on gridded macroclimate data (Worldclim: Fick & Hijmans 2017; CHELSA; Karger et al. 2017; and TerraClimate; Abatzoglou et al. 2018) based on weather stations located outside forests above short grass. Such weather stations only reflect macroclimatic conditions misrepresenting the sub-canopy climatic conditions (i.e. microclimatic conditions). However, a correct representation of the temperature at the understory is key, especially for forest regeneration studies. Indeed, the mismatch between the environmental requirements of tall adults *vs.* juveniles on the forest floor is extremely important in that respect (Geiger, Aron, & Todhunter, 2003; Lenoir, Hattab, & Pierre, 2017; Uvarov, 1931; Zellweger et al., 2020). Fortunately, recent advances have made it possible to use local forest microclimatic data obtained from a network of microclimate sensors located in forest understories across Europe. Based on that information, a relationship between macroclimate, forest cover and microclimate was established (see Zellweger et al. 2019). To correctly evaluate the impacts of climate change on the adult and juvenile life stages (i.e. ontogenetic shifts in the context of climate change), it is necessary to have repeated records (resurveys) of both layers (canopy and understory) in undisturbed forest and with sufficient time between records (several decades) in order to capture the effects of climate warming on species occurrences. Moreover, if resurveys with long intervals between surveys are combined, with accurate records of temperature over multiple regions, it is possible to increase the representativeness, and thus generality, of the results (Verheyen et al., 2017).

Here we specifically address the long-term, large-scale, multitaxa dynamics of the difference between the temperatures perceived by adults and juveniles, for 25 of the most common European temperate forest tree species. To this end, we took advantage of a unique database containing 2195 pairs of resurveyed plots in 48 regions (12 countries) across Europe. Our database contains species presence and cover data (visual estimates of percentage ground cover by each species) of adults and juveniles <1.3 m) with a mean time interval between the baseline survey and the resurvey of 37 years. For both surveys, we extracted macroclimatic temperatures from global climate grids and calculated microclimate temperatures in the forest understory (representative of the juvenile layer) across the continent using, for the first time at such scale, the established relationship between macroclimatic temperature, tree canopy cover and the temperature offset inside the forest (see Zellweger *et al.* 2019). This relationship was fitted by calculating the difference of temperature outside and inside the forest by combining microclimate data obtained from a sensor network with weather station records across Europe. We determined: (i) the degree of warming as perceived by the canopy of the adult (macroclimate temperature) and juvenile (microclimate temperature) layers between the baseline and resurvey period (thermal shift over time for each life stage); (ii) the difference in the perceived temperature between the adult and juvenile layers during each survey (ontogenetic shift); (iii) whether the difference in temperature as experienced by adults and juveniles changed over time (ontogenetic shift over time) and (iv) whether any difference in ontogenetic shift over time was correlated with species properties and key morphological and physiological traits important for dispersal and establishment and for coping with environmental conditions (i.e. LHS - leaf-height-seed traits and species' shade tolerance).

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

## 2. Materials and methods

### *Database characterization and plots selection*

We used data from the forestREplot database (Verheyen et al., 2017). This database contains species presence and cover data (percentage of ground cover by the canopy of each species estimated consistently, in both surveys, in the same plots) from forest resurveys in permanent or quasi-permanent plots (no pseudoreplicates) with variable plot sizes (between 1 m$^2$ and 1000 m$^2$ but in most cases the plots were either a 10×10 m or a 9m radius plot) located in natural or semi-natural forests in temperate deciduous forests across Europe (see details of the database at www.forestreplot.ugent.be). The vast majority of the plots in this database are in ancient and mainly undisturbed or very low-managed forests (between surveys).

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

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

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

*Temperature data*

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

The microclimate temperature within the understory layer (where juveniles grow) at the baseline survey and resurvey were calculated at the plot level for plots where each species was present in either the baseline or the resurvey. To compute microclimate temperatures near the forest floor at both time periods, we used the information of canopy cover at each plot (visual estimates of percentage ground cover by each species) recorded *in situ* when each survey (baseline and resurvey) took place (reflecting all the conditions that influenced the canopy cover e.g. management, soil nutrient, rainfall variability, $CO_2$ and Nitrogen deposition) and the empirical relationship established by Zellweger et al. (2019)

between macroclimate temperature, canopy cover, distance to the cost and sub-canopy temperature. The microclimatic information used by Zellweger et al. (2019) was obtained from a network of sensors installed in ten plots representing a regional gradient of canopy cover distributed in ten regions across Europe (all included in this study). The air temperature at 1m above the ground was recorded hourly from February 2017 to February 2018, then, aggregated to minimum (Tmin), mean (Tmean) and maximum (Tmax) daily temperature. Next, the temperature offset values were calculated as the difference between the daily temperature statistics (Tmin, Tmean, Tmax) recorded inside the forest and the respective temperature statistic recorded by the closest weather station (macroclimate above-canopy temperature). Finally, the daily temperature offsets were aggregated to calculate monthly means (Zellweger et al. 2019).

The data obtained was used to build a set of models that analysed the temperature offset as function of two groups of explanatory variables i) local canopy structure and composition and ii) landscape structure and topography. Next, the best performing model ($R^2$=0.33, RMSE gamm 0.92) with local canopy cover and distance to the coast as predictors was selected after evaluation using the cross-validation approach such that a model was calibrated based on data from nine out of 10 regions and validated based on the remaining one (‘leave one out’ approach). This model developed by Zellweger et al., (2019) was used to calculate the below-canopy (juvenile layer) maximum temperature during summer of the five years precedent to the year of each survey (to iron out any extremes that happen during the year of the survey) as it was proven to correctly predict the temperature offset in summer. Additionally, this model reflects principal physical mechanisms for driving the radiation regime below the canopy, which is a key determinant of the below canopy temperature offsets. During warm and clear days, a large part of the incoming short- wave radiation is absorbed and reflected by the canopy, while increasing evapotranspirative cooling, resulting in a cooling of the understory maximum temperature (De Frenne et al., 2021; De Frenne, Zellweger, Rodríguez-Sánchez, Scheffers, Hylander, Luoto, Vellend, Verheyen, Lenoir, et al., 2019). Moreover, as the variables used to fit the model are the plot-specific distance to the coast (invariable), the canopy cover (*in situ* recorded at the moment of each survey, in 100 plots included in this study) and the macro maximum summer temperatures extracted from TERRACLIMATE or CRU (extracted for each survey), and the model relies on the physics of radiative transfers through vegetation canopies, the model despite its limitations, can be used to estimate the temperature at the juvenile layer during both surveys.

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

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

*Data analyses*

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

We analysed:

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

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

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

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

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

Finally, for all 25 species and then also for the 8 species that showed significant changes in thermal ontogenetic shifts between surveys (i.e. analysis iii), we correlated this difference (one value per species) with a shade tolerance index, and the mean and the standard deviation of key functional traits (leaf mass area, leaf area, plant height and seed mass, Table S2) (Westoby 1998, Díaz et al. 2016). Pearson correlation was used for height while Spearman correlations were used for leaf mass area, leaf area and seed mass due to the non-normality of those data. The values of the key functional traits were extracted from Díaz et al. (2016). The functional trait values provided by Díaz et al. (2016) are the geometric mean extracted from the Plant Trait Database TRY (https:// www.try-db.org) supplemented by published data not included in TRY and a small number of original unpublished data (Díaz et al., 2016). All data were standardized and subjected to error detection and quality control (see details in Díaz et al. 2016). The standard deviation values were calculated from the individual records of traits values available in the TRY database. The number of observations per trait and species range from a single one (in the case of rare, geographically restricted species) to 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).

## 3. Results

Across all species, the adult layer temperature increased by 1.56 °C ± SD 0.53 (0.38 °C/decade) between the baseline and the resurvey while the juvenile layer temperature increased by 1.34°C ± SD 0.42 (0.35 °C/decade) between surveys (Table S3 and Table S12). However, the rate of temperature change in both layers was species-specific (Table S3, Fig. 2 and Table S12). In the adult layer, *Quercus rubra* experienced the highest degree of warming (3.59 °C, i.e. 0.78 °C/decade) while *Tilia cordata* exhibited the strongest warming in the juvenile layer (2.19 °C, i.e. 0.67°C/decade) (Table S3, Fig. 2 and Table S12).

The adult layer experienced significantly higher temperatures than the juvenile layer in both the baseline survey (+2.19 °C ± SD 0.74) and the resurvey (+2.41 °C ± SD 0.73) across species (Table S3). However, the difference between the temperature experienced by the adults and juveniles was again species-specific (Table S3, Fig. 2 and Table S12). In the baseline survey, the highest difference between the temperature experienced by the adults and the juveniles was recorded in *Populus tremula* (+3.84 °C) and in the resurvey in *Tilia platyphyllos* (+3.92 °C) (Table S3, Fig. 2 and Table S12).

Temperature differences between adults and juveniles changed significantly between surveys when all the species are considered together (Table S3). We found that the temperature difference experienced by adults vs juveniles increased over time for 17 (68%) of the 25 analysed European tree species. However, this difference was significant for eight out of 25 species only (Table S3 and Fig. 3). These eight species exhibited an average increase of 0.18°C in the temperature difference between adult and juvenile layers when comparing the baseline survey to the resurvey (Fig. 3). In other words, the thermal ontogenetic shift between putative “mothers” and “daughters” significantly increased over time for eight tree species. The only species in which this temperature difference significantly decreased, by 0.14 °C, was *Acer campestre* (Fig. 3).

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

## 4. Discussion

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

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

The warming recorded here in both layers is in line, but slightly higher than, the global mean land surface air temperature increase of 1.29 °C measured between 1940 and 2016 (the time period considered in this study) (IPCC, 2019). The higher degree of warming recorded in this work is likely due to the fact that we analysed maximum summer temperatures. The detected temperature increase was species-specific and, considering the close relationship between latitude and observed and projected temperatures (De Frenne, Graae, et al., 2013; Monleon & Lintz, 2015), it is likely that recorded species-specific warming is also linked to the spatial distribution of a species and its dispersal and establishment capacity (Table S8) despite the fact that our database did not cover the complete distribution of the species. This species-specific response, might also be linked to the species-specific crown architecture (e.g. *Betula* species transmit more light to the forest floor than for example *Abies alba*). However, the influence of crown architecture on the change in the temperature over time is beyond the scope of this work but should be considered in future studies. The observed species-specific pattern of temperature increase between surveys should be considered with caution because the estimates are based on temperature datasets that have a relatively coarse resolution (~4x4 km for TERRACLIMATE). In our study focused on thermal shifts, we only consider one of the multiple factors that influence the presence of an individual, i.e. temperature, while other factors and processes could also influence the establishment of new individuals including masting, herbivory, the past legacy of human interventions and forest management (Lombaerde et al., 2020).

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

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

Our trait-based analyses shed light on the causes of the divergent responses in the difference of the temperature experienced by adults *vs.* juveniles between surveys. Large-leafed species exhibited an increase of the difference between the temperature experienced by adults *vs.* juveniles over time, likely because large leaves provide competitive advantages in dealing with the darker conditions of the understory (Bequet et al., 2011; Li, Liu, & Berninger, 2004). Seedlings with larger leaves can overtop neighbouring vegetation and get better access to light at the forest floor (Leishman, Wright, Moles, & Westoby, 2000; Poorter & Rose, 2005). Additionally, larger leaves have usually a thicker boundary layer that slows sensible heat exchange with the surrounding air, developing larger leaf-to-air temperature differences than smaller leaves. The wider leaf-to-air temperature differences of larger leaves may allow them to more quickly heat up during cool mornings to favourable temperatures for photosynthesis, what might allow for higher photosynthetic returns (Wright et al., 2017). The intraspecific variability of leaf area, included in our analysis as the traits' standard deviation, apparently, does not affect the difference between the temperature experienced by adults *vs*. juveniles over time (no significant correlation). Leaf traits as well as other species traits and properties (e.g., shade tolerance) can vary not only intraspecifically but also along the species life cycle (i.e., ontogenetic shift in traits values). This variation of traits along the species life cycle is somehow present in our standard deviation analysis as the traits' database used here combines adult and juveniles' traits values as well as data collected in controlled experiments and in nature. However, a detail analysis of how ontogenetic changes in functional traits affect the difference between the temperature experienced by juveniles *vs.* adults is beyond the scope of this work. Finally, we did not find a significant relationship between the shade tolerance of the species and the changes in the adults *vs.* juveniles thermal differences among surveys. We had, however, a relatively small species sample size (n= 25 or n= 8) (Wasserstein & Lazar, 2016) and further analysis should be done with larger sample size to confirm these results.

## Conclusions

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

By disentangling the impacts of climate change on different phases of plants' life cycle, our work sheds light onto the ontogenetic changes across large geographical and temporal scales in the context of climate change. This information is key to advance our understanding of the ecology and dynamics of temperate forests in the face of climate warming. Our findings could also assist forest managers in predicting future species composition based on climatic projections, and in promoting tree regeneration by creating suitable tree species-specific microclimatic conditions, helping to mitigate, at least partially, the change at the understory level driven by changes in macroclimate.

## Acknowledgements

Mercedes Caron was supported by FONCyT PICT-2017-2245 and by CESAM Visiting Staff Platform (2019) - Ghent University

Florian Zellweger received funding from the Swiss National Science Foundation (project 172198 and 193645)

Kris Verheyen and Michael Perring were supported by the European Research Council (ERC) UnderSCORE grant #861957

Sandra Díaz was supported by FONCyT PICT-2017-1084

Radim Hédl, Martin Macek, Petr Petřík, and Martin Kopecký were supported by the long-term research development project No. RVO 67985939 of the Czech Academy of Sciences.

František Máliš was funded by Slovak Research and Development Agency grant No. APVV-19-0319.

Pieter De Frenne received funding from the European Research Council (ERC) under the European Union’s Horizon 2020 research and innovation programme (ERC Starting Grant FORMICA 757833).

**Conflict of Interest:** The authors declare that they don’t have any conflict of interest.

**Author Contributions statement**: MMC and PDF designed the study. MMC performed the analysis. FZ provided the climatic database. KV, LB, RH, MB-R, IB, JB, GD, TD, TD, TH, BJ, MK, JL, MM, MM, MF, NTA, PP, KR, RP, WS, KS, BT, MW and PDF collected the vegetation information available in the ForestREplot database. FZ, LB, SD, JL, MPP and PDF contributed to the initial discussion of the paper design. All the authors provided comments.

**Data Availability statement**: All vegetation data used in this paper is available in the forestREplot database (www.forestreplot.ugent.be). Macro and micro temperature data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.rfj6q57bh (Caron, M. M., et al., 2021). The rest of the 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

| 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) | ∆ 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) | ∆ Temperature (macroclimate temperature – microclimate temperature) | Survey | Region |

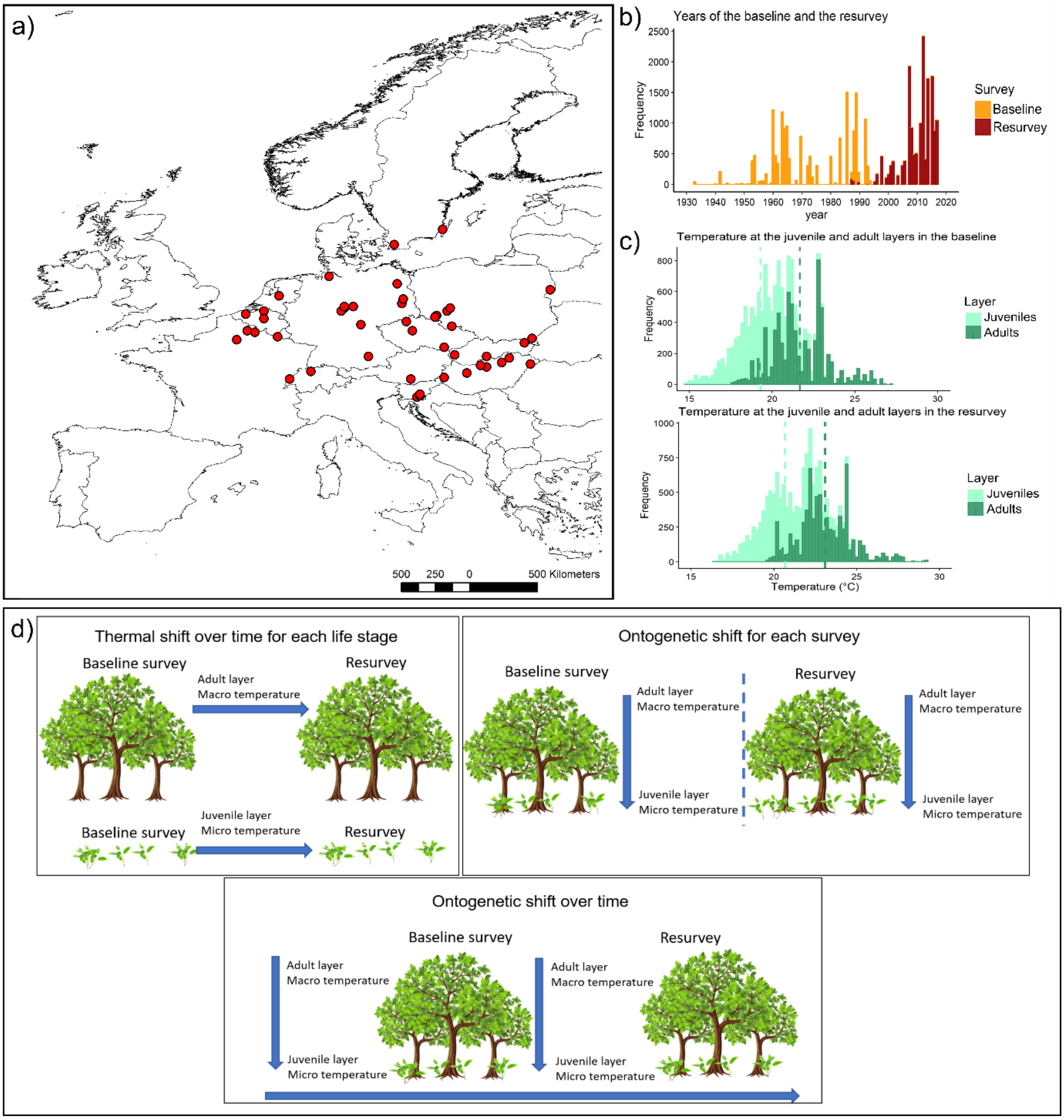

Fig. 1: a) Locations of the datasets used for the analysis, b) Histogram of number of plots with years of the baseline survey and resurvey and c) Histogram showing number of plots with given maximum summer temperature in the adult (i.e. macroclimate) and juvenile (i.e. microclimate) layer at the time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

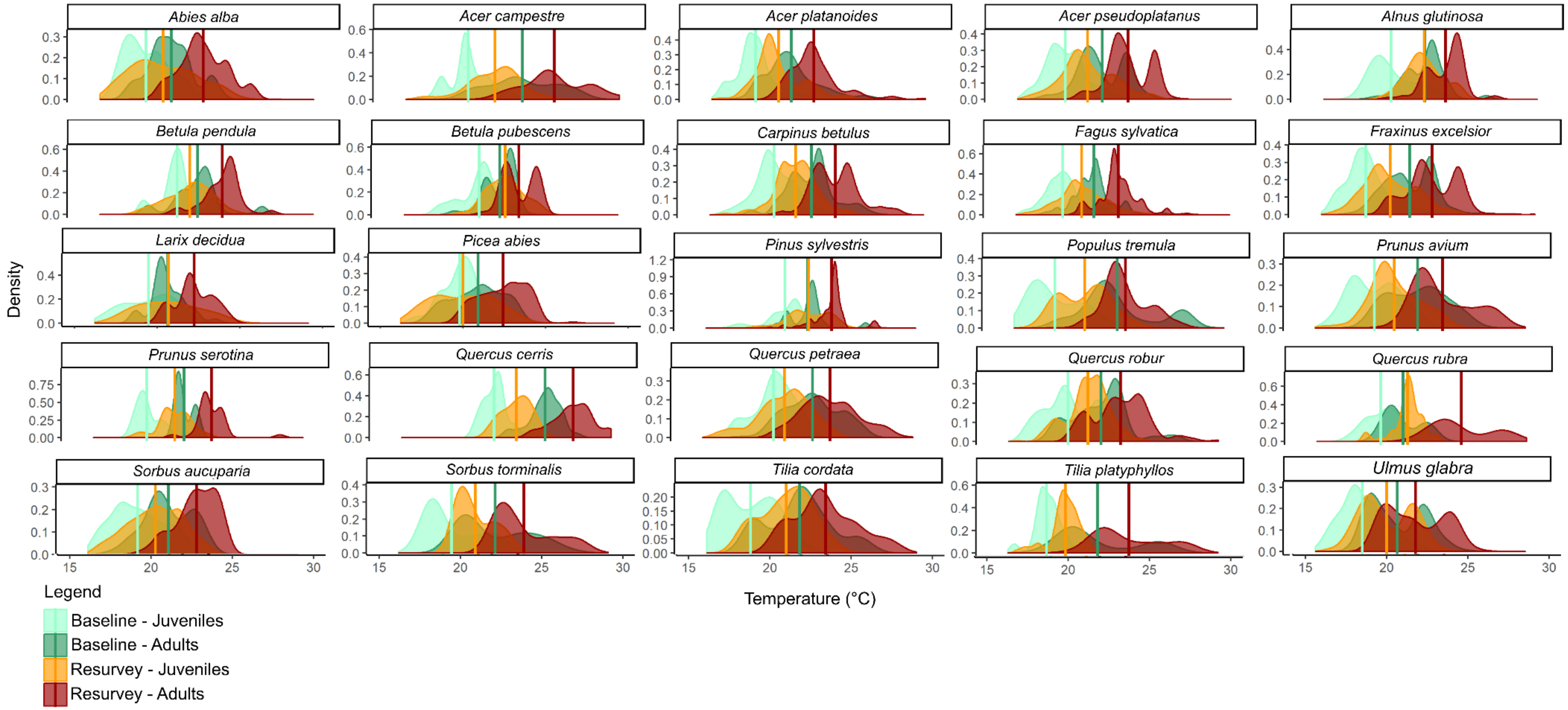

Fig. 2: Juvenile layer temperature (subcanopy microclimate temperature) and adult layer temperature (above-canopy macroclimate temperature) for the 25 most common tree species in the baseline survey and resurvey. Vertical lines represent the species means of each layer and survey.

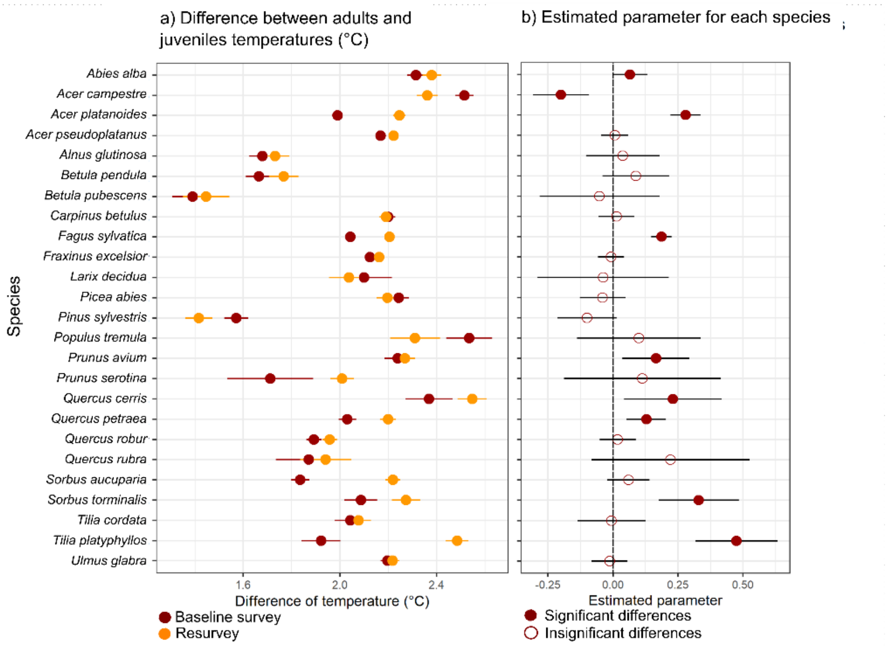

Fig. 3: a) Difference between the adult layer temperature and the juvenile layer temperature (calculated as adult layer minus juvenile layer such that positive values reflect warmer temperatures for the overstory trees) in the baseline survey (red) and the resurvey (yellow); error bars denote standard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

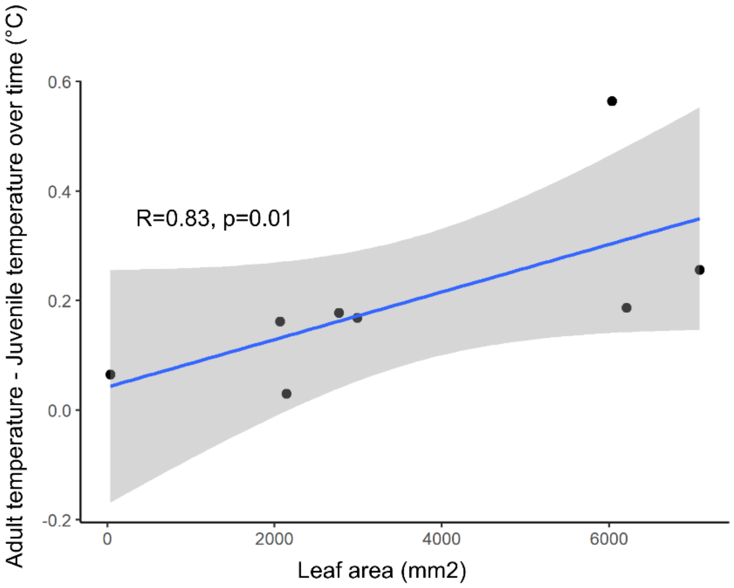

Fig. 4: Positive relationship between the temperature difference of adults minus juvenile trees over time (resurvey minus baseline survey) and leaf area (mm²). Shown here only for the eight species with a significant change in the ontogenetic thermal niche over time (n = 8).