ECOGRAPHY

Research

Divergent occurrences of juvenile and adult trees are explained by both environmental change and ontogenetic effects

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Ecography
2022: e06042
doi: 10.1111/ecog.06042
Subject Editor: Daniel Stouffer
Editor-in-Chief:
Jens-Christian C Svenning
Accepted 14 December 2021

Recent climate warming has fueled interest into climate-driven range shifts of tree species. A common approach to detect range shifts is to compare the divergent occurrences between juvenile and adult trees along environmental gradients using static data. Divergent occurrences between life stages can, however, also be caused by ontogenetic effects. These include shifts of the viable environmental conditions throughout development ('ontogenetic niche shift') as well as demographic dependencies that constrain the possible occurrence of subsequent life stages. Whether ontogenetic effects are an important driver of divergent occurrences between juvenile and adult trees along large-scale climatic gradients is largely unknown. It is, however, critical in evaluating whether impacts of environmental change can be inferred from static data on life stage occurrences. Here, we first show theoretically, using a two-life stage simulation model, how both temporal range shift and ontogenetic effects can lead to similar divergent occurrences between adults and juveniles (juvenile divergence). We further demonstrate that juvenile divergence can unambiguously be attributed to ontogenetic effects, when juveniles diverge from adults in opposite direction to their temporal shift along the environmental gradient. Second, to empirically test whether ontogenetic effects are an important driver of divergent occurrences across Europe, we use repeated national forest inventories from Sweden, Germany and Spain to assess juvenile divergence and temporal shift for 40 tree species along large-scale climatic gradients. About half of the species-country combinations had significant juvenile divergences along heat sum and water availability gradients. Only a quarter of the tree species had significant detectable temporal shifts within the observation period. Furthermore, significant juvenile divergences were frequently associated with opposite temporal shifts, indicating that ontogenetic effects are a relevant cause of divergent occurrences between life stages. Our study furthers the understanding of ontogenetic effects and challenges the practice of inferring climate change impacts from static data.

Keywords: climate change, Europe, national forest inventories, ontogenetic niche shift, range shift, tree demography

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Introduction

Recently, global climate change has put rapid external pressure on ecosystems (Walther et al. 2002, Feehan et al. 2009, Lindner et al. 2010). In addition, European ecosystems have experienced regional changes in land-use practices (Smith et al. 1999, Hodgson et al. 2005, Turner et al. 2007). In response to pressure from environmental change, species can shift their ranges. Plant species have been shown to shift ranges over time in response to land-use change (Cudlín et al. 2017, Perring et al. 2018), and there has been elevated interest in climate change-driven range shifts – in particular in tree species (Lenoir et al. 2008, Chen et al. 2011, Gibson-Reinemer and Rahel 2015). In order to show climate-driven range shifts in trees, many recent studies have compared the occurrence of different size classes within a species along environmental gradients (Lenoir et al. 2009, Monleon and Lintz 2015, Smithers et al. 2018). In these studies, tree size is assumed to reflect tree age, so that larger trees are used as a proxy for conditions further in the past, compensating the lack of historical tree occurrence data. Many studies have found that the distribution of smaller trees (here called 'juveniles') was shifted to higher elevations (Lenoir et al. 2009, Wason and Dovciak 2017), higher latitudes (Woodall et al. 2009, Monleon and Lintz 2015) or lower temperatures compared to the distribution of larger 'adult' trees (Bell et al. 2014, Mathys et al. 2018). Given that trees are sessile organisms with long life cycles, it is assumed that their ranges respond slowly to environmental pressure. And since the size class of juvenile trees has faster turnover than adults, under a changing environment the range of juveniles is thought to track the niche conditions more closely (Monleon and Lintz 2015). Consequently, divergent occurrences of two size classes or life stages are commonly interpreted as an indicator of a temporal range shift of the entire population because juveniles have established in a new range (Peñuelas et al. 2007, Smithers et al. 2018).

Assuming that divergent occurrences of juveniles and adults result from temporal change alone is however problematic. During ontogeny, i.e. the progress through stages of development (Gatsuk et al. 1980), here reflected by size classes, the occurrence of trees can also be influenced by different types of ontogenetic effects (Fig. 1). In particular, one of these ontogenetic effects, different responses of life stages to the environment, sometimes referred to as 'ontogenetic niche shift' (Werner 1984, Parish and Bazzaz 1985), can cause divergent occurrences of juveniles and adults as well (Eriksson 2002, Young et al. 2005, Miriti 2006, Bertrand et al. 2011, Ni and Vellend 2021). Ontogenetic niche shift is a likely mechanism acting on tree species (Stohlgren et al. 1998, Cavender-Bares and Bazzaz 2000, Bertrand et al. 2011), because a tree species' phenotype undergoes marked change during its life history from seedling to adult stage (Thomas and Winner 2002, Augspurger and Bartlett 2003, Lusk 2004, Niinemets 2006, Niklas and Cobb 2010, Vitasse 2013, Leuschner and Meier 2018). This is why Máliš et al. (2016) have recently highlighted that divergent occurrences between juvenile and adult trees can not simply be interpreted as temporal range shifts. Instead, they have demonstrated that observed distributional differences between seedlings and adults along an elevation gradient in the Western Carpathians are better explained by their life stage than temporal range shift (Sittaro et al. 2017). Nevertheless, subsequent studies have interpreted ontogeny as a proxy for time when analyzing range shifts in trees on larger scales (Wason and Dovciak 2017, Mathys et al. 2018, Smithers et al. 2018), while the relative importance of ontogenetic effects for divergent occurrences along large-scale climatic gradients remains still unknown.

Here, we evaluate at a continental scale whether impacts of climate and land-use change on tree species ranges can be inferred from static data, by dissecting which processes are important drivers of divergent occurrences of tree life stages across Europe: temporal range shifts or ontogenetic effects. Expanding on the argument of Máliš et al. (2016) who concentrated on the ontogenetic effects niche shift, niche expansion and contraction, we analyze an additional ontogenetic effect: demographic dependencies between life stages, which can also lead to divergent occurrences of juvenile and adult trees (Fig. 1).

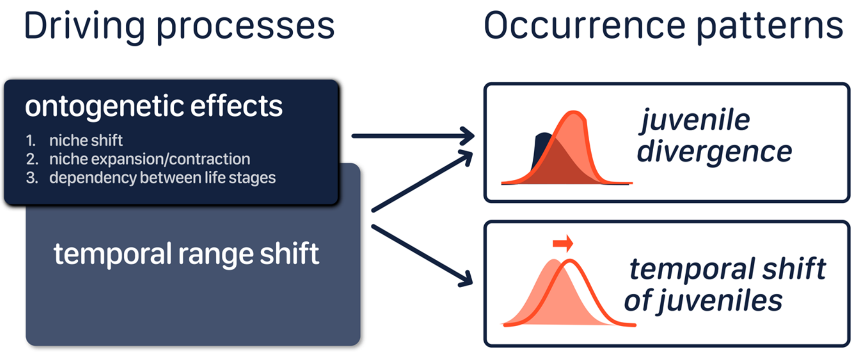


Figure 1. Ontogenetic effects and temporal range shift can have different observable effects on occurrence patterns of sessile organisms like trees: juvenile divergence, i.e. the observed difference of juvenile occurrence compared to adult occurrence along an environmental gradient, can be driven by both ontogenetic effects and advancing juveniles under a temporal range shift of the entire population. An observed temporal shift of juveniles along the gradient, however, unambiguously indicates a temporal range shift.

To understand how ontogenetic effects can cause divergent occurrences of life stages in environmental space, it is necessary to, first, clarify the distinction between Hutchinson niche and occurrence of a species and, second, break down the Hutchinsonian niche concept to life stages:

The Hutchinson niche is a hypervolume in environmental space representing the environmental conditions where the entire population of a species is potentially able 'to survive and reproduce' (Hutchinson 1957). But the actually observable occurrence space of a species is not equivalent to the niche (Soberón and Peterson 2005): limited dispersal will reduce occurrence compared to the niche, not all niche conditions might actually be realized in geographical space, and finally, in a changing environment, occurrence can be out of equilibrium and trailing the niche conditions.

Second, the niche concept can be applied to individual life stages within a population. Maguire (1973) introduced the analytical view of breaking down the niche into multiple hypervolumes representing the responses of ontogenetic stages to the environment, here called 'ontogenetic niches'. Ontogenetic niches can be defined analogously to the fundamental niche (Hutchinson 1957) of a whole population: as the fundamental niche comprises the environmental conditions at which an ideal population would persist independent of dispersal and species interactions (Hutchinson 1957, Soberón and Peterson 2005), we define ontogenetic niches as the environmental conditions where ideal populations of life stages would persist if they were independent of all other life stages. Thus, independence of other life stages is a key distinguishing property of ontogenetic niches compared to life stage occurrences, which are necessarily interdependent through transitions between them.

Independent shift, expansion or contraction of niches between life stages through different demographic responses to the environment (Grubb 1977, Parish and Bazzaz 1985, Miriti 2006, Bertrand et al. 2011, Vecchio et al. 2020) can lead to observed divergent occurrences between juveniles and adults (Bertrand et al. 2011, Pironon et al. 2017). The occurrence of a life stage, however, is constrained by the occurrence of earlier life stages (Young et al. 2005) and the environmentally-dependent probability of proceeding to later life stages. Demographic dependencies between life stages can therefore also lead to divergent occurrences of life stages.

Here, we aim to disentangle the contribution of temporal range shift and ontogenetic effects to the patterns of divergent occurrences between juvenile and adult trees (juvenile divergence; Fig. 1), with regression models applied to both theoretical data from simulations and empirical data from repeated forest inventories. First, we explore with a theoretical two-life stage simulation model how life stage occurrences along an environmental gradient respond to temporally shifting environmental conditions and ontogenetic effects. Our simulations illustrate how both temporal range shift and ontogenetic effects can cause divergent occurrences of two life stages, and how temporal range shift and ontogenetic niche shift can act simultaneously. Second, we empirically evaluate with a regression model whether temporal range shifts or ontogenetic effects are responsible for juvenile divergences observed along two large-scale climatic gradients, i.e. long-term averages of heat sum and water availability, across European forests. To this end, we estimated the effect of time and life stage on species' occurrence centers along each climatic gradient using two repeated surveys of national forest inventories (NFIs) from Sweden, Germany and Spain. Since the vast majority of forests in these countries have been managed (McGrath et al. 2015), we expect that the estimated occurrences of life stages will be impacted by management and thus that temporal shifts could emerge from both climate change and changes in management regime (e.g. forest encroachment at higher altitudes after abandonment; Améztegui et al. 2010). To attribute the pattern of juvenile divergence to either temporal range shift or ontogenetic effects, we propose a framework of hierarchical tests, that takes advantage of the observed temporal shifts of juveniles from repeated surveys and compares differences in occurrence patterns instead of trying to infer different niches. Applying this framework to occurrence patterns of tree species along two large-scale climatic gradients, we assess the relevance of ontogenetic effects compared to environmental change-driven temporal range shifts for divergent occurrences between life stages in Europe. Our results challenge the common practice of inferring climate change impacts on tree species from divergent occurrence of tree life stages using static data.

Methods

We used a two-life stage population model to show with theoretical simulations how temporal range shifts and ontogenetic effects can drive divergent occurrences between life stages and how these can be deteceted with beta regression models. We used the same beta regression models with data from three NFIs to empirically quantify temporal range shifts and ontogenetic effects in European forests. All simulations and data analyses have been performed with R ver. 4.0.2 (<www.r-project.org>).

Two-life stage simulation model

For a simple model of a population with two interdependent life stages, we used ordinary differential equations expressing the transitions between two states, abundances of juveniles and adults. Juvenile J and adult A abundances were coupled via growth, i.e. transition rate g, and regeneration rate r. The life stages' carrying capacities k (juveniles), $\hat{k}$ (adults), expressing density dependence within life stages, and their respective density-independent mortality rates m, $\hat{m}$ were modeled as a function of a theoretical environmental gradient $\vec{e}$. The environmental gradient was discretized into n equal-width cells, so that the abundance change rates in the ith cell were described by

$$\frac{\mathrm{d}J_i}{\mathrm{d}t} = \left(rD_i - m(t,e_i) \times J_i - gJ_i\right)\left(1 - \frac{J_i}{k(t,e_i)}\right) \qquad (1)$$

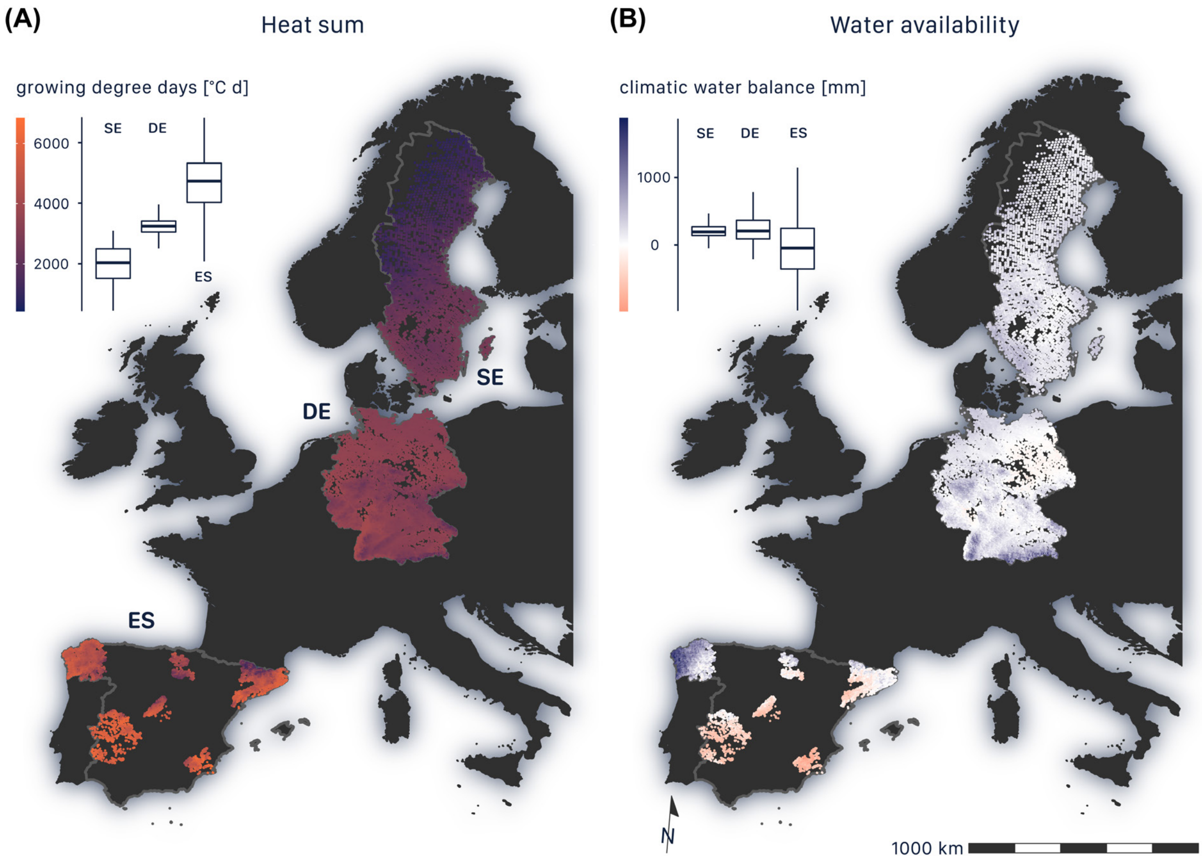


Figure 2. Tree plot locations of the three national forest inventories (NFIs) – Sweden (SE), Germany (DE), Spain (ES) – coloured by the climatic variables (A) heat sum (growing degree days) and (B) water availability (climatic water balance). Box plots show the distribution of climatic variables by country. The map projection is a Lambert azimuthal equal-area projection.

$$\frac{\mathrm{d}A_i}{\mathrm{d}t} = \left(gJ_i - \hat{m}(t,e_i)\right) \times \left(1 - \frac{A_i}{\hat{k}(t,e_i)}\right) \tag{2}$$

D represents the diaspores dispersed from A that are recruited into J. Dispersal was modelled as a centered rolling average of A with window width d, so that the ith cell of D was the average of the d cells around the ith cell of A.

To simulate ontogenetic niches, we made the parsimonious assumption that two demographic parameters related to survival are dependent on the environmental gradient: the carrying capacity k, which expresses density-dependent survival, and the density-independent mortality m, so that both density-dependent and density-independent niche effects were accounted for. The responses to the environment were bell-shaped for carrying capacity and reversely bell-shaped for mortality, scaled by the same environmental response function f. This way, carrying capacity k reaches its maximum and density-independent mortality m its minimum M under the same optimal environmental conditions:

$$k, \hat{k}(t,e) = K \times f(t,e) \tag{3}$$

$$m, \hat{m}(t,e) = M \times \left(1 - f(t,e)\right) \tag{4}$$

$$f(t,e) = \exp\left(-\frac{1}{2}\left(\frac{e-\mu(t)}{\sigma}\right)^2\right) \tag{5}$$

$$\mu(t) = a_\mu + b_\mu t \tag{6}$$

Different positions of the demographic niches per life stages were thus achieved by life stage-specific a_μ. As indicated by the function argument t, the demographic responses k and m could not only have different position parameters μ per life stage but could also vary with time by altering μ with the slope . Temporally shifting the environmental driver of the demographic response relative to the original time was thus achieved by linearly shifting the response function f with time.

To simulate initial life stage abundances prior to any temporal environmental change, populations of both life stages were let grown from a very low and environmentally-constant abundance state $J = A = 0.5$ at time $t = 0$ to a stable state at $t = 10\ 000$. We simulated three scenarios of shifts by varying the life stage-specific niche position μ and the temporal slope b to yield visibly diverging occurrences (for parameterization see the Supporting information): (A) temporal shift of the environment was simulated by linearly shifting the response function over time with a slope $b_\mu > 0$ (Fig. 3A). (B) Ontogenetic niche shift was simulated by assigning juveniles and adults a different optimum value a_μ for the response function f (Fig. 3B). (C) The joint effect of temporally shifting environment and ontogenetic niche shift was simulated by first running the model to a stable state with ontogenetic niche shift as in case B, and then altering the stage response functions over time with the same temporal shift of the environment acting on both life stage populations, while the two different ontogenetic niches remained offset (Fig. 3C). In all three shift scenarios, the maximal carrying capacity was kept at $K = 10\ 000$ for juveniles and $\hat{K} = 7000$ for adults to reflect that the carrying capacity decreases with tree size (Fig. 3A–C). In addition, to explore the effect of demographic dependency on occurrence widths of both life stages, even with equal environmentally-dependent mortality, we simulated one further scenario without any temporal or ontogenetic shifts or changes of niche width (Fig. 3D) using the same response function f, carrying capacity K and mortality M for juveniles and adults.

To detect temporal shifts and juvenile divergence in the simulated data we used the same regression method used in the empirical analyses (estimates of juvenile divergences and temporal shifts from beta regression models section). We generated presence data by randomly resampling values of the theoretical environmental gradient with a sampling probability proportional to the abundance. The resulting distribution of environmental values is equivalent to an 'occurrence distribution of environmental values' at presences, as used with the empirical analyses (estimates of juvenile divergences and temporal shifts from beta regression models section) and shown as probability density curves in Fig. 3A–C.

To visualize ontogenetic niches (Fig. 3A–D, dashed lines), defined as the environmental space where ideal populations of juveniles or adults would persist if they were independent of each other, we simulated two independent models for each life stage for each scenario. Each life-stage was simulated from the same model with the same environmental response as the size-structured populations, but to remove the interdependence between life stages, regeneration r was simulated from J itself instead of D, and transition g was simulated from A instead of J.

Ordinary differential equations were integrated with lsoda as provided by the package 'deSolve' ver. 1.28 (Soetaert et al. 2010). For model code see the Supporting information.

Analyses of European national forest inventory data

Tree species data

To infer occurrence patterns of juvenile and adult trees in Europe, we used two repeated national forest inventory (NFI) surveys from three countries (Fig. 2): Sweden, Germany and Spain (survey design detailed in Fridman et al. 2014, Riedel et al. 2017, Ruiz-Benito et al. 2017). The geographical extent of the countries is spanning a broad climatic gradient of arid, warm temperate and boreal climates (Kottek et al. 2006). The survey repetitions were selected from two (Sweden) or three (Germany and Spain) repetitions to cover the maximum time period per species. This resulted in different periods between two surveys per sample plot and country (Supporting information): 10 years in Sweden (periodically-regular and geographically-random rolling surveys between 2003 and 2017), 10 or 25 years in Germany (two out of three full surveys in 1987, 2002 and 2017, depending on species), and varying period between 14 and 34 years in Spain (survey dates between 1980 and 2017). To ensure that a constant environmental sampling space for species presences was maintained across survey repetitions, we included only those plots that had been surveyed at both times.

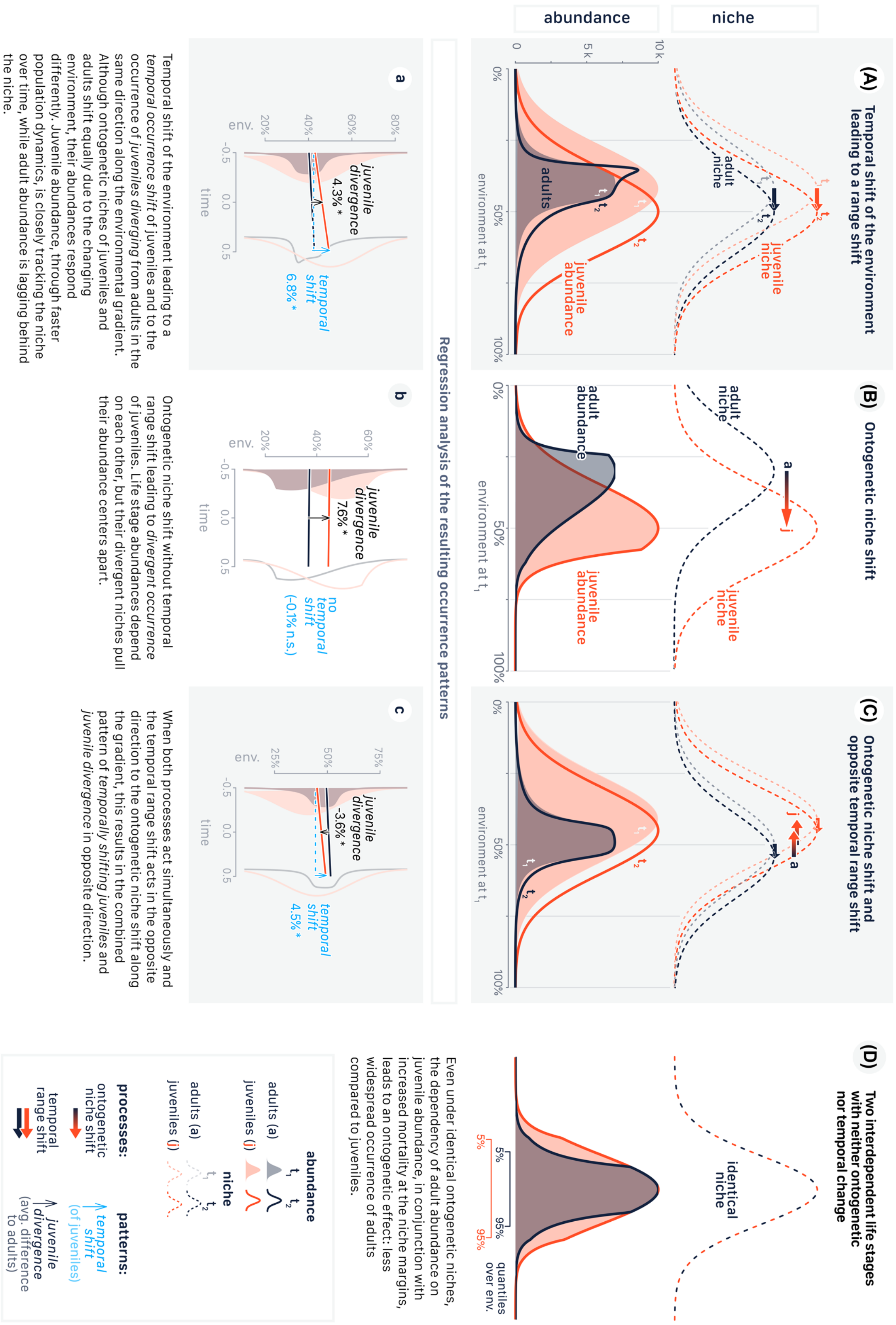
We used presence data for two life stages of 40 tree species. Trees were classified as juveniles when their height was below 130 cm in Sweden and Germany, and when their diameter at breast height (DBH) was below 2.5 cm in Spain. The lower sampling bounds for small trees were 10 cm height (Sweden), 20 cm height (Germany), while there was no lower bound in Spain. Different definitions of juveniles per country were necessary because small trees were counted in different size classes in the three NFIs (for sampling thresholds see the Supporting information). Trees were classified as adults in all three NFIs when their height was above 130 cm and their DBH exceeded 15 cm, resulting in a size gap between juveniles and adults.

Since taxonomic concepts, the set of species, and the sampled life stages within species changed over the repeated inventory surveys, tree observations were subset to maintain a constant environmental sampling space across life stages and surveys based on the following criteria within countries: 1) survey repetitions were included for a species, when both life stages had been sampled, 2) two surveys were chosen to cover the longest possible time period and 3) species had to be present on at least 20 plots per life stage and survey.

Climatic variables

To assess occurrence of both tree life stages along large-scale climatic gradients, we used long-term averages of heat sum and water availability. These variables are widely considered key climatic determinants of plant and vegetation distribution at larger scales (climatic water availability: Woodward and Williams 1987, Guisan et al. 2007; heat sum: Woodward 1988, Sykes et al. 1996). Both variables were derived from long-term averages over the period 1979–2013 from the CHELSA high resolution climatologies (Karger et al. 2017), which comprise 12 monthly averages over the entire 34 years at a spatial resolution of 30 arcsec (1 km).

Heat sum was measured as growing degree days (GDD) within the frost-free period. To obtain GDD from the



Temporal shift of the environment leading to a *temporal occurrence shift* of juveniles and to the occurrence of *juveniles diverging* from adults in the same direction along the environmental gradient. Although ontogenetic niches of juveniles and adults shift equally due to the changing environment, their abundances respond differently. Juvenile abundance, through faster population dynamics, is closely tracking the niche over time, while adult abundance is lagging behind the niche.

Ontogenetic niche shift without temporal range shift leading to *divergent occurrence* of juveniles. Life stage abundances depend on each other, but their divergent niches pull their abundance centers apart.

When both processes act simultaneously and the temporal range shift acts in the opposite direction to the ontogenetic niche shift along the gradient, this results in the combined pattern of *temporally shifting juveniles* and *juvenile divergence* in opposite direction.

Even under identical ontogenetic niches, the dependency of adult abundance on juvenile abundance, in conjunction with increased mortality at the niche margins, leads to an ontogenetic effect: less widespread occurrence of adults compared to juveniles.

Figure 3. Simulated abundances of trees along an environmental gradient under (A) temporal range shift, (B) ontogenetic niche shift, (C) opposite temporal range shift and ontogenetic niche shift and (D) under no shift at all. The three scenarios of shifts (A–C) lead to specific divergence patterns in beta regression of the occurrence distribution of environmental variables, i.e. the environmental values sampled proportional to abundance, here shown as probability densities (a–c), while scenario D illustrates the ontogenetic effect of the demographic dependency between life stages.

monthly climatologies, daily values for mean and minimum temperature were derived from the corresponding monthly values by linear interpolation. For interpolation, the differences between the values of two consecutive months were divided by the number of days between the 15th of the two months to obtain an average daily change rate. Daily temperatures between the two boundary dates were then calculated by cumulatively adding the daily changes to the climatology of the first of the two boundary dates. Daily mean temperature values were summed up from the first day following latest spring frost (as determined using daily minimum temperatures) until the day before the earliest autumn frost to obtain GDD [°C d].

Water availability was measured as annual climatic water balance, i.e. the difference between precipitation and potential evapotranspiration (Thornthwaite 1948). First, monthly climatic water balance was obtained from the climatologies by calculating potential evapotranspiration according to Hargreaves (Hargreaves 1994) as implemented in the package SPEI (Beguería and Vicente-Serrano 2017) using minimum and maximum temperatures, precipitation and latitude. The monthly climatic water balance (mm) was then summed up over all months to obtain annual water availability.

Environmental variable values at the locations of sample plots were extracted from the raster cell covering the respective point using the extract function from package 'raster' (Hijmans 2020). This resulted in sampled climatic gradients ranging over heat sums from 453 to 6819°C d, and water availability from −966 to 1863 mm (Fig. 2).

Using static gradients of long-term climatic variables to compare species distributions through time will lead to species shifting their range along the gradients under the assumptions of temporal climate change and tracking of climatic niches. Growing degree days significantly increased in Europe between 1950 and 2010, in particular in the Mediterranean region (Spinoni et al. 2015). Increasing temperatures in southern Europe have increased drought frequency through higher evapotranspiration, while drought frequency has decreased in northern Europe through increased precipitation between 1958 and 2014 (Stagge et al. 2017). Since both, heat sum and water availability, have changed in Europe throughout the NFI survey periods, species are expected to shift along the static gradients, e.g. towards colder conditions along the heat sum gradient.

Estimates of juvenile divergences and temporal shifts from beta regression models

To infer the effects of time and life stage on centers of tree occurrence along climatic gradients, we fitted beta regression models (Ferrari and Cribari-Neto 2004) with the package 'glmmTMB' ver. 1.0.2.1 (Brooks et al. 2017).

Most of the studies that compare the occurrences of different life stages compare the means or quantiles of the environmental variables at the occurrences of the life stages (Lenoir et al. 2009, Bell et al. 2014, Monleon and Lintz 2015, Máliš et al. 2016, Sittaro et al. 2017, Wason and Dovciak 2017) Here, we use an analogous approach where the long-term climatic variables at plot locations where a species was present, i.e. the occurrence distribution of climatic variables, were taken as response variables of regression models. Pivoting the climatic variables from predictors to the responses and comparing the distribution centers, has several advantages compared to fitting a more complicated species distribution model with abundance or occurrence as the response: 1) as the sampling intensities (area) of juvenile trees and adults are different (in addition to changing intensities across countries and surveys; Supporting information), reducing the data to presences and then taking the occurrence distribution of climatic variables will yield the same distribution regardless of the sampling intensity, which is independent of the environmental gradient. But Ni and Vellend (2021) have shown by resampling that extreme quantiles (e.g. the 95th percentile of heat sum) will underestimate the occurrence width of juveniles, when their sampling intensity in NFIs is lower than that of adults. We avoid the bias that is introduced by extreme quantiles by using the more robust centers of distributions along a climatic gradient as responses of the beta regression models. Although occurrence centers are not as sensitive to environmental changes as range margins, the occurrence centers will still reflect changes over the full distribution, including the margins. 2) Comparing the effects that a predictor has on the position of these distributions is straight-forward in regression models for which hypothesis tests are readily available. However, using a species distribution model with occurrence or abundance as a response for the same objecive, would require first to harmonize the data by modelling (partly unknown) different sampling intensities, then to reduce the possible resulting response curves to a central measure, and third develop hypothesis tests to compare the effect of time or life stage on this central measure.

Occurrence distributions of climatic variables were scaled across surveyed plots including all countries and species to have the range $[\varepsilon, 1 - \varepsilon]$ (with computer precision $\varepsilon = 2.220446 \times 10^{-16}$), so that the environment along the entire sampled European gradient was expressed as a variable between zero and one. We used a beta-distribution, which has two properties that account for different shapes that the occurrence distributions of climatic variables can take over a climatic gradient with fixed limits: 1) the distribution can be symmetrical or skewed, and 2) the distribution can have high or even maximal density towards one of the limits of the gradient, which reflects that the sampled range can be a subsample of the entire range of a species. Hence, the expected value y (position along the gradient expressed by parameter μ) and the shape (width and skewness expressed by precision parameter ϕ, which was unconstrained to provide any skewed shape) of the occurrence distribution of climatic variables were made dependent on life stage (juvenile or adult), time (year of the survey) and their interaction: y ~ time × life stage, with a dispersion model for the shape ~ life stage × time (R-style notation, Wilkinson and Rogers 1973). This can be written as a beta model with mean μ and precision parameter ϕ:

$$y \sim B(\mu = p + X\beta, \phi = q + X\gamma) \quad (7)$$

where p, q are the respective intercepts, β, γ are vectors of coefficients and the design matrix X consists of a column vector for time θ, as well as a dummy-coded vector of the two life stage levels λ and their interaction with time:

$$X = \{[\theta][\lambda][\theta \cdot \lambda]\} \quad (8)$$

Models were fitted independently per country and species, but the response (the respective climatic variable) and time were scaled with data pooled across all countries, so that the effect sizes are comparable across countries and species. To account for the geographical clustering of sample plot locations in the Spanish NFI (Fig. 2), the factor region was included as an additional fixed effect in the models for Spain. The continuous predictor time (year of the survey) was first centered at the level of independent models, i.e. per species (within cluster for Spanish data) within country, and then scaled linearly in such a way that the most frequent sampling period, 25 years, corresponded to the range between −0.5 and +0.5. This way, the slope for time estimates the average linear shift over 25 years, independently for each species–country combination. This harmonization makes the effect sizes for time comparable across countries and species, while the uncertainty of the estimates still depends on the original time period between surveys.

Model assumptions were checked with simulated quantile residuals provided by the package 'DHARMa' (Hartig 2020), and consequently three out of the 58 fits for heat sum and none of the fits for water availability were discarded because they violated the assumption of a beta-distributed error (Supporting information).

To quantify temporal shifts and juvenile divergences, we used marginal effects of time and life stage on the position parameter μ, as well as post-hoc significance tests ($\Pr(>|z|) = p < 0.05$) provided by the package 'emmeans'. The differences in marginal means of the two life stages (approximately equivalent to the difference between life stage-level intercepts; Fig. 3A–C) was interpreted as the divergence of juveniles compared to adults (juvenile divergence). The marginal trend of juvenile occurrence over time (approximately equivalent to the slope over time within the juvenile stage level; Fig. 3A–C) was interpreted as the temporal shift. Species-specific juvenile divergences and temporal shifts were averaged per country by weighting with the inverse of the associated squared standard error 1/SE, and the frequency of effect directions was counted (Fig. 4B–D and 5B–D). Since both, juvenile divergence and temporal shift were transformed to the response scale, they can readily be interpreted as a change of occurrence center in % along the entire sampled gradient across all three countries, where 0% corresponds to the minimum and 100% to the maximum of the environmental gradient.

Results

Simulated divergent occurrences

Simulations of the two-life stage population model showed that both environmental-change driven temporal range shift and ontogenetic niche effects, in particular ontogenetic niche shift, can cause divergent occurrences of juveniles from adults. The simulated data from three different scenarios of shifts led to three different combinations of occurrence patterns detected by the beta regression: (A) temporal environment shift resulted not only in a temporal shift of juveniles, i.e. the shift of juvenile occurrence over time along the environmental gradient, but also in juvenile divergence in the same direction, i.e. the difference between marginal means of occurrence from adults to juveniles (Fig. 3A). (B) In contrast, ontogenetic niche shift led to juvenile divergence only – in the direction of the ontogenetic niche shift (Fig. 3B). Ontogenetic niche shift and temporal range shift can act simultaneously. (C) Only when both processes acted in opposite directions, they could be disentangled because they led to oppositely directed juvenile divergence and temporal shift (Fig. 3C).

In addition to ontogenetic niche shift, our simulations demonstrate another ontogenetic effect: under stable environmental conditions, the occurrence width can contract from juveniles to adults due to the demographic dependency of the adult on the juvenile population, even when the niche width remains constant over ontogeny (Fig. 3D). Despite identical ontogenetic niches of juveniles and adults, the environmentally-dependent mortality led to a stable state population where juveniles occurred more widespread towards the extreme conditions of the environmental gradient. Adults occurred in a smaller range because the increased juvenile mortality at the niche margins also decreased transition from juveniles to adults.

Divergent occurrences in NFIs

In the three European countries, tree species had both significant temporal shifts of juveniles over the respective time periods between surveys and significant juvenile divergences along the two gradients of long-term climatic variables. Significant temporal shifts were less frequent – 24% (heat sum) and 21% (water availability) of all 55 species-country combinations – than significant juvenile divergences – 53% (heat sum) and 48% (water availability) of the cases – (Fig. 4C and 5C). The effect sizes of juvenile divergence and temporal shift, scaled to express changes over 25 years, were similar with up to 6.6% of the entire climatic range across all surveyed plots in all three countries. Most strikingly, the overall frequency of significant juvenile divergences associated with an opposite temporal shift was similar to the frequency of significant divergences associated with a temporal shift in the same direction along both heat sum (59% versus 41% of the significant juvenile divergences; Fig. 4D) and water availability (39% versus 61%; Fig. 5D).

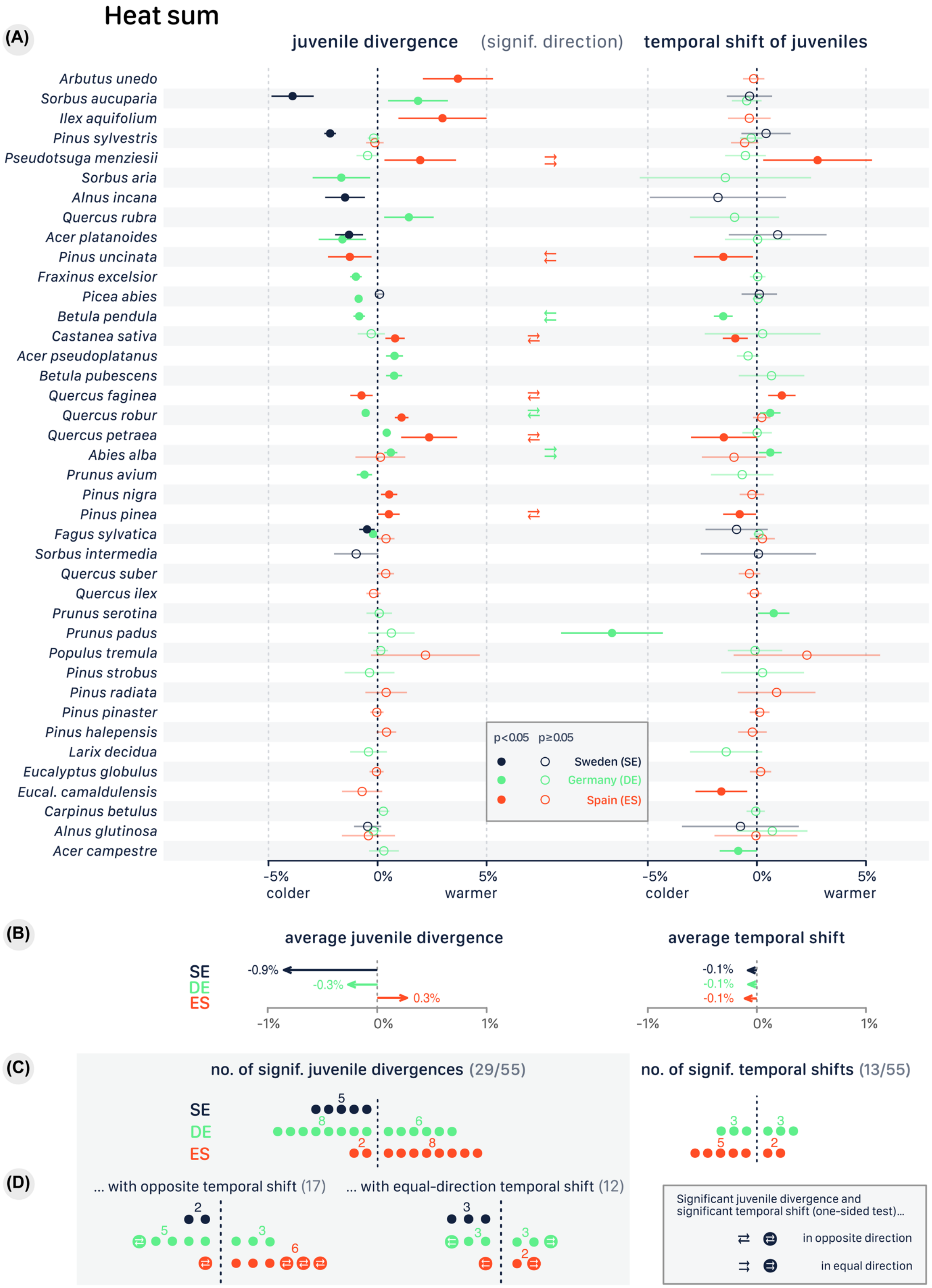


Figure 4. Juvenile divergence and temporal shift of juvenile trees along a European heat sum gradient: (A) effect sizes by species and country in % of the full gradient range across all three countries, ordered by effect size and significance of the juvenile divergence. Pairs of arrows mark those significant juvenile divergences that are associated with a significant temporal shift (one-sided test) and whether the effects are in equal or opposite direction. (B) Average effect sizes by country and direction, weighted by the inverse of the squared standard error. (C) Count of significant juvenile divergences and significant temporal shifts by country and direction. (D) Comparison of the frequency between significant juvenile divergences with associated opposite temporal shift and with equidirectional temporal shift (additional significant tests for direction of the temporal shift are emphasized with arrow symbols). Significance of the estimates was tested with a two-sided test, significance of the directions with a one–sided test ($\Pr(>|z|) = p < 0.05$).

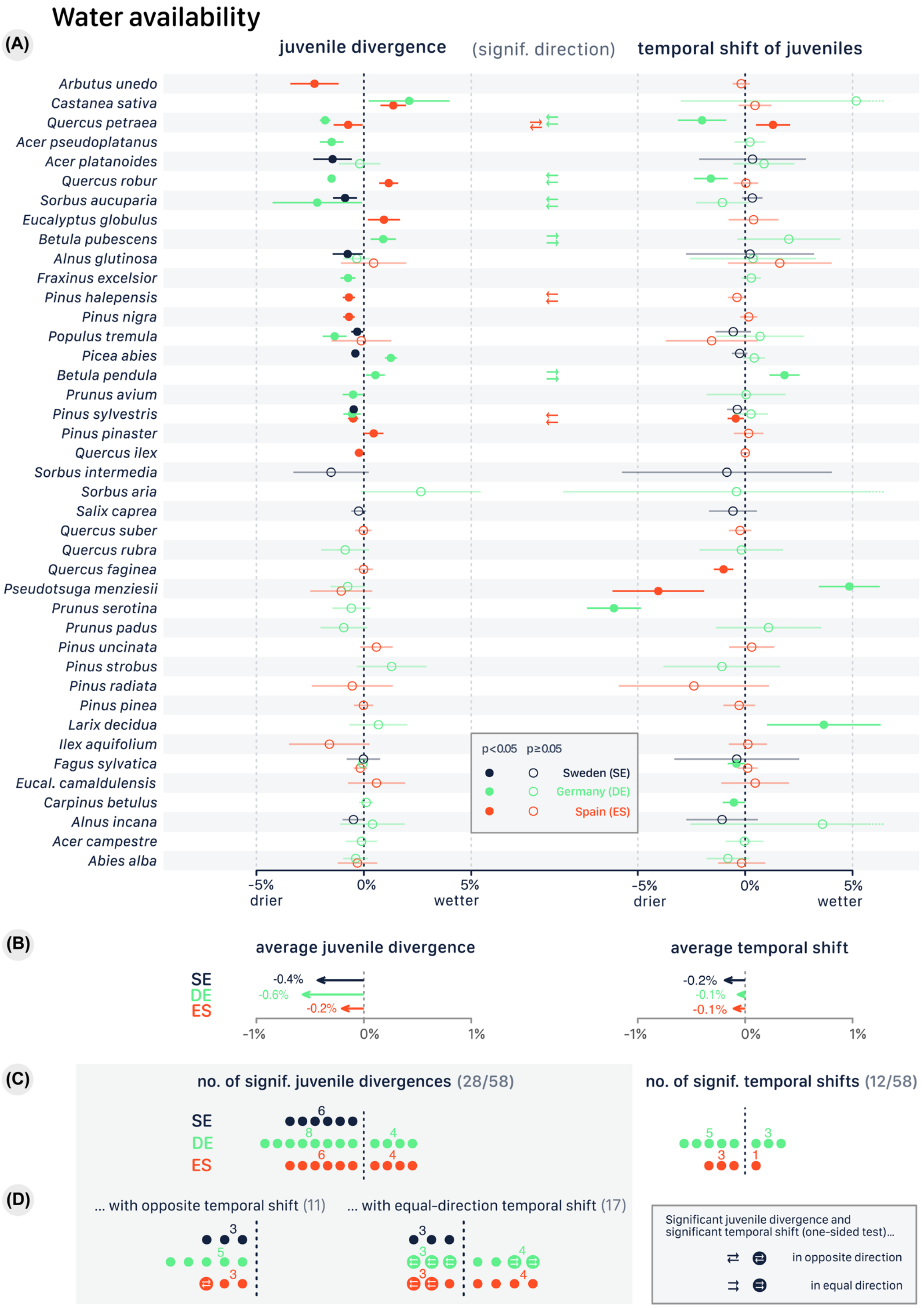


Figure 5. (A) Juvenile divergence and temporal shift of juvenile trees along a European water availability gradient: (A) Effect sizes by species and country in % of the full gradient range across all three countries, ordered by effect size and significance of the juvenile divergence. Pairs of arrows mark those significant juvenile divergences that are associated with a significant temporal shift (one-sided test) and whether the effects are in equal or opposite direction. (B) Average effect sizes by country and direction, weighted by the inverse of the squared standard error. (C) Count of significant juvenile divergences and significant temporal shifts by country and direction. (D) Comparison of the frequency between significant juvenile divergences with associated opposite temporal shift and with equidirectional temporal shift (additional significant tests for direction of the temporal shift are emphasized with arrow symbols). Significance of the estimates was tested with a two-sided test, significance of the directions with a one-sided test (Pr(> |z|) = p < 0.05). Large confidence intervals where cut off only at the upper limit of 6.5%, as indicated by dotted error bars.

The predominant direction of juvenile divergences along heat sum strongly varied between countries: all five significant juvenile divergences in Sweden had juveniles occurring in colder conditions than adults, while eight out of ten significant juvenile divergences in Spain were to warmer conditions (Fig. 4C–D). In Germany, the direction of juvenile divergences along heat sum was balanced. This pattern was also observed in the average juvenile divergences over all species per country with juvenile divergence towards colder in Sweden and warmer in Spain, and moderately colder in Germany (Fig. 4B) – and even within species: juveniles of, e.g. *Fagus sylvatica* and *Quercus robur* diverged towards warmer conditions in Spain but towards colder conditions in the other countries.

Along water availability, juveniles commonly occurred in drier conditions than adults across all countries. This pattern was consistent across averages per country (Fig. 5B) and frequencies of significant juvenile divergences. Of the significant divergences, 100% (Sweden), 67% (Germany) and 60% (Spain) were towards drier conditions (Fig. 5C). Equally, all of the significant juvenile divergences in opposite direction to the *temporal shift* were towards drier conditions 5D), and many of the species with significant juvenile divergences in more than one country shifted exclusively to drier conditions: *Sorbus aucuparia*, *Populus tremula*, *Quercus petraea* and *Pinus sylvestris* (but cf. *Castanea sativa* and *Quercus robur*).

Significant temporal shifts (Fig. 4C and 5C) only occurred in Germany and Spain, not in Sweden, the country with the shortest period between observations of 10 years (Supporting information). Average temporal shifts per country were consistently towards colder and predominantly towards drier conditions across countries (Fig. 4B and 5B). There were significant temporal shifts in all directions along the two gradients, but a small majority was towards colder and drier conditions (Fig. 4C and 5C). Certain species had extraordinary large temporal shifts (around 5% of the gradient range): *Castanea sativa*, *Pseudotsuga menziesii*, *Prunus serotina*, *P. padus* and *Larix decidua* in Germany; and *Pseudotsuga menziesii* in Spain.

Discussion

Both temporal range shift and ontogenetic effects, such as ontogenetic niche shifts, can lead to similar divergent occurrences of juveniles and adults along an environmental gradient, as demonstrated by our two-life stage simulation model. The analysis of European NFI data revealed that significant juvenile divergences were as frequently opposite to temporal shifts as they were in the same direction. This is a strong indication that juvenile divergence can not simply be interpreted as a sign of environmental change-driven range shift, but that ontogenetic effects frequently play a major role in divergences between juveniles and adults.

Simulated divergences between life stages

Our simulations illustrate how both temporal shifts of the environment and ontogenetic niche shifts can cause divergent occurrences between life stages, and how the demographic dependency of life stages alone can lead to differently widespread occurrences. Many empirical studies, however, assume that different occurrences are exclusively the result of a temporal shift caused by environmental changes (Zhu et al. 2014, Mathys et al. 2018). This is based on the assumption that, when species change their ranges to maintain niche conditions, juveniles will respond faster and track these conditions more closely than adults (Monleon and Lintz 2015). These temporal range shifts that become evident as shifts of occurrence centers can also include shifts that only occur at either the leading margins, i.e. juveniles filling a new range, or at the trailing margins, i.e. juveniles regressing where adults persist (Lenoir et al. 2009). Under ongoing environmental shift, juveniles will permanently lead the trailing adults throughout time. This permanent and increasing juvenile divergence is illustrated in Fig. 3A, where the environment had already been shifted before the first observation so that juveniles do not only diverge on average (Fig. 3A, juvenile divergence), but already at the first observation (Fig. 3A, at $t_1 = -0.5$). Permanent divergence through time alone can thus not be interpreted as necessarily caused by ontogenetic niche shift either. Inferring ontogenetic niche shifts from permanent divergence of life stages may however be considered if there are only negligible temporal shifts over a long period (cf. Máliš et al. 2016).

As shown in our simulations, the pattern of divergent occurrences can also emerge when the niche shifts between ontogenetic stages (Fig. 3B). Ontogenetic niche shifts, i.e. juvenile plants requiring or enduring different environmental conditions to grow or survive than adults of the same species, have been reported in many empirical studies (Eriksson 2002, Miriti 2006, Ewald 2007, Máliš et al. 2016, Andivia et al. 2020). In addition, it is also possible that observed divergences between life stages could reflect ontogenetic niche shift of unobserved life stages. These life stages include, e.g. ontogenetic niche shifts of seedlings below the sampling threshold, the germination of seedlings (Valdez et al. 2019, Vecchio et al. 2020), but even the environmentally dependent ability of trees of to produce the life stage of seeds (Rosbakh et al. 2018, Bajocco et al. 2021). Furthermore, other ontogenetic effects like ontogenetic niche contraction or expansion (Eriksson 2002, Bertrand et al. 2011), and the demographic dependency between life stages can lead to juvenile divergences, when the sampled geographical range does not include the entire niche (more widespread occurrence of juveniles along European climatic gradients section). Evidence of life stage divergence (as illustrated in Fig. 3A–B; juvenile divergence) can therefore not simply be interpreted as a result of temporal change but ontogenetic effects must also be considered as a potential cause.

Attributing juvenile divergence to temporal range shift or ontogenetic effects

Since both processes, temporal range shift and ontogenetic effects, can cause divergent occurrences between life stages along the climatic gradient, the observed pattern of juvenile divergence, i.e. the difference in centers of adult and juvenile occurrence along the gradient averaged over time, can not directly be attributed to either one of the processes (Fig. 1). The challenge of attributing juvenile divergence to either temporal range shift or ontogenetic effects can be partly overcome with repeated surveys. With repeated observations, the trend of juvenile occurrence over time can be quantified and directly be interpreted as a temporal shift (Fig. 3A, temporal shift). When temporal range shift and ontogenetic effects act simultaneously, they can either be directed in the same direction, amplifying juvenile divergence. But they can also act in opposite direction, leading to juvenile divergence that is opposite to the direction of the temporal shift (Fig. 3C) or even to divergences that cancel each other out (for a discussion of the consequences for inference see Temporal range shifts and ontogenetic effects are at least equally relevant for divergent occurrences section). These associations of directions provide a tool for inferring ontogenetic effects within species: If a species has significant juvenile divergence associated with a significant temporal shift in opposite direction, we can attribute the juvenile divergence to ontogenetic effects because the divergence has not likely emerged from the temporal range shift. In addition, the frequencies of juvenile divergences and associated directions of temporal shifts can be used for inference within a set of species: comparing the overall frequencies of juvenile divergences with opposite to those with equidirectional temporal shifts is an indication of the relative contribution of ontogenetic effects and temporal range shifts to observed divergences between life stages.

Divergent occurrences between life stages in European forests

Temporal range shifts and ontogenetic effects are at least equally relevant for divergent occurrences

There were about twice as many significant juvenile divergences than significant temporal shifts along both climatic gradients across species and the three NFI countries. Significant estimates of juvenile temporal shift in 24% (heat sum) and 21% (water availability) of all species–country combinations are a unequivocal indicator of temporal range shifts. The high frequency of juvenile divergences – observed in 53% (heat sum) and 48% (water availability) of all cases – is however no sufficient evidence of ontogenetic effects, such as ontogenetic niche shifts. Ontogenetic effects and temporal range shift can both cause juvenile divergences, and furthermore, the significance of a temporal shift depends on the length of the observed time period, which varies between species and country combinations (Supporting information). Particularly in Sweden the short observation period of only 10 years could lead to temporal shifts that are not significant. But the contribution of ontogenetic effects to juvenile divergences can be inferred from the direction of associated temporal shifts within the same species.

At the individual species level, we found significant juvenile divergences in opposite direction to the temporal shift for five species along the heat sum gradient and for one species along the water availability gradient. These juvenile divergences can clearly be attributed to ontogenetic niche shifts, because they could not have arisen from the temporal range shift. The overall importance of ontogenetic effects, however, is probably greater than apparent from these individual cases, because our rigorous test for ontogenetic effects within species will exclude several cases. For instance, ontogenetic niche shifts and other ontogenetic effects will not be detected when no significant temporal shift occurred simultaneously in opposite direction to the ontogenetic niche shift. Additionally, even if ontogenetic niche shift and temporal shift were in opposite directions, the juvenile divergence could become too small to be significant under fast temporal shifts. Fast shifting juveniles can diminish the divergence caused by ontogenetic effects so that both processes cancel each other out, and they could even overtake the slowly shifting adults along the gradient, so that not every opposite ontogenetically-caused divergence can be observed as juvenile divergence in the opposite direction to the temporal shift.

To further evaluate the relative importance of ontogenetic effects for juvenile divergences across all species and countries, the odds of a juvenile divergence being associated with a temporal shift in opposite direction rather than in the same direction can be considered, regardless of significance or effect size of the temporal shift. Assuming that all juvenile divergences were caused only by temporal range shifts, all observed patterns of temporal shifts would be in the same direction as the juvenile divergences (the odds would converge to 0). In contrast, if we assume that all juvenile divergences were caused by ontogenetic effects – and the temporal range shift was an additional independent process not causing any divergences – the directions of the temporal shifts of juveniles would split equally among equidirectional and opposite patterns of temporal shift (the odds would converge to 1).

In our results, the odds of temporal shifts opposite to the juvenile divergence are $17:12 = 1.42$ along the heat sum gradient and $11:17 = 0.64$ along the water availability gradient. This suggests that along both gradients the majority of juvenile divergences are unlikely caused by a temporal range shift, and in the case of heat sum there are even more juvenile divergences opposite to the temporal shift than expected from independent processes ($1.42 > 1$). We can thus conclude that ontogenetic effects, like ontogenetic niche shifts, are at least as relevant for causing divergent occurrences of life stages as environmental change-driven temporal range shifts.

That occurrence centers of tree species' life stages can diverge along an environmental gradient because of ontogenetic niche shift has been suggested by other empirical studies (Urbieta et al. 2011, Zhu et al. 2014, Máliš et al. 2016). The importance of ontogenetic effects for divergent occurrences of tree life stages has far-reaching consequences for scientific inference: environmental change impacts can not simply be inferred from static data on occurrence of tree life stages. Having established that both temporal range shifts and ontogenetic effects exist in European forest tree species, we will discuss plausible causes of those processes in the following sections.

Temporal shifts in response to environmental change

Under climate warming with increased evaporation, tree species are expected to shift over time towards colder and wetter conditions along static long-term climatic gradients to maintain the conditions of their climatic niche. In line with this expectation, temporal range shifts towards long-term colder conditions have been reported for several species based on repeated observations at northern range limits (Boisvert-Marsh et al. 2014, Sittaro et al. 2017) or at high elevations along mountain slopes (Julio Camarero and Gutiérrez 2007, Du et al. 2018). As expected from climate change-driven range shifts, the average temporal shifts in the three NFI countries were consistently towards colder conditions. For instance, *Prunus padus*, *P. avium*, *Betula pendula* and *Pinus uncinata* (but cf. Améztegui et al. 2010) shifted towards colder conditions. *Prunus padus* had a particularly pronounced shift in Germany, probably due to its effective long-distance seed dispersal (Nestby 2020). Contrary to expectations, average temporal shifts along water availability were mainly towards drier conditions (Fig. 4B and 5B). This may be partly explained by regional differences in long-term trends of climatic water availability, e.g. decreased drought frequency in northern Europe (Spinoni et al. 2015, Stagge et al. 2017). The temporal shifts in Sweden were not significant for any of the species, probably due to the comparatively short period between surveys (10 years; Supporting information), which leads to larger uncertainties in the temporal shift estimates. Across all countries, individual species significantly shifted towards both colder and warmer (8:5) and drier and wetter (8:4) conditions. This adds to the body of studies that have found inconsistent directions among species in the divergence between adults and juveniles (Rabasa et al. 2013, Wason and Dovciak 2017, O'Sullivan et al. 2020) and in temporal shifts from repeated observations (Woodall et al. 2013, Gibson-Reinemer and Rahel 2015). Although hypotheses have been proposed about how climate warming can cause shifts to warmer and drier conditions along long-term climatic gradients – like competitive release at the warmer margin or other climate-driven habitat modifications that indirectly allow for range shifts (Lenoir et al. 2010, Crimmins et al. 2011) – it is problematic to assume that any temporal range shift is driven by climate warming.

Instead, the set of species associated with many of the most pronounced temporal shifts suggests a connection to land-use change, including 1) introduction and promotion of individual species through forestry and 2) management regime change. First, silviculturally introduced species are likely to change their range to new environmental conditions because the climatic conditions at planting locations frequently differ from the their actual niche conditions (Ruiz-Benito et al. 2012). Unsurprisingly, introduced timber species are responsible for almost all of the large temporal shifts in Germany and Spain (Fig. 4, 5; Germany: *C. sativa*, *P. menziesii*, *P. serotina*, *L. decidua*; Spain: *P. menziesii*). The exotic conifer species *P. menziesii* has naturalized and expanded in mountainous regions in Germany (Knoerzer 1999) and Spain (Broncano et al. 2005). *Larix. decidua* has been planted outside the native range within central Europe (Jansen and Geburek 2016). The deciduous species *C. sativa* (Seemann et al. 2001) and *P. serotina* have been introduced in Germany, where *P. serotina* in particular has become invasive (Starfinger et al. 2003). Second, in addition to introduction and promotion of individual species, changing forest management regimes, especially abandonment, has been changing species composition of forests, e.g. through giving up traditional fire management in Spain (Seijo et al. 2018) or coppice management in central Europe (Müllerová et al. 2015). Consistently, native, resprouting species that had benefited from these traditional management regimes, e.g. *Quercus* spp. and *Carpinus betulus* also show significant *temporal shifts*. Overall, the underlying drivers of range shifts – climate, land use or any other temporal pressure – can not be inferred from the effect of time on the occurrence distributions of environmental variables alone, and the underlying causes remain speculative.

More widespread occurrence of juveniles along European climatic gradients

Juveniles generally occurred in more extreme conditions than adults within countries and therefore along a wider range of the entire European climatic gradients (Fig. 4). The number of juvenile divergences per direction and country along a latitudinal gradient from low mean heat sum in Sweden towards high mean heat sum in Spain followed a striking opposite pattern (Fig. 2). Although in Sweden plant productivity may be limited by heat sum (Woodward 1987), all juvenile divergences were towards colder conditions. In Spain, however, where plant productivity is more likely limited by evapotranspiration associated with high heat sum (Larcher 2003), the majority of juvenile divergences were towards warmer conditions. Germany, where the directions of juvenile divergences along heat sum were balanced (Fig. 4C, also takes an intermediate position on the heat sum gradient. Along water availability, juveniles overwhelmingly diverged towards drier conditions (Fig. 5C), which – again – is a divergence towards more hostile conditions, because at a large scale only drought but not climatic water excess is a limiting factor for tree growth in Europe (Kottek et al. 2006). Juvenile divergences towards more hostile growing conditions were also expressed in the per-country average juvenile divergences, and particularly distinct in the significant juvenile divergences opposite to the temporal shift, which are even more likely to correspond to definite ontogenetic effects (Fig. 4 and 5D).

This pattern – more widespread occurrence of juveniles along large-scale climatic gradients – can be caused by ontogenetic niche shifts but also by other ontogenetic effects, namely 1) ontogenetic niche contraction from juveniles to adults, including 2) the special case of reduced growth at niche margins, but also by 3) demographic dependency between life stages. First, changes in width of the viable conditions along environmental gradients over life history, i.e. ontogenetic niche expansion and contraction, have widely been evoked as an explanation of observed differences in occurrence widths (Stohlgren et al. 1998, Copenhaver-Parry et al.

2020). In particular, wider juvenile occurrence has been explained by ontogenetic niche contraction (Eriksson 2002, Young et al. 2005, Quero et al. 2008, Bertrand et al. 2011, Máliš et al. 2016), which can emerge through more severe mortality of adults under the same conditions. For example, Bertrand et al. (2011) have suggested that species' niches ontogenetically converge towards better nutritional conditions because the nutrient demand of adults may be higher. Furthermore, it has been shown that larger trees are more susceptible to drought-induced mortality (Bennett 2015), partly because ontogenetically increasing leaf area is directly linked to higher evapotranspirative demand (Buras et al. 2018). This will result in juvenile occurrences at environmental conditions that can not supply the development into adults, which can be regarded as sink populations (Soberón and Peterson 2005). Second, reduced growth at the niche margins can be interpreted as a special case of ontogenetic niche shift or niche contraction, when ontogenetic progression is not measured in terms of age but, as in this case, in terms of size as a measure for the progress through stages of development (Gatsuk et al. 1980). If under extreme water- or heat supply-limited conditions growth rates are diminished (Coomes and Allen 2007), or trees adaptively never exceed certain sizes at the niche margins (Lines et al. 2012), small individuals are more likely to be found at extreme climate conditions than larger individuals, leading to an ontogenetic niche change between size stages. Relatively higher abundance of small-sized trees toward climate extremes is an additional challenge to any approach using static data on tree size as a substitute for age to infer temporal shifts of range limits (Rabasa et al. 2013, Mathys et al. 2018).

Third, adults can occur under narrower and less extreme environmental conditions than juveniles simply because the abundance of adults is not only determined by their own ontogenetic niche, but also dependent on the abundance of earlier life stages (Young et al. 2005). Adults are confined to the intersection of their own ontogenetic niche with that of prior life stages, potentially limiting adult occurrence to a smaller range on the gradient than any of these filters (Young et al. 2005) alone. In our two-life stage simulation (Fig. 3D), we have shown that the effect of narrower occurring adults due to the dependency on juvenile abundance even arises under ontogenetically identical niches of juveniles and adults, if, due to environmentally-dependent mortality alone, disproportionally fewer juveniles transition to adults at the niche margins (Zhu et al. 2014, 'turnover effect').

While only the first of the three mechanisms – ontogenetic niche contraction – is ontogenetic niche change or shift in the strict sense, all of them are ontogenetically acting effects: For all three mechanisms, trees transition less frequently to later life stages at the niche margins, leading to the same pattern of more widely occurring juveniles along environmental gradients. Any one of these processes – acting individually or simultaneously – could thus be responsible for the observed juvenile divergence towards colder in Sweden, towards hotter in Spain, and towards drier conditions across all three countries.

Here, instead of modelling life stage's niches, we modelled the change in the occurrence distribution of climatic variables over time and per life stage, because this allows for differences in sampling protocols between life stages and countries (estimates of juvenile divergences and temporal shifts from beta regression models section) as well as the fact that the sampling does not cover the entire climatic range of all species. Without these data limitations, however, a niche modelling approach that characterizes ontogenetic niches would be preferable to accurately predict species occurrences. Furthermore, to separate the ontogenetic effects that act on the occurrences of life stages into ontogenetic niche differences and demographic dependencies between life stages, an ontogenetic niche modelling approach will also have to account for these demographic dependencies. For example, recently, it has been discussed whether juvenile trees have wider or narrower ontogenetic niches than adult trees (Bertrand et al. 2011, Copenhaver-Parry et al. 2020, Ni and Vellend 2021). We have shown that to answer this question, the vital performance of life stages along environmental gradients has to be assessed separately, because occurrence of a particular life stage is also constrained by its dependency on other life stages.

Conclusions

We conclude that divergent occurrences between life stages are caused by both temporal range shifts and ontogenetic effects – including ontogenetic niche shift, expansion or contraction, and demographic dependency between observed or unobserved life stages. That juvenile divergences associated with temporal range shifts in opposite direction are as frequent as divergences in the same direction, indicates that ontogenetic effects are at least as relevant for divergent occurrences between life stages as temporal range shifts.

The important role of ontogenetic effects at the continental scale emphasizes that impacts from changing climate on forest ecosystems can not simply be inferred from divergent occurrence of life stages in static data on tree occurrences. Instead, future studies should recognize demographic dependencies between life stages and that early tree life stages can have different ontogenetic niches than adult trees that could cause even more sensitive responses to environmental change (Grubb 1977, Lines et al. 2019).

Acknowledgements – We thank Florian Hartig for advice on theoretical concepts. We also thank Thomas Riedel for providing environmental data raster values at German NFI locations. Spanish forest inventory data were provided by the Spanish Ministry for the Ecological Transition and the Demographic challenge (MITECO) and the Spanish Ministry of Agriculture, Fisheries and Food (MAPA; <www.mapa.gob.es/es/desarrollo-rural/temas/politica-forestal/inventario-cartografia/inventario-forestal-nacional/default.aspx>).

Funding – LHe, LHü and AB were funded by the Bavarian Ministry of Science and the Arts within the Bavarian Climate Research Network (bayklif). PRB was supported by the Community of Madrid Region under the framework of the multi-year Agreement with the University of Alcalá (Stimulus to Excellence for Permanent University Professors, EPU-INV/2020/010) and RTI2018-096884-B-C32 (MICINN, Spain). GK received support from the ANR through REFORCE – EU FP7 ERA-NET Sumforest 2016 and ANR AAPG2020 DECLIC.

Author contributions

Lukas Heiland: Conceptualization (lead); Data curation (equal); Formal analysis (lead); Methodology (lead); Visualization (equal); Writing – original draft (equal); Writing – review and editing (lead). **Georges Kunstler**: Conceptualization (equal); Methodology (supporting); Supervision (equal); Writing – review and editing (lead). **Paloma Ruiz-Benito**: Conceptualization (supporting); Data curation (equal); Methodology (supporting); Writing – review and editing (equal). **Allan Buras**: Data curation (equal); Methodology (supporting); Writing – review and editing (equal). **Jonas Dahlgren**: Data curation (equal); Writing – review and editing (supporting). **Lisa Hülsmann**: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Methodology (equal); Project administration (lead); Supervision (lead); Writing – review and editing (lead).

Transparent Peer Review

The peer review history for this article is available at <https://publons.com/publon/10.1111/ecog.06042>.

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.31zcrjdnc> (Heiland et al. 2021).

Supporting information

The supporting information associated with this article is available from the online version.

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