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RESEARCH ARTICLE

Growth–survival trade-off in temperate trees is weak and restricted to late-successional stages

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Abstract

1. Life-history strategies emerge from eco-evolutionary constraints, where organisms allocate limited resources to growth, survival, and reproduction, resulting in trade-offs such as the growth–survival trade-off. There is still a limited understanding of whether and how disturbance regimes and successional stages might mediate such trade-offs, with potential consequences for species population dynamics and community assembly.
2. Here, we investigate how disturbances shape the growth–survival trade-off by comparing early and late-successional forest stands across the eastern United States. Using large-scale sampling to capture the realised niche of 68 temperate species, we estimated species-specific mortality probabilities under zero growth (a proxy for resource-poor environments) applying a Bayesian multilevel modelling framework. We tested trade-offs between these estimates and species' maximum growth capacity (a proxy for resource-rich environments), within and across early and late-successional stands.
3. Overall, we found a weak growth–survival trade-off among temperate tree species ($R^2=0.07$). No clear evidence of this trade-off was found in early successional stands ($R^2=0.02$), while late-successional stands showed a relatively stronger—though still weak—positive association between species' maximum growth and mortality under zero growth conditions ($R^2=0.17$). Disturbances therefore seem

to mediate a filtering of tree life-history strategies. Consequently, an increase in disturbance rates or changes in their regime could disrupt the growth–survival trade-off in temperate forests.

4. *Synthesis*: Life-history strategies arise from eco-evolutionary constraints and can lead to trade-offs like tree growth and survival. While temperate tree species in late-successional or low-disturbance-frequency forests do show a growth–survival trade-off, this trade-off is weak and was not found in early successional or high-disturbance-frequency stands, nor across all stages combined. Our findings highlight a role of disturbances in filtering life-history strategies and their potential impact on forest dynamics and global carbon cycling but also a need to better understand the mediating processes of tree demographic trade-offs.

KEYWORDS

angiosperms, community assembly, demographic trade-offs, forest disturbance, gymnosperms, life-history strategies, stand development

1 | INTRODUCTION

The forest carbon sink is governed ultimately by the behaviour of the species in each forest community (Bialic-Murphy et al., 2024; Pan et al., 2024). Therefore, an improved understanding of species demography can help refine our comprehension of the mechanisms by which tree species occur and coexist in forests (Kobe, 1999; Silvertown, 2004), and to predict the future of forest species composition in the face of rapidly changing environmental conditions (Bauman, Fortunel, Cernusak, et al., 2022; Bauman, Fortunel, Delhaye, et al., 2022). Similarly, a better understanding of how fast species assimilate carbon, via growth, and release carbon, via mortality, can help us predict the future of the forest carbon sink (Rüger et al., 2020). Ecological theory predicts that the way species invest in the acquisition of resources and their allocation to growth, survival, and reproduction will be tightly linked and have mutual dependencies (Rüger et al., 2018; Salguero-Gómez et al., 2015; Wright et al., 2010). For instance, light-demanding species tend to invest resources into radial growth: they can grow fast under high light availability, but may fail to grow with concomitant high mortality when light is limited (Brienen et al., 2020; Kobe, 1996; Pacala et al., 1994). In contrast, shade-tolerant species usually allocate more resources to stem structure and defences, leading to higher longevity at the expense of slower growth rates (Iida et al., 2014; Kobe et al., 1995; Poorter et al., 2008). Ultimately, such trade-offs are expected to shape the demographic performance of tree species (Bialic-Murphy et al., 2024; Kitajima, 1994; Kobe, 1999; McMahon et al., 2011; Russo et al., 2021).

An implication of the growth–survival trade-off is that species' maximum growth rates can predict whether and how the risk of mortality of individual trees varies with resource availability (e.g. water, nutrients, light). For instance, slow-growing species may experience low mortality in low-resource environments, but have a greater mortality risk in resource-rich environments due to limited competitive advantage (Russo et al., 2008). Conversely, fast-growing species would have a higher competitive advantage in resource-rich environments, at the expense of increased mortality risk in low-resource environments (Russo et al., 2008). Consequently, the probability of mortality of individuals in the absence of growth could produce insights into the allocation strategies of each species (Kobe et al., 1995; Russo et al., 2021). In addition, the mortality risk when growth is extrapolated to be zero (i.e. the intercept) allows us to infer tolerance to conditions of resource limitation, whether by light, nutrients, or water supply (Kitajima, 1994; Kitajima & Poorter, 2008; Kobe et al., 1995; Russo et al., 2005, 2008), as the lower the species-specific mortality probability at zero growth, the greater the tolerance to resource limitation (Russo et al., 2021). More widely, how different species covary in terms of growth and mortality over environmental resource gradients may ultimately shape the overall local and large-scale dynamics of forests (Rüger et al., 2020; Russo et al., 2021).

The existence and strength of demographic trade-offs have been explored across Amazonia and in other lowland tropical forests (Coelho de Souza et al., 2016; Kambach et al., 2022; Rüger et al., 2020; Russo et al., 2008, 2021; Wright et al., 2010), suggesting a widespread tropical pattern, at least in non-cyclone-affected forests (i.e. forests experiencing low-severity disturbances). While the growth–survival trade-off has been observed in temperate regions at local and regional scales (McMahon et al., 2011; Wijenayake et al., 2023), it has not been explored nor quantified over large biogeographical scales. Such a test is important because, as well as being structurally and floristically very different from tropical forests (Spicer et al., 2020), temperate forests are often disturbed by intense events (Sommerfeld et al., 2018). There is evidence that some ecological strategies typical of old-growth ecosystems, such as the presence of slow-growing and shade-tolerant species, are lost after major disturbances that cause high tree mortality (e.g. hurricanes, insect outbreaks, and droughts) (Needham et al., 2022; Russo et al., 2021). To the extent that disturbances may cause reversion to earlier developmental or successional stages dominated by fast-growing pioneer species, we can expect to observe reduced demographic trade-offs due to the absence of slow-growing and shade-tolerant species (see Figure 1). In extremis, the growth–survival trade-off might be absent in disturbed forests (Russo et al., 2021).

In forests, the growth–survival trade-off might also vary due to the differences among species, including the presence of distinct clades of both angiosperms and gymnosperm species, which may have fundamentally different ecological strategies and competitive abilities (Becker, 2000; Bond, 1989; Laughlin et al., 2020). For instance, gymnosperms are expected to have higher survival and outcompete angiosperms in resource-poor environments (Bond, 1989), such as low soil fertility and frequent frost conditions, as they have conservative traits that allow them to persist in stressful environments, in addition to successful strategies for colonising disturbed environments (Brodribb et al., 2012). On the other hand, gymnosperms typically exhibit lower photosynthetic and hydraulic capacity due to the presence of small vessels, affecting the conductance of water through the plant (Lusk, 2011; Lusk et al., 2003). These physiological and morphological traits may confer a competitive disadvantage in resource-rich environments (Becker, 2000; Lusk, 2011; Stephenson & Van Mantgem, 2005), which would, in turn, be dominated by angiosperm species. Thus, studying demographic trade-offs in temperate forests at large biogeographical scales is crucial for understanding how these dynamics vary among species. In addition, since temperate forests are often prone to disturbances and structurally distinct from tropical forests, insights into growth–survival trade-offs of each tree species here may clarify how disturbances impact community structure and dynamics across forest ecosystems more generally.

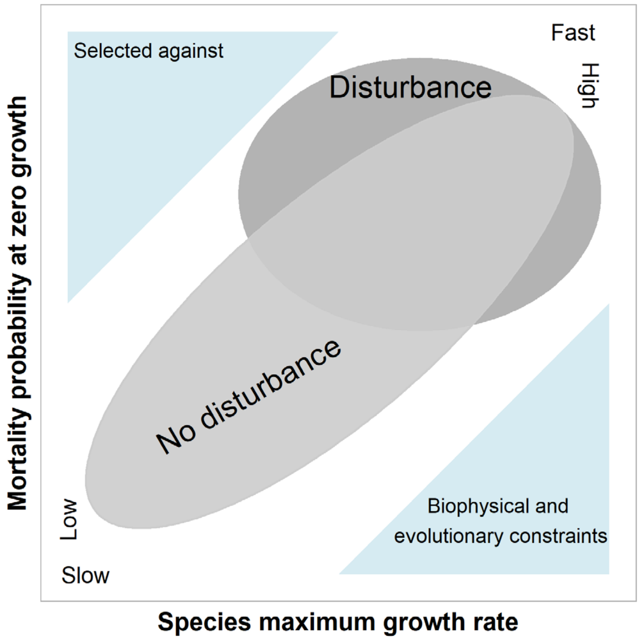

FIGURE 1 Expected interspecific relationships between maximum growth rate and mortality probability at zero growth. Here, maximum growth rate is a proxy for species growth rate in resource-rich environments, and mortality probability at zero growth is a proxy of mortality probability in resource-poor environments. Species' life-history strategies vary according to how they allocate resources, along a continuum from low investment in growth and high investment in defences, to high investment in growth and low investment in defences. Species mortality rates are expected to vary from low to high across this continuum, reflecting a trade-off between growth and survival investments. Species that fall within the upper-left light-blue triangle would be selected against, as having slow growth and high mortality may reduce the population size and are not viable for sustaining a population in the long term (Russo et al., 2021). In contrast, the bottom-right light-blue triangle indicates a region where species would not be successful under low resource due to investments in survival, leading to a fast growth but low reproductive success (Reich, 2014; Rose et al., 2009). If a disturbance of sufficient intensity drives forests to an early successional stage, there would be a loss of slow-growth, low-mortality species, resulting in forests dominated by fast-growing, high-mortality species. Figure adapted from Russo et al. (2021).

Here we analysed data from 12,035 permanent inventory plots distributed across the eastern United States from the Forest Inventory and Analysis (FIA) Program (Burrill et al., 2021) to understand how species' tolerance to resource limitation varies across temperate tree species, and to test and quantify the growth–survival trade-off across 68 dominant species. We further analysed a subset of these species to test whether this trade-off differed between forest stands in early and late-successional stages—here used as a proxy of disturbance regimes across forests.

2 | METHODS

2.1 | Study region and demographic data

We used data from the US FIA National Program (USDA Forest Service, research.fs.usda.gov/products/dataandtools/fia-datamart) of the US Department of Agriculture, Forest Service (Bechtold & Patterson, 2005; Burrill et al., 2021). This dataset is derived from the National Forest Inventory of the United States and includes 12,035 long-term plots of 0.067 ha in temperate forests distributed across the eastern US, totalling 215,339 stems belonging to 68 species (Figure 2; Tables S1 and S2). This extensive sampling enabled us to evaluate species within their realised distributions, encompassing most of their niche space. All stems with a diameter at breast height (dbh) ≥12.7 cm from plots with at least three censuses were included in our analyses. We used the last three censuses for each plot and excluded plots that had been harvested or had management records, as our aim was to study tree demography without direct human influence. Furthermore, the sampling period varied widely among plots (census 1: 2001–2008; census 2: 2006–2013; census 3: 2011–2018), ensuring our sample was unlikely to be biased by extreme weather events along the sampling period.

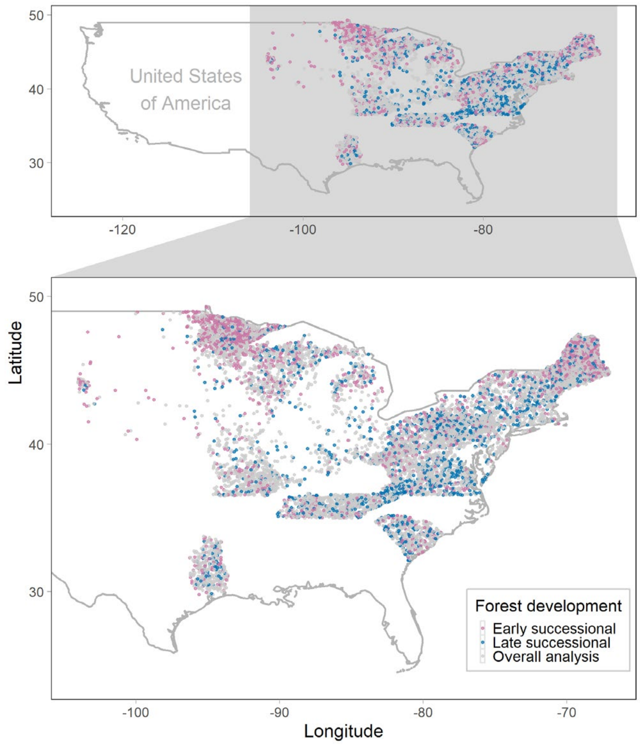

FIGURE 2 Distribution of forest sampling units across the eastern United States. Please note that all sampling units (i.e. grey, pink, and blue dots) were used to assess the mortality probability of zero growth and maximum growth for the overall test of growth–survival trade-off. However, only early-development plots (in pink) were used to assess the trade-offs in early successional stands, while only late-development plots (in blue) were used to assess the trade-offs in late-successional stands.

To obtain annualized absolute growth rate (cm year^{-1}) of individuals between two censuses, we calculated the difference in stem dbh from the two most recent censuses, divided by the number of years between censuses. We used the 95th quantile of the distribution of growth rate across all trees within a given species as an estimate of the species-level maximum growth rate. These metrics were used to estimate the interspecific relationship between the maximum growth in a resource-rich environment (95th quantile of growth rates) and the tolerance to resource limitations (mortality probability at zero growth estimated from a statistical model; see below).

2.2 | Prior disturbance assessment

To determine the successional stage of each plot, we compared the total basal area of each plot to the potential basal area of the forests within the environmental envelope in which the forest is located, following the procedure developed by Astigarraga et al. (2024) and available for usage. Such an initial approximation of successional stage assumes that the total basal area of a forest increases during stand development up to a threshold depending on the resource availability within its environmental envelope. Specific details and methods about the stand development assessment can be found in Astigarraga et al. (2024). Briefly, the environmental envelope clustered plots within similar climatic (mean annual temperature and annual precipitation) and edaphic (nitrogen availability) conditions, which resulted in maximum potential basal area per cluster. While mean annual temperature, mean precipitation, and nitrogen availability capture broad environmental gradients (Babst et al., 2013; Berendse & Aerts, 1987), local factors are also expected to affect individual growth and mortality. Each forest inventory plot was characterised regarding the stand successional value ranging from 0 to 1 by dividing the basal area of each plot by the maximum basal area of its corresponding cluster (i.e. 95th percentile of the basal area of the cluster to which this plot belonged). Plots with a basal area above the 95th percentile of their respective cluster were assigned a value of 1. While this measurement only approximates the successional stage of each stand, it acts as a good proxy of their structural state, as lower basal area is often related to sites typically younger or recovering from past disturbances. Early stand succession was defined by sites with low stand basal area values (i.e. below or equal to 0.25 of stand development) in the climate space in which the stand was located. Late stand succession was defined by sites with high stand basal area values (i.e. above or equal to 0.75 of stand development when considering all species together) in the climate space in which the stand was located.

2.3 | Data analyses

2.3.1 | Modelling species mortality and tolerance to resource-poor environments

We estimated species-specific annual mortality probability at zero growth using predictions from a Bayesian multilevel model of individual survival. In this model, the binary outcome of tree death from the period of censuses 2–3 was used as the response variable to estimate annualised mortality probability as a function of previous growth rate (i.e. from census 1 to census 2) and tree size (i.e. dbh at census 2) (Equation 1.1). The multilevel model structure allows each species to have its own baseline mortality probability (i.e. varying intercept) as well as mortality response (i.e. varying slopes) to both previous growth and dbh (Equations 1.2 and 1.3). It also estimates responses across species (the grand means or hyperparameters of the theoretical distributions of parameters from which species-level slopes are assumed to arise; Equations 1.7 to 1.9). Thus, we modelled the death status at the end of the second interval, *t* (from census 2 to census 3), for individuals *i* of species *s* in plots *k*, as follows:

Likelihood:

$$\text{mortality}_{i,s,k,\ t} \sim \text{Bernoulli}\left(1-\left(1-p_{i,t}\right)^{\text{years}_i}\right) \tag{1.1}$$

$$\text{Log}-\text{odd linear model:}$$

$$\text{logit}\left(p_{i,t}\right)=\alpha_{s[i]}+\beta_{\text{dbh}_{s[i]}}\,\text{dbh}_{i,t}+\beta_{\text{gr}_{s[i]}}\,\text{gr}_{i,t-1}+\gamma_k \tag{1.2}$$

$$\text{Population of species varying effects:}$$

$$\begin{pmatrix}\alpha_s\\ \beta_{\text{dbh}_s}\\ \beta_{\text{gr}_s}\end{pmatrix}\sim\text{MV Normal}\begin{pmatrix}\begin{pmatrix}\alpha_0\\ \beta_{\text{dbh}0}\\ \beta_{\text{gr}_0}\end{pmatrix},S\end{pmatrix}\text{ for } s=\text{species }1\text{–}68 \tag{1.3}$$

$$\text{Construct covariance matrix of species' parameters:}$$

$$S=\begin{pmatrix}\sigma_\alpha & 0 & 0\\ 0 & \sigma_{\beta_{\text{dbh}}} & 0\\ 0 & 0 & \sigma_{\beta_{\text{gr}}}\end{pmatrix}R\begin{pmatrix}\sigma_\alpha & 0 & 0\\ 0 & \sigma_{\beta_{\text{dbh}}} & 0\\ 0 & 0 & \sigma_{\beta_{\text{gr}}}\end{pmatrix} \tag{1.4}$$

$$\text{Correlation matrix among species' parameters:}$$

$$R=\begin{pmatrix}0 & \rho_{\beta_{\text{dbh}},\alpha} & \rho_{\beta_{\text{gr}},\alpha}\\ \rho_{\alpha,\beta_{\text{dbh}}} & 0 & \rho_{\beta_{\text{gr}},\beta_{\text{dbh}}}\\ \rho_{\alpha,\beta_{\text{gr}}} & \rho_{\beta_{\text{dbh}},\beta_{\text{gr}}} & 0\end{pmatrix} \tag{1.5}$$

$$\text{Prior for correlation matrix:}$$

$$R\sim\text{LKJ}(2) \tag{1.6}$$

$$\text{Prior for average intercept:}$$

$$\alpha_0\sim\text{Normal}(-1,2) \tag{1.7}$$

$$\text{Prior for average slope of dbh:}$$

$$\beta_{\text{dbh}_0}\sim\text{Normal}(0,1) \tag{1.8}$$

$$\text{Prior for average slope of previous growth:}$$

$$\beta_{\text{gr}_0}\sim\text{Normal}(0,1) \tag{1.9}$$

$$\text{Prior SD among species' parameters:}$$

$$\sigma_\alpha,\sigma_{\beta_{\text{dbh}}},\sigma_{\beta_{\text{gr}}}\sim\text{Half Normal}(0,1) \tag{1.10}$$

$$\text{Adaptive prior for plots' varying intercept:}$$

$$\gamma_k\sim\text{Normal}\left(0,\sigma_\gamma\right)\text{ for } k=\text{plots 1 to 12,035} \tag{1.11}$$

$$\text{Prior SD among intercepts per plot:}$$

$$\sigma_\gamma\sim\text{Half Normal}(0,1) \tag{1.12}$$

In this model, $\text{dbh}_{i,t}$, and $\text{gr}_{i,t-1}$ are the dbh of individual *i* measured at census 2 and the growth rate of that same individual at the end of the first interval, *t*−1 (i.e. from census 1 to 2). In addition, the multivariate normal distribution assumed for species-level intercepts and slopes (Equation 1.3) and associated covariance matrix *S* allow linking those parameters and allow them to share information, leading to partial pooling and parameters shrinkage, hence improving model fit while limiting risks of overfitting (McElreath, 2020). We also included the inventoried plot as a varying intercept (Equations 1.1 and 1.2) in the model to account for within-plot environmental heterogeneity. The likelihood (Equation 1.1) was built to make use of the fact that mortality probability is compounded over time, here allowing the use of the exponential effect of the time between the second and the third censuses to model annualised mortality probability. We applied a log-transformation to dbh and an exponential transformation to growth (gr^0.47, empirically tested for the data) to limit heteroscedasticity and skewness. This analysis was restricted to species with at least 200 stems alive and five dead stems at the third census (Russo et al., 2021), to limit risks of high uncertainties or unstable estimates from underrepresented species. Using the joint posterior distribution of the fitted mortality model, we used the Equations 1.2–1.5 and the species-level parameter posteriors to generate species-specific posterior probabilities of mortality at zero growth, at a dbh of 12.7 cm, in an 'average plot' (ignoring the plots' varying intercept γ). These species-level mortality probabilities at zero growth were used together with the maximum growth rates per species to fit the growth–survival trade-off.

2.3.2 | Testing of the growth–survival trade-off

To assess the growth–survival trade-off among species, we analysed the relationship between mortality probability at zero growth and maximum growth rates for all stems of the 68 studied species. To quantify the trade-off, we fitted a standardised major axis regression (SMA) between the species' annual mortality probability at zero growth and the species' maximum growth. We used SMA for the analyses because (1) it does not impose a predictive relationship of *X* on *Y*, and (2) it accounts for measurement error in both the *X* and *Y* axes. All the SMA regressions included the species clade (angiosperms or gymnosperms; 51 and 17 species, respectively) as a covariate, as comparing those clades is part of the questions of the study.

To examine the effect of disturbance on the strength of the trade-off, we divided the initial dataset into two for the early and the late-successional stage stands, respectively (early stage: 22 species and 14,866 stems; late stage: 33 species and 37,645 stems). We re-calculated maximum growth rates, re-ran the multilevel survival model, and re-estimated mortality probabilities at zero growth separately from each dataset. We then re-ran the SMA separately for early and late stand successional-based estimates to test the growth–survival trade-off within each stand successional stage. Finally, to assess differences in maximum growth and mortality probability at zero growth within species according to the stand succession, we subset the species occurring in both early and late stands (18 species) and compared their successional stage-specific growth and survival estimates by using paired *t*-tests.

The mortality model was created in STAN (Carpenter et al., 2017), run using the R package *rstan* (Stan Development Team, 2024) (commented R code is available in the Zenodo repository, see Bordin, 2025). Convergence and efficiency diagnostics of the Bayesian models consisted of visual assessment of chain mixing through trace plots and ensuring that all parameters' R-hats were smaller than 1.01. The posterior probability distribution of parameters or predictions of interest was summarised through the posterior's mean and the 90%-highest posterior density interval (90%-HPDI), that is, the narrowest uncertainty interval of parameter values compounding 90% of probability mass. All analyses were conducted in R version 4.2.2 (R Core Team, 2023), with the help of packages *tidybayes* (Kay & Mastny, 2024), *smatr* (Warton et al., 2018), and *tidyverse* (Wickham et al., 2019).

3 | RESULTS

The strategies to deal with low-resource availability, here represented by the annual mortality probability at zero growth, varied considerably across species, ranging from 0.01 [0.004–0.018] (posterior mean and 90%-HPDIs) for *Nyssa biflora* to 0.36 [0.26–0.46] for *Populus grandidentata* (Figure 3; Table S1; Figure S1). The fastest growing species was *Pinus taeda* [1.33 cm year^{-1}, varying from 1.29 to 1.38 cm year^{-1}], and the slowest growing species was *Ostrya virginiana* [0.3 cm year^{-1}, varying from 0.27 to 0.33 cm year^{-1}]. We find that even a slight increase in growth rates may reduce substantially the mortality probability within temperate species (Figure 3 [inset]). The mean annual mortality probability at zero growth across angiosperms is 0.09 [0.06–0.12], and gymnosperms is 0.07 [0.05–0.09]. The mean maximum growth rate is 0.7 cm year^{-1} [0.64–0.75 cm year^{-1}] and 0.64 cm year^{-1} [0.61–0.67 cm year^{-1}], for angiosperms and gymnosperms, respectively.

Species with higher growth rates showed a weak trend of having lower tolerance to resource limitation, as shown by a slight positive relationship between the maximum growth rate of a species and their probability of mortality at zero growth (SMA slope = 0.35, $R^2 = 0.02$, $p = 0.02$) (Figure 4a). However, when analysing angiosperms and gymnosperms separately, this relationship became even weaker than when evaluating all species together (Figure 4b,c).

The relative strength of the growth–survival trade-off among species depended on the stage of stand development. The trade-off between demographic strategies appeared as weak overall, but it was relatively stronger—though still low—across species from late-successional stands (SMA slope = 0.53, $R^2 = 0.17$, $p = 0.01$), compared to early successional stands where no clear evidence of a trade-off was found (SMA slope = 0.33, $R^2 = 0.02$, $p = 0.49$) (Figure 5a,c; Figures S2 and S3). There is one angiosperm species from late-successional stands (*Nyssa aquatica*) that showed both very low mortality (0.03 [0.01–0.06]) and fast maximum growth (1.05 cm year^{-1} [0.76–1.57 cm year^{-1}]) in late-successional stands, which was unexpected (Figure 1). As expected, if we remove this species and re-run

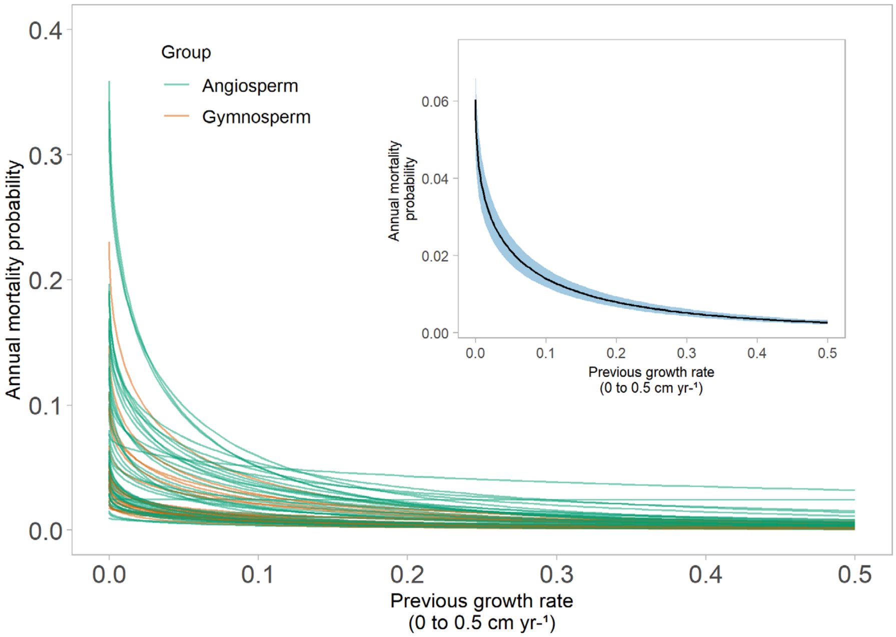

FIGURE 3 Estimated annual mortality probability as a function of previous growth rate for 68 North American temperate tree species. Each curve corresponds to the mean of the species-specific posterior prediction of mortality probability at 100 regularly spaced growth rate values between 0 and 0.5 cm year^{-1}, at a dbh of 12.7 cm. Each corresponding intercept represents species' mortality probability at zero growth, that is, the predicted posterior of interest to then assess the growth–survival trade-off. We considered that the lower the mortality at zero growth, the higher the tolerance to resource limitation (Russo et al., 2021). The green lines represent angiosperm species, orange lines represent gymnosperm species, and the inset plot shows the average species predicted curve (with 95% confidence intervals in blue).

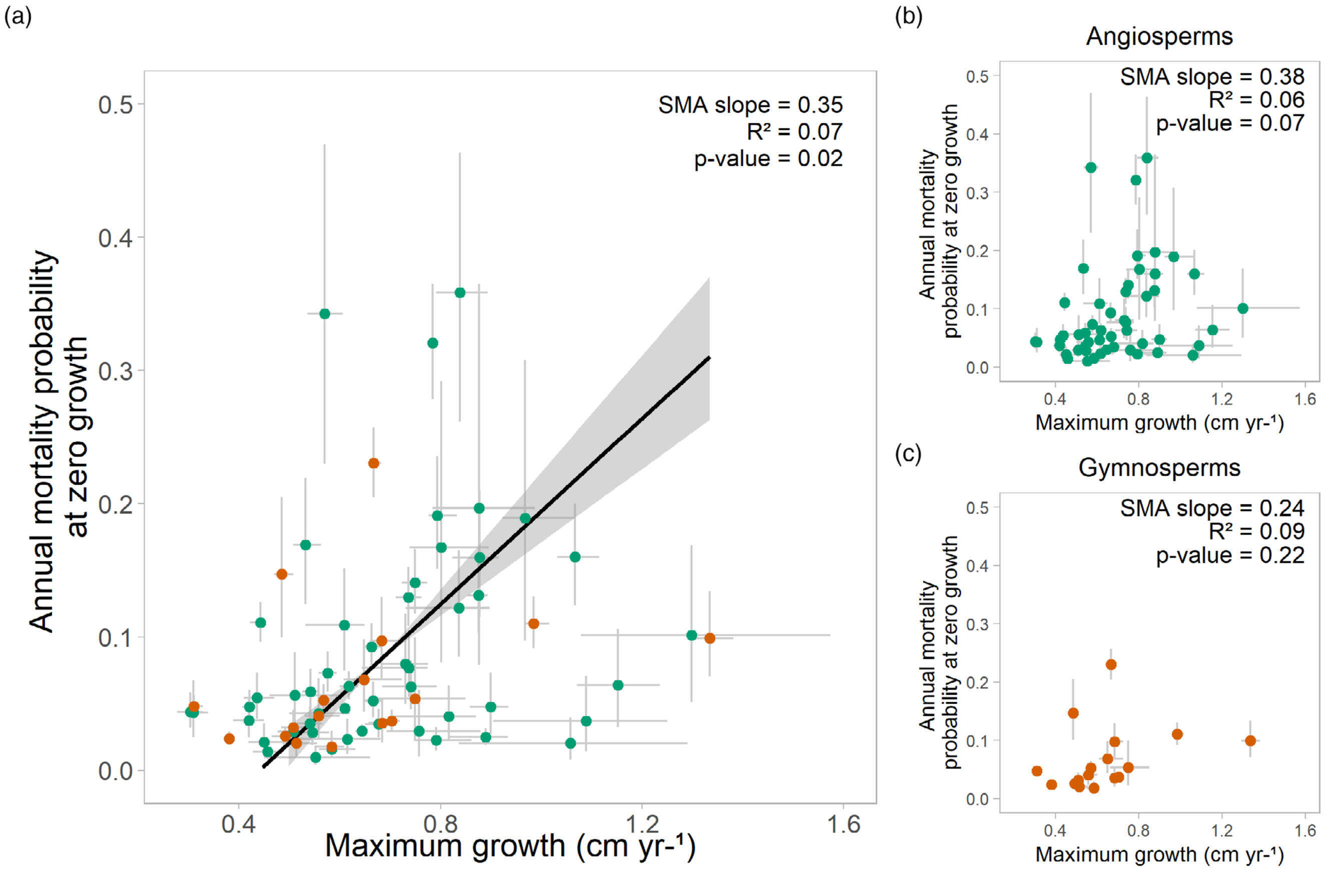

FIGURE 4 Growth and survival trade-off across temperate species. (a) Relationship between maximum growth (95th percentile of tree growth) and annual mortality probability at zero growth estimated from the mortality model for the 68 temperate species. The regression line shows the trade-off between investment in maximum growth under high resource and mortality probability under low resource. Analyses were repeated only for angiosperms, in green (b) and gymnosperms, in orange (c). For mortality probabilities, circle and vertical bars are the mean and 90% highest posterior density intervals of the species' predictions' posteriors. For growth rates, circle and horizontal lines are the 95% confidence intervals of the calculated 95th percentile of species growth rates.

the SMA on the remaining 32 species, the growth–survival trade-off across species at late-successional stands became stronger (SMA slope = 0.59, $R^2 = 0.28$, p-value = 0.001). Finally, on average, the same set of species tends to have higher maximum growth in stands under early succession, while mortality probability remains unaltered (Figure 5b,d).

4 | DISCUSSION

Here we performed an assessment of the trade-off between tolerance to resource limitation and maximum growth capacity under favourable conditions across 68 dominant temperate tree species in the eastern United States. We observed large variation in the tolerance of temperate tree species to resource limitation, with mean estimates of mortality probability at zero growth varying between 0.01 and 0.36, as well as a broad range of maximum growth, which varied from 0.3 to 1.33 cm year^{-1}. We further found either no evidence of a relationship between mortality in resource-limited environments and growth potential under resource-rich conditions, pointing to a weak demographic trade-off among temperate tree species. While no evidence of a trade-off was found in early successional stands, the trade-off was relatively stronger at late-successional stands. This implies that an increase in frequency and magnitude of forest disturbances over time (Sommerfeld et al., 2018) could potentially disrupt and weaken the growth–survival trade-off in temperate forests, with consequences for future forest dynamics, composition, and global carbon cycling.

The mortality probability across tree species increases steeply under zero growth rates, such as illustrated for the angiosperm *P. grandidentata*, a light-demanding species, whose annual mortality surged from 0.05 to 0.36 under previous growth of 0.1 and 0 cm year^{-1}, respectively. This is consistent with other studies from tropical and temperate forests showing that reduced vigour related to growth stress leads to a higher mortality probability (Chao et al., 2008; Kobe et al., 1995; Kobe & Coates, 1997). In addition, even a slight increase in growth rates is enough to substantially reduce the mortality probability for most species, highlighting the importance of previous growth and size as powerful predictors of individual tree mortality risk in temperate forests (Kobe et al., 1995;

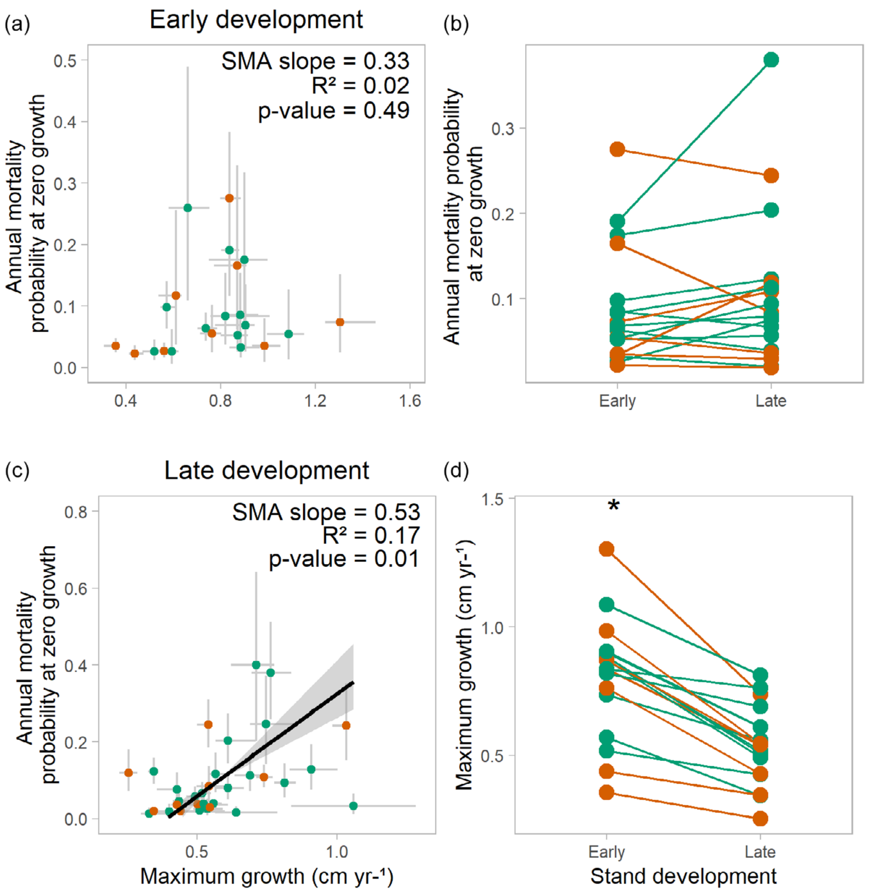

FIGURE 5 Growth and survival trade-offs across species in different stand successional stages. Relationship between maximum growth rate and annual mortality probability at zero growth for 55 temperate species in (a) early successional stands ($n=22$) and (c) late-successional stands ($n=33$). Comparison of the (b) mortality probability at zero growth and (d) maximum growth rate between the same set of species ($n=18$) in early and late-successional stands. The regression line in black shows the direction and magnitude of the relationship between maximum growth and annual mortality probability at zero growth, obtained from a standardised major axis regression. Differences between maximum growth rates across species in early and late stand development are highlighted with the asterisk (*). In all panels, angiosperms are shown in green and gymnosperms in orange. For mortality probabilities, circle and vertical bars are the mean and 90% highest posterior density intervals of the species' predictions' posteriors. For growth rates, circle and horizontal lines are the 95% confidence intervals of the calculated 95th percentile of species growth rates.

Russo et al., 2021). Consequently, management actions could leverage the relationship between increasing mortality probability and the absence of growth to develop more effective strategies for forest stand management, such as selective logging activities.

The weak trade-off between growth and survival across eastern US temperate tree species suggests that species with faster growth rates in resource-rich environments have slightly higher mortality probability in low-resource environments. In addition, this relationship is a little weaker ($r=0.27$) than the mean relationship reported for undisturbed tropical forests ($r=0.41$) (Russo et al., 2021). This may be explained, in part, by the fact that the forest plots analysed by Russo et al. (2021) included saplings, for which growth–survival trade-offs are often stronger (Kobe, 1999; Kobe et al., 1995; Kobe & Coates, 1997; Wright et al., 2010), underscoring that the growth–survival relationship may be size-dependent (Niinemets, 2006). Additionally, the differences in demographic trade-offs may be linked to the increasing growth rates observed in temperate species as a consequence of recent climatic changes, due to CO_2 enrichment in the atmosphere (Arco Molina et al., 2024; McMahon et al., 2010). This may lead some species that allocate resources to functions that favour faster growth to increase their risk of higher mortality rates in stressful environments under adverse conditions in the future. For instance, species that exhibit less dense wood may show increased growth rates but also a higher vulnerability to windthrows or extreme droughts (Bennett et al., 2015; Esquivel-Muelbert et al., 2020). Therefore, this strategy may make these species more vulnerable to environmental change, potentially reducing their chances of survival and recruitment in the future (Rose et al., 2009; Salguero-Gómez, 2017).

In addition, those species may also depend on other axes of life-history trade-offs. For instance, the stature-recruitment trade-off suggests that fast-growing and long-lived species may invest less in recruitment (Rüger et al., 2018; Stott et al., 2024). This stature-recruitment axis also predicts that slow-growing species with high-mortality rates could invest more in recruitment (Rüger et al., 2018, 2020), although they might be selected against, as this strategy is not successful in the long term and may reduce the population size (Russo et al., 2021; Figure 1). As expected, these patterns of slow growth and high mortality were rare across our set of temperate tree species. Additionally, our results show that some—though few—species exhibit both fast growth and low mortality (such as *N. aquatica*, see Section 3). If those species have also allocated fewer resources to recruitment, it could explain their high investments in both growth and survival (Rüger et al., 2020). This recruitment dimension of demography and life-history trade-offs, however, remains comparatively little understood and will require seedling data and thoroughly test potential trade-offs of allocation among growth, survival, and reproduction.

When we evaluated species from different evolutionary lineages—angiosperms and gymnosperms, we observed low within-group variability for annual mortality probabilities at zero growth and maximum growth rates, pointing to a weak demographic trade-off within these clades, for example, with species showing both fast growth and low-mortality probability. For instance, the angiosperm *Quercus nigra* showed a mean mortality probability at zero growth of 0.10 and maximum growth of 1.30 cm year^{-1}, and the gymnosperm *P. taeda* showed a mortality probability at zero growth of 0.10 and maximum growth of 1.33 cm year^{-1} (Table S1). This illustrates how mortality does not increase with higher growth rates for all species, potentially reflecting higher persistence of these species over time in the communities (Becker, 2000; Bond, 1989). Beyond this belonging to angiosperms or gymnosperms, disturbances also affected the estimated strength of the trade-off. Disturbance events alter forest structural complexity, which underlies the strength of demographic trade-offs by filtering out some strategies in disturbed ecosystems (Needham et al., 2022; Russo et al., 2021). Thus, species are not limited to the top-right part of the diagram as we expected (cf. Figure 1) but display a lower range of mortality probabilities and larger maximum growth rates, rather than a restricted population of functional space not allowing it to manifest, as observed by Russo et al. (2021). An implication of this result is that we may expect that the observed increasing disturbances associated with climate change (e.g. windstorms, insect outbreaks, heat waves, droughts) will affect demographic dynamics across temperate forests.

We found that the same species exhibited faster growth in stands under early succession than their conspecifics in stands under late succession. In addition, some species (for instance, from the genus *Populus*) showed an increase in mortality probability in late-developing stands (Figures S2 and S3). As these species are light-demanding pioneer species, this result is not unexpected. Differences in environmental conditions related to both natural and human-led disturbance events, such as light availability, can alter the species composition and stem density across species, which in turn affect their demographic rates (Carreño-Rocabado et al., 2012; Fang et al., 2024; Nemetschek et al., 2024). In addition, local processes such as conspecific negative density dependence may influence species' mortality rates (i.e. self-thinning) (Magee et al., 2024; Westoby, 1984), which can increase local resource availability and potentially result in higher growth rates, as well as reduced growth in larger trees due to higher maintenance costs (West, 2020). Moreover, our sample is limited to relatively large individuals (i.e. dbh ≥12.7 cm) and abundant species, which might not encompass the full range of potential demographic trade-offs among eastern US temperate species. This could explain some unexpected maximum growth and mortality probability values, such as those observed for *N. aquatica*. Despite this constraint, our results address an important gap in understanding the effects of disturbances on demographic trade-offs across temperate tree species. In addition, future demographic studies should make a greater effort to include smaller individuals from less abundant species in order to improve our understanding of how these trade-offs shape the structure and dynamics of forest ecosystems under different levels and types of disturbance.

Better understanding the mortality probability of temperate species under a scenario of very slow to no growth may provide valuable information to guide management actions (e.g. adaptive management stocking indexes (Chivhenge et al., 2024)), providing important insights into how forests might respond to global change. For instance, some evidence that growth rates are increasing across tree species could potentially arise as a consequence of climate change and CO_2 enrichment (Hubau et al., 2020; McMahon et al., 2010). While this fertilisation may increase the risk of higher tree mortality in tropical forests due to faster life cycles (Brienen et al., 2020; Esquivel-Muelbert et al., 2020), similar outcomes may not occur in temperate forests, where faster growth shows a weak trade-off with reduced survival. Furthermore, these changes may have even more pronounced effects in early developing stands, where species exhibit faster growth alongside high survival, as highlighted in our findings, which may impact the future of global forest dynamics and carbon cycling.

AUTHOR CONTRIBUTIONS

Kauane Maiara Bordin and Adriane Esquivel-Muelbert designed this study with inputs from David Bauman, Thomas A. M. Pugh, Oliver L. Phillips and Sandra C. Müller. Adriane Esquivel-Muelbert, Thomas A. M. Pugh, Daijun Liu, Julen Astigarraga, Lalasia Bialic-Murphy, Kauane Maiara Bordin, and Christopher W. Woodall compiled and standardised the data. Kauane Maiara Bordin and David Bauman developed and ran the statistical analyses, analysed results, and created the figures. Kauane Maiara Bordin wrote the manuscript with supervision from Adriane Esquivel-Muelbert, David Bauman, and Sandra C. Müller. All authors read, provided feedback, and approved the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The raw data is available at https://research.fs.usda.gov/products/dataandtools/fia-datamart. The processed data and R codes used to conduct data analyses are publicly available at Bordin (2025), https://doi.org/10.5281/zenodo.14402211.

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REFERENCES

Arco Molina, J. G., Saurer, M., Altmanova, N., Treydte, K., Dolezal, J., Song, J.-S., & Altman, J. (2024). Recent warming and increasing CO$_2$ stimulate growth of dominant trees under no water limitation in South Korea. *Tree Physiology*, *44*, tpae103.

Astigarraga, J., Esquivel-Muelbert, A., Ruiz-Benito, P., Rodríguez-Sánchez, F., Zavala, M. A., Vilà-Cabrera, A., Schelhaas, M. J., Kunstler, G., Woodall, C. W., Cienciala, E., Dahlgren, J., Govaere, L., König, L. A., Lehtonen, A., Talarczyk, A., Liu, D., & Pugh, T. A. M. (2024). Relative decline in density of northern hemisphere tree species in warm and arid regions of their climate niches. *Proceedings of the National Academy of Sciences*, *121*, e2314899121.

Babst, F., Poulter, B., Trouet, V., Tan, K., Neuwirth, B., Wilson, R., Carrer, M., Grabner, M., Tegel, W., Levanic, T., Panayotov, M., Urbinati, C., Bouriaud, O., Ciais, P., & Frank, D. (2013). Site- and species-specific responses of forest growth to climate across the European continent. *Global Ecology and Biogeography*, *22*, 706–717.

Bauman, D., Fortunel, C., Cernusak, L. A., Bentley, L. P., McMahon, S. M., Rifai, S. W., Aguirre-Gutiérrez, J., Oliveras, I., Bradford, M., Laurance, S. G. W., Delhaye, G., Hutchinson, M. F., Dempsey, R., McNellis, B. E., Santos-Andrade, P. E., Ninantay-Rivera, H. R., Chambi Paucar, J. R., Phillips, O. L., & Malhi, Y. (2022). Tropical tree growth sensitivity to climate is driven by species intrinsic growth rate and leaf traits. *Global Change Biology*, *28*, 1414–1432.

Bauman, D., Fortunel, C., Delhaye, G., Malhi, Y., Cernusak, L. A., Bentley, L. P., Rifai, S. W., Aguirre-Gutiérrez, J., Menor, I. O., Phillips, O. L., McNellis, B. E., Bradford, M., Laurance, S. G. W., Hutchinson, M. F., Dempsey, R., Santos-Andrade, P. E., Ninantay-Rivera, H. R., Chambi Paucar, J. R., & McMahon, S. M. (2022). Tropical tree mortality has increased with rising atmospheric water stress. *Nature*, *608*, 528–533.

Bechtold, W. A., & Patterson, P. L. (2005). *The enhanced forest inventory and analysis program—National sampling design and estimation procedures* (p. 85). USDA General Technical Report, SRS-80.

Becker, P. (2000). Competition in the regeneration niche between conifers and angiosperms: Bond's slow seedling hypothesis. *Functional Ecology*, *14*, 401–412.

Bennett, A. C., McDowell, N. G., Allen, C. D., & Anderson-Teixeira, K. J. (2015). Larger trees suffer most during drought in forests worldwide. *Nature Plants*, *1*, 1–5.

Berendse, F., & Aerts, R. (1987). Nitrogen-use-efficiency: A biologically meaningful definition? *Functional Ecology*, *1*, 293–296.

Bialic-Murphy, L., McElderry, R. M., Esquivel-Muelbert, A., van den Hoogen, J., Zuidema, P. A., Phillips, O. L., de Oliveira, E. A., Loayza, P. A., Alvarez-Davila, E., Alves, L. F., Maia, V. A., Vieira, S. A., Arantes da Silva, L. C., Araujo-Murakami, A., Arets, E., Astigarraga, J., Baccaro, F., Baker, T., Banki, O., … Crowther, T. W. (2024). The pace of life for forest trees. *Science*, *386*, 92–98.

Bond, W. J. (1989). The tortoise and the hare: Ecology of angiosperm dominance and gymnosperm persistence. *Biological Journal of the Linnean Society*, *36*, 227–249.

Bordin, K. (2025). kmbordin/UStemperate_demographic_trade-offs: v2. https://doi.org/10.5281/zenodo.16422978

Brienen, R. J. W., Caldwell, L., Duchesne, L., Voelker, S., Barichivich, J., Baliva, M., Ceccantini, G., Di Filippo, A., Helama, S., Locosselli, G. M., Lopez, L., Piovesan, G., Schöngart, J., Villalba, R., & Gloor, E. (2020). Forest carbon sink neutralized by pervasive growth-lifespan trade-offs. *Nature Communications*, *11*, 1–10.

Brodribb, T. J., Pittermann, J., & Coomes, D. A. (2012). Elegance versus speed: Examining the competition between conifer and angiosperm trees. *International Journal of Plant Sciences*, *173*, 673–694.

Burrill, E. A., DiTommaso, A. M., Turner, J. A., Pugh, S. A., Menlove, J., Christiansen, G., Perry, C. J., & Conkling, B. L. (2021). *The forest inventory and analysis database: Database description user guide for phase 2*. U.S. Department of Agriculture, Forest Service.

Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., & Riddell, A. (2017). Stan: A probabilistic programming language. *Journal of Statistical Software*, *76*, 1–32.

Carreño-Rocabado, G., Peña-Claros, M., Bongers, F., Alarcón, A., Licona, J.-C., & Poorter, L. (2012). Effects of disturbance intensity on species and functional diversity in a tropical forest. *Journal of Ecology*, *100*, 1453–1463.

Chao, K. J., Phillips, O. L., Gloor, E., Monteagudo, A., Torres-Lezama, A., & Martínez, R. V. (2008). Growth and wood density predict tree mortality in Amazon forests. *Journal of Ecology*, *96*, 281–292.

Chivhenge, E., Ray, D. G., Weiskittel, A. R., Woodall, C. W., & D'Amato, A. W. (2024). Evaluating the development and application of stand density index for the Management of Complex and Adaptive Forests. *Current Forestry Reports*, *10*, 133–152.

Coelho de Souza, F., Dexter, K. G., Phillips, O. L., Brienen, R. J., Chave, J., Galbraith, D. R., Lopez Gonzalez, G., Monteagudo Mendoza, A., Pennington, R. T., Poorter, L., Alexiades, M., Álvarez-Dávila, E., Andrade, A., Aragão, L. E., Araujo-Murakami, A., Arets, E. J., Aymard, C., Baraloto, C., Barroso, J. G., … Baker, T. R. (2016). Evolutionary heritage influences Amazon tree ecology. *Proceedings. Biological sciences*, *283*, 20161587.

Esquivel-Muelbert, A., Phillips, O. L., Brienen, R. J. W., Fauset, S., Sullivan, M. J. P., Baker, T. R., Chao, K. J., Feldpausch, T. R., Gloor, E., Higuchi, N., Houwing-Duistermaat, J., Lloyd, J., Liu, H., Malhi, Y., Marimon, B., Marimon Junior, B. H., Monteagudo-Mendoza, A., Poorter, L., Silveira, M., … Galbraith, D. (2020). Tree mode of death and mortality risk factors across Amazon forests. *Nature Communications*, *11*, 5515.

Fang, S., Ren, J., Cadotte, M. W., Yuan, Z., Hao, Z., Wang, X., Lin, F., & Fortunel, C. (2024). Disturbance history, neighborhood crowding and soil conditions jointly shape tree growth in temperate forests. *Oecologia*, *205*, 295–306.

Hubau, W., Lewis, S. L., Phillips, O. L., Affum-Baffoe, K., Beeckman, H., Cuní-Sanchez, A., Daniels, A. K., Ewango, C. E. N., Fauset, S., Mukinzi, J. M., Sheil, D., Sonké, B., Sullivan, M. J. P., Sunderland, T. C. H., Taedoumg, H., Thomas, S. C., White, L. J. T., Abernethy, K. A., Adu-Bredu, S., … Zemagho, L. (2020). Asynchronous carbon sink saturation in African and Amazonian tropical forests. *Nature*, *579*, 80–87.

Iida, Y., Poorter, L., Sterck, F., Kassim, A. R., Potts, M. D., Kubo, T., & Kohyama, T. S. (2014). Linking size-dependent growth and mortality with architectural traits across 145 co-occurring tropical tree species. *Ecology*, *95*, 353–363.

Kambach, S., Condit, R., Aguilar, S., Bruelheide, H., Bunyavejchewin, S., Chang-Yang, C. H., Chen, Y. Y., Chuyong, G., Davies, S. J., Ediriweera, S., Ewango, C. E. N., Fernando, E. S., Gunatilleke, N., Gunatilleke, S., Hubbell, S. P., Itoh, A., Kenfack, D., Kiratiprayoon, S., Lin, Y. C., … Rüger, N. (2022). Consistency of demographic trade-offs across 13 (sub)tropical forests. *Journal of Ecology*, *110*, 1485–1496.

Kay, M., & Mastny, T. (2024). *tidybayes: Tidy data and "Geoms" for Bayesian models*.

Kitajima, K. (1994). Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia*, *98*, 419–428.

Kitajima, K., & Poorter, L. (2008). Functional basis for resource niche partitioning by tropical trees. In W. Carson & S. Schnitzer (Eds.), *Tropical forest community ecology* (pp. 160–181). Wiley-Blackwell.

Kobe, R. K., Pacala, S. W., Silander, J. A., Jr., & Canham, C. D. (1995). Juvenile tree survivorship as a component of shade tolerance. *Ecological Applications*, *5*, 517–532.

Kobe, R. K. (1996). Intraspecific variation in sapling mortality and growth predicts geographic variation in Forest composition. *Ecological Monographs*, *66*, 181–201.

Kobe, R. K. (1999). Light gradient partitioning among tropical tree species through differential seedling mortality and growth. *Ecology*, *80*, 187–201.

Kobe, R. K., & Coates, K. D. (1997). Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. *Canadian Journal of Forest Research*, *27*, 227–236.

Laughlin, D. C., Delzon, S., Clearwater, M. J., Bellingham, P. J., McGlone, M. S., & Richardson, S. J. (2020). Climatic limits of temperate rainforest tree species are explained by xylem embolism resistance among angiosperms but not among conifers. *New Phytologist*, *226*, 727–740.

Lusk, C. H. (2011). Conifer–angiosperm interactions: Physiological ecology and life history. *Smithsonian Contributions to Botany*, *95*, 157–164.

Lusk, C. H., Wright, I., & Reich, P. B. (2003). Photosynthetic differences contribute to competitive advantage of evergreen angiosperm trees over evergreen conifers in productive habitats. *New Phytologist*, *160*, 329–336.

Magee, L. J., LaManna, J. A., Wolf, A. T., Howe, R. W., Lu, Y., Valle, D., Smith, D. J. B., Bagchi, R., Bauman, D., & Johnson, D. J. (2024). The unexpected influence of legacy conspecific density dependence. *Ecology Letters*, *27*, e14449.

McElreath, R. (2020). *Statistical rethinking: A Bayesian course with examples in R and STAN* (2nd ed.). CRC Press.

McMahon, S. M., Metcalf, C. J. E., & Woodall, C. W. (2011). High-dimensional coexistence of temperate tree species: Functional traits, demographic rates, life-history stages, and their physical context. *PLoS One*, *6*, e16253.

McMahon, S. M., Parker, G. G., & Miller, D. R. (2010). Evidence for a recent increase in forest growth. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 3611–3615.

Needham, J. F., Johnson, D. J., Anderson-Teixeira, K. J., Bourg, N., Bunyavejchewin, S., Butt, N., Cao, M., Cárdenas, D., Chang-Yang, C. H., Chen, Y. Y., Chuyong, G., Dattaraja, H. S., Davies, S. J., Duque, A., Ewango, C. E. N., Fernando, E. S., Fisher, R., Fletcher, C. D., Foster, R., … McMahon, S. M. (2022). Demographic composition, not demographic diversity, predicts biomass and turnover across temperate and tropical forests. *Global Change Biology*, *28*, 2895–2909.

Nemetschek, D., Derroire, G., Marcon, E., Aubry-Kientz, M., Auer, J., Badouard, V., Baraloto, C., Bauman, D., le Blaye, Q., Boisseaux, M., Bonal, D., Coste, S., Dardevet, E., Heuret, P., Hietz, P., Levionnois, S., Maréchaux, I., McMahon, S. M., Stahl, C., … Fortunel, C. (2024). Climate anomalies and neighbourhood crowding interact in shaping tree growth in old-growth and selectively logged tropical forests. *Journal of Ecology*, *112*, 590–612.

Niinemets, Ü. (2006). The controversy over traits conferring shade-tolerance in trees: Ontogenetic changes revisited. *Journal of Ecology*, *94*, 464–470.

Pacala, S. W., Canham, C. D., Silander, J. A., Jr., & Kobe, R. K. (1994). Sapling growth as a function of resources in a north temperate forest. *Canadian Journal of Forest Research*, *24*, 2172–2183.

Pan, Y., Birdsey, R. A., Phillips, O. L., Houghton, R. A., Fang, J., Kauppi, P. E., Keith, H., Kurz, W. A., Ito, A., Lewis, S. L., Nabuurs, G. J., Shvidenko, A., Hashimoto, S., Lerink, B., Schepaschenko, D., Castanho, A., & Murdiyarso, D. (2024). The enduring world forest carbon sink. *Nature*, *631*, 563–569.

Poorter, L., Wright, S. J., Paz, H., Ackerly, D., Condit, R., Ibarra-Manríquez, G., Ackerly, D. D., Harms, K. E., Licona, J. C., Martínez-Ramos, M., Mazer, S. J., Muller-Landau, H. C., Peña-Claros, M., Webb, C. O., & Wright, I. J. (2008). Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. *Ecology*, *89*, 1908–1920.

R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Reich, P. B. (2014). The world-wide 'fast–slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, *102*, 275–301.

Rose, K. E., Atkinson, R. L., Turnbull, L. A., & Rees, M. (2009). The costs and benefits of fast living. *Ecology Letters*, *12*, 1379–1384.

Rüger, N., Comita, L. S., Condit, R., Purves, D., Rosenbaum, B., Visser, M. D., Wright, S. J., & Wirth, C. (2018). Beyond the fast–slow continuum: Demographic dimensions structuring a tropical tree community. *Ecology Letters*, *21*, 1075–1084.

Rüger, N., Condit, R., Dent, D. H., DeWalt, S. J., Hubbell, S. P., Lichstein, J. W., Lopez, O. R., Wirth, C., & Farrior, C. E. (2020). Demographic trade-offs predict tropical forest dynamics. *Science*, *368*, 165–168.

Russo, S. E., Brown, P., Tan, S., & Davies, S. J. (2008). Interspecific demographic trade-offs and soil-related habitat associations of tree species along resource gradients. *Journal of Ecology*, *96*, 192–203.

Russo, S. E., Davies, S. J., King, D. A., & Tan, S. (2005). Soil-related performance variation and distributions of tree species in a Bornean rain forest. *Journal of Ecology*, *93*, 879–889.

Russo, S. E., McMahon, S. M., Detto, M., Ledder, G., Wright, S. J., Condit, R. S., Davies, S. J., Ashton, P. S., Bunyavejchewin, S., Chang-Yang, C. H., Ediriweera, S., Ewango, C. E. N., Fletcher, C., Foster, R. B., Gunatilleke, C. V. S., Gunatilleke, I. A. U. N., Hart, T., Hsieh, C. F., Hubbell, S. P., … Zimmerman, J. (2021). The interspecific growth–mortality trade-off is not a general framework for tropical forest community structure. *Nature Ecology & Evolution*, *5*, 174–183.

Salguero-Gómez, R. (2017). Applications of the fast–slow continuum and reproductive strategy framework of plant life histories. *New Phytologist*, *213*, 1618–1624.

Salguero-Gómez, R., Jones, O. R., Blomberg, S. P., Hodgson, D. J., Zuidema, P. A., & Kroon, H. D. (2015). Fast–slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proceedings of the National Academy of Sciences of the United States of America*, *114*, E9753.

Silvertown, J. (2004). Plant coexistence and the niche. *Trends in Ecology & Evolution*, *19*, 605–611.

Sommerfeld, A., Senf, C., Buma, B., D'Amato, A. W., Després, T., Díaz-Hormazábal, I., Fraver, S., Frelich, L. E., Gutiérrez, Á. G., Hart, S. J., Harvey, B. J., He, H. S., Hlásny, T., Holz, A., Kitzberger, T., Kulakowski, D., Lindenmayer, D., Mori, A. S., Müller, J., … Seidl, R. (2018). Patterns and drivers of recent disturbances across the temperate forest biome. *Nature Communications*, *9*, 4355.

Spicer, M. E., Mellor, H., & Carson, W. P. (2020). Seeing beyond the trees: A comparison of tropical and temperate plant growth forms and their vertical distribution. *Ecology*, *101*, e02974.

Stephenson, N. L., & Van Mantgem, P. J. (2005). Forest turnover rates follow global and regional patterns of productivity. *Ecology Letters*, *8*, 524–531.

Stott, I., Salguero-Gómez, R., Jones, O. R., Ezard, T. H. G., Gamelon, M., Lachish, S., Lebreton, J. D., Simmonds, E. G., Gaillard, J. M., & Hodgson, D. J. (2024). Life histories are not just fast or slow. *Trends in Ecology & Evolution*, *39*, 830–840.

Stan Development Team. (2024). *RStan: The R interface to Stan*. R package version 2.32.6. Retrieved October 27, 2024, from mc-stan.org.

Warton, D., Duursma, R., & Taskinen, D. F. (2018). *smatr: (standardised) Major axis estimation and testing routines*.

West, P. W. (2020). Do increasing respiratory costs explain the decline with age of forest growth rate? *Journal of Forest Research*, *31*, 693–712.

Westoby, M. (1984). The self-thinning rule. In A. MacFadyen & E. D. Ford (Eds.), *Advances in ecological research* (pp. 167–225). Academic Press.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., McGowan, L., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K., Ooms, J., Robinson, D., Seidel, D., … Yutani, H. (2019). Welcome to the tidyverse. *Journal of Open Source Software*, *4*(43), 1686.

Wijenayake, P. R., Masaki, T., Shibata, M., & Kubota, Y. (2023). Does life form affect tree species assembly? A demographic study across the life history of a temperate forest in Japan. *Ecosphere*, *14*, e4579.

Wright, S. J., Kitajima, K., Kraft, N. J. B., Reich, P. B., Wright, I. J., Bunker, D. E., Condit, R., Dalling, J. W., Davies, S. J., Díaz, S., Engelbrecht, B. M. J., Harms, K. E., Hubbell, S. P., Marks, C. O., Ruiz-Jaen, M. C., Salvador, C. M., & Zanne, A. E. (2010). Functional traits and the growth-mortality trade-off in tropical trees. *Ecology*, *91*, 3664–3674.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Species information from the complete dataset used to test for the growth–survival trade-off across temperate tree species.

Figure S1. Graphical result of the species-level mortality probability and 95% confidence interval for all species within the dataset.

Figure S2. Graphical result of the species-level mortality probability and 95% confidence interval for species from early-development stands.

Figure S3. Graphical result of the species-level mortality probability and 95% confidence interval for species from late-development stands.

Table S2. Species information, growth, and mortality probability estimates used to test for the growth–survival trade-off across temperate tree species. Please see the readme spreadsheet for additional information.

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