Species- and community-level demographic responses of saplings to drought during tropical secondary succession

Hao Ran Lai[a,b,*] Alexander W. Cheesman[c,d] Jefferson S. Hall[e]

Martijn Slot[e] Michiel van Breugel[e,f,*]

Affiliations:

[a] Centre for Integrative Ecology, School of Biological Sciences, University of Canterbury, Christchurch 8140, Aotearoa New Zealand

[b] Bioprotection Aotearoa, Centre of Research Excellence, Aotearoa New Zealand

[c] College of Life and Environmental Sciences, University of Exeter, Exeter EX4 4QE, UK

[d] College of Science & Engineering and Centre for Tropical Environmental and Sustainability Science, James Cook University, Cairns, QLD, Australia

[e] ForestGEO, Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancón, Republic of Panama

[f] Department of Geography, National University of Singapore, Singapore, Singapore

[*]Correspondence: Hao Ran Lai, hrlai.ecology@gmail.com; Michiel van Breugel, mvbreugel@gmail.com

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Abstract

Naturally regenerating secondary vegetation dominates the tropical forest landscapes, showing a remarkable capacity to sequester carbon, but such a role is threatened by increasing drought predicted with climate change. To understand how secondary forest species and communities respond to drought, we leverage a long-term chronosequence of tropical successional forests from Central Panama that coincided with the 2015/16 El Niño extreme drought event to analyse the diameter growth and mortality of 113,505 saplings and 60 species under water stress. As expected, drought negatively impacted most species in either diameter growth, mortality, or both. However, we additionally found that neighbourhood basal area ameliorated or exacerbated the effect of drought on diameter growth of some species. These species-level demographic responses aggregated to a community-level shift from the dominance of drought-susceptible saplings to more drought-tolerant saplings during stand development. Our study highlights that sapling communities in older secondary forests were less sensitive to drought: they suffered less growth reduction possibly due to denser canopies that mitigated evapotranspiration, and they also experienced lower mortality due to a higher relative abundance of drought-resistant species. Saplings in young secondary forests were overall more susceptible to drought, but their responses were also highly variable, suggesting a potential in understanding why some young secondary forest communities are more drought-tolerant, a knowledge that can be leveraged to restore resilient forests necessary to withstand a future of increased drought frequency and severity under a changing climate.

Keywords: El Niño Southern Oscillation, tree diameter growth, mortality, population dynamics, rainfall, resilience, vital rates

Introduction

Around 10% of the world's forests are naturally regenerating early secondary forests less than 30 years old (Heinrich et al., 2023). These regenerating forests show remarkable potential for carbon sequestration, biodiversity maintenance and the provision of ecosystem services

(Girardin et al., 2021; Hall et al., 2022; Poorter et al., 2021). In parallel, planted forests continue to increase in area (FAO, 2020), with several ambitious reforestation initiatives aiming to slow or even reverse the losses in ecosystem functions (Brancalion et al., 2019; Busch et al., 2019). However, these carbon mitigation strategies depend critically on the ability of planted and naturally-regenerating secondary forests to serve as net carbon sinks, a role that is increasingly undermined by climate change (Corlett, 2016; Reichstein et al., 2013; Xu et al., 2019). Drought, for example, is one of the major drivers of increasing tree mortality in tropical forests (Bauman et al., 2022; Browne et al., 2021; McDowell et al., 2018) and in many tropical regions, longer and more severe drought events are expected to become more frequent in the future (Allen et al., 2010; McDowell et al., 2022). We therefore urgently need to understand how tree species and forest communities respond to climate change in order to predict whether current reforestation efforts will meet climate targets. To this end, long-term forest monitoring programmes that coincide with and field experiments that test unusually strong or long periods of drought provide valuable data on the effects of climate change on tree performances and forest carbon dynamics (Anderson-Teixeira et al., 2015; Bonal et al., 2016), which in turn can improve dynamic vegetation models and facilitate data-driven policies on forest restoration (Neeff & Piazza, 2020).

Although there has been increasing evidence of drought-induced mortality and reduced growth in tropical forest trees (Allen et al., 2010; Corlett, 2016; Zuidema et al., 2022), we still know little about the relative importance and interaction of drought with other determinants of individual tree performance (McDowell et al., 2018). The effects of drought on tree growth and survival may depend on an individual tree's size and canopy position, as the microclimate experienced by understory trees is very different to that of canopy trees (O. L. Phillips et al., 2010). Canopy or emergent trees experience less light competition but are more directly exposed to the sun and wind, thereby are subjected to greater evapotranspiration rates and heat stress (Bennett et al., 2015; Itoh et al., 2012; Vinod et al., 2023). However, larger trees may mitigate drought impacts by accessing deeper groundwater (Chitra-Tarak et al., 2021), or increased sapwood water storage (N. G. Phillips et al., 2003). On the other hand, saplings generally have smaller root systems and hence are more vulnerable to drying topsoils when exposed (Bretfeld et al., 2018), while for understory species, it may be more costly to shed leaves as a drought avoidance strategy (Williams et al., 1989). However, shading mitigates heat stress and maintains air humidity, thus slowing the drying of topsoils and evapotranspiration rates. Complex outcomes may also arise when drought increases mortality or leaf loss in canopy trees, thereby reducing light competition in favor of the understory trees. In highly diverse tropical secondary forests, these interactions can be especially meaningful as coexisting tree species with different successional statuses and life history strategies naturally occur under contrasting canopy conditions (Blondeel et al., 2024; Bretfeld et al., 2018; Sinacore et al., 2020).

In tropical moist secondary forests, the differential responses of tree species to drought events due to variation in life history strategies and successional contexts may affect successional trajectories, likely leading to compositional shifts at the community level towards more drought-tolerant, deciduous canopy trees and losses of evergreen species (Bartlett et al., 2019; Fauset et al., 2012). This, in turn, may modify the canopy cover and microclimate in the understory during dry periods, altering the relative roles of light and water limitation on species performances over the course of succession. An increasing frequency or length of periods with water deficits may thus alter the plant–environment feedback dynamics that drive succession (Breugel et al., 2024) by shifting forest compositions towards species with ecophysiological adaptations to drought stress (Aguirre-Gutiérrez et al., 2020; Bartlett et al., 2019; Batllori et al., 2020). Understanding how physiological drought responses at the tree level scale up to influence successional feedbacks at the system level is an enormous task, but one way to begin is to quantify the tree performance of multiple species across both rainfall and successional gradients, and then aggregate the interspecific variations to a net response at the community level. This requires longitudinal studies that coincide with periods of drought along a chronosequence of diverse secondary forest establishment, with sufficient replication to include spatial variability across the landscape.

Here we leverage one of the few studies in the Tropics that has such a capacity: the long-term chronosequence data from Agua Salud, Central Panama (Breugel et al., 2013), wherein secondary forest plots of 1–32 years post-abandonment were intensively monitored from 2009 to 2017. This period included the 2015/16 El Niño event with comparably extreme drought conditions as the 1982/83 and 1997/98 events (Santoso et al., 2017), which previously caused long-lasting impacts on tree mortality and growth in tropical forests worldwide (Condit et al., 2017; O. L. Phillips et al., 2010). Recent studies on seedlings in the region have revealed widespread increased mortality during the 2015/16 El Niño (Browne et al., 2021), warranting a deeper investigation into larger size classes and across successional stages. In contrast to old-growth studies, our large secondary forest dataset provides a broader community gradient required to untangle both abiotic (drought) and biotic (neighbourhood competition) effects on tree growth and mortality. Our forests also contain high replication of a large number of species, some of which have high potentials for active restoration once we quantify their demographic responses to drought and competition (Marshall et al., 2022). Our study sought to address three main questions:

1. How does drought affect growth and mortality of saplings across tree species?
2. Are species' growth and mortality responses to drought moderated by local neighbourhood competition?
3. How do these species-level demographic responses to drought scale up to the community level?

Material and Methods

Site description and tree census data

Our data originated from the Agua Salud Project's long-term Secondary Forest Dynamics Study in the central Panama Canal watershed (9° 13′ N, 79° 47′ W, 330 m asl). Annual precipitation averages 2,700 mm per year, with a dry season from mid-December to early May (Ogden et al., 2013). The area is characterised by an undulating topography, with short, steep slopes intersected by a dense network of narrow streams (Hassler et al., 2011). Soils are silty clays to clays, strongly weathered, well drained, phosphorus-poor and nitrogen-limited (Batterman et al., 2013; Breugel et al., 2019). The landscape is dominated by active and abandoned cattle pastures and naturally regenerating secondary forest of different ages (Breugel et al., 2013).

Fifty-two sloped sites were chosen within secondary forest regenerating on abandoned pastures across an area of 15 km^2. In 2009, two plots of 50 m $\times$ 20 m were established at each site; one plot near the bottom of the slope and another near the top of the slope. The initial age of the secondary forests in our sites varied from one to 32 years, with sites well distributed along this age range. From 2009 to 2017, each plot was monitored annually, with the exception of 2013 (thus excluded from analyses), resulting in six annual census intervals for analyses. During 2015, the strong El Niño event resulted in only 1,800 mm of precipitation, with 2014–16 being the driest contiguous period since the first instrumental weather data in 1925 on the nearby Barro Colorado Island [BCI; Bretfeld et al. (2018)]. During plot censuses, trees and shrubs with a diameter-at-breast-height (DBH) $\geq$ 5 cm were recorded in each plot while all trees and shrubs 1–4.9 cm were recorded in one-half of each plot (Breugel et al., 2013). For this study we only use stems in the 1–4.9 cm DBH range (hereafter referred to as "saplings") and selected species with at least 100 observed individuals. This resulted in a focal data set of 113,505 trees from 60 species spanning 28 families, present in 98 plots across 49 sites.

Measures of drought and neighbourhood basal area

To examine the influence of water availability on tree growth and mortality, we defined the magnitude of drought as the deviation in precipitation from the long-term average. Since our study location did not have a long-term local rainfall record, we approximated it with the long-term precipitation data from BCI (1971–2020), 6-km from Agua Salud. Censuses were not repeated each year on the same dates and consequently census intervals (i.e., number of days between a given census and the previous census) varied per plot and year. Per plot and census interval, we calculated the mean of the daily rainfall values measured over the actual census interval (O) and the mean of the long-term averages of the daily rainfall values measured on the same calendar days over the 1971-2020 period (L). Subsequently, we calculated the normalised deviation in precipitation across the census interval as $(L-O)/L$. As such, positive and negative values denote drier and wetter census intervals, respectively.

To examine the influence of local competition or microclimate on tree growth and mortality, neighbourhood basal area (m^2 ha^{-1}) was calculated for each individual focal tree by summing the basal area of all trees and shrubs within the same 5 m × 5 m quadrant as the focal tree and in the eight adjacent quadrants. We used two candidate measures of neighbourhood basal area for each focal tree: the first measure summed the basal area of all neighbouring trees, whereas the second only included trees that were larger in DBH than the focal tree. Because the two neighbourhood basal area measures were autocorrelated, we compared and selected the one with a better ability to extrapolate out-of-sample to a validation dataset (explained below).

Statistical analyses

Diameter growth model

For tree i of species j observed in plot p nested within site q and census year t, we modelled its annual diameter growth, G (cm yr^{-1}), as a function of its DBH, D (cm), and then allowed the size–growth relationship to be influenced by drought R, neighbourhood density A, and their interactions as follows:

$$G_{ijpqt} \sim \text{Student-}t\left(2,\ \mu_{ijpqt},\ \sigma^2\right) \tag{1}$$

$$\log \mu_{ijpqt} = \log a_j + b_j \log D_{ijpqt} - c_j D_{ijpqt} + \alpha_j A_{ipqt} + \beta_j R_{pqt} + \gamma_j A_{ipqt} R_{pqt} + \varepsilon_p + \varepsilon_q\,, \tag{2}$$

where we assume a Student-*t* generative process for diameter growth with mean μ, standard deviation σ, and two degrees-of-freedom (Lai et al., 2024). A Student-*t* distribution allows us to (1) include both negative and positive growth values while (2) accounting for extreme growth values that would violate the kurtosis assumption of a Gaussian model. A Student-*t* model is also a form of robust regression because it reduces the influence of extreme observations on parameter estimation while avoiding the arbitrary removal of “outliers”.

We let the mean of log diameter growth, $\log \mu_{ijpqt}$, be dependent on tree diameter in the component $\log a_j + b_j \log D_{ijpqt} - c_j D_{ijpqt}$ following Zeide (1993), where $b_j \log D$ is the growth expansion component, $\log a_j$ is the instantaneous log diameter growth rate at small diameters, and $-c_j D$ is growth decline with increasing diameter associated with maintenance costs. When the species-specific growth parameters, b_j and c_j, are constrained to be positive, the Zeide (1993) diameter–growth equation produces a hump-shaped growth curve that is commonly observed in trees. The log-link constraints μ to positive diameter increments, but with a large-enough standard deviation σ will accommodate non-positive growth values. As such, σ accounts for both measurement errors and real biological processes that result in negative diameter growth. Next, we included the main effects of neighbourhood basal area, drought, and their interaction effects on each species as α_j, β_j, and γ_j respectively. In a pilot analysis, we attempted to include the interactions between diameter, drought and neighbourhood basal area to explore if tree size affects growth responses (and mortality below), but did not proceed with this formulation due to difficulties in model convergence and a lack of interpretability (see elaboration in Appendix S1). This also motivated us to restrict the analyses to a smaller range of diameters, i.e., “saplings” in the size class of 1–4.9 cm. That being said, the inclusion of interaction between drought and neighbourhood basal area (of larger trees; see *Variable Selection* below) in our model would still capture the differential microclimate experienced by smaller and larger focal trees. Lastly, we included random plot and site intercepts, ε_p and ε_q respectively, to account for spatial non-independence in diameter growth.

Mortality model

Individual trees’ annual mortality rate was also modelled as a function of diameter, neighbourhood basal area, drought, and the interaction between the latter two in a Bernoulli regression with logit link:

$$M_{ijpqt} \sim \text{Bernoulli}\left(1 - (1 - p_{ijpqt})^{\tau}\right) \tag{3}$$

$$\text{logit}\left(p_{ijpqt}\right) = \log v_j - u_j \log D_{ijpqt} + w_j D_{ijpqt} + \delta_j A_{ipqt} + \zeta_j R_{pqt} + \theta_j A_{ipqt} R_{pqt} + e_p + e_q\,, \tag{4}$$

where p is the annual probability of mortality (yr^{-1}) and τ is the census interval in years. We followed previous studies (Iida et al., 2014; Kohyama et al., 2015; Rüger et al., 2011) and modelled the mortality–diameter relationship as a U-shaped curve given by $\log v_j - u_j \log D + w_j D$, where u_j and w_j were constrained to be positive. Similar to the diameter-growth model, we included the main effects of neighbourhood density, drought, and their interaction effects on each species' mortality as δ_j, ζ_j, and θ_j respectively, as well as random plot and site intercepts, e_p and e_q respectively, to account for spatial non-independence in mortality.

Model fitting and variable selection

To select either all-tree or larger-tree neighbourhood basal area in the final model, we compared their prediction accuracies when extrapolating out-of-sample to validation data. To this end, we randomly split 70% of the data into a training set and the rest into a testing set, and then calculated the root mean square error (RMSE) as a measure of prediction accuracy. Data partitioning was stratified by species, such that each species retained 70% of observations in the training set. We fitted a model using all-tree and then another using larger-tree neighbourhood basal area onto the training set, and then validated them against the testing set and calculated RMSE. Models were fit via maximum *a posteriori* estimation using the `opt` function in the `greta` v0.4.2 package (Golding, 2019) in `R` v4.2.0. Prior to model fitting, D was scaled to unit standard deviation (SD), while A and R were centered to zero mean and scaled to unit SD to assist convergence. The model including larger-tree neighbourhood basal area had the lowest RMSE, so we refit the model with larger-tree neighbourhood basal area to the entire dataset for a more accurate parameter estimation. We checked model assumptions using the Dunn–Smyth residuals (Dunn & Smyth, 1996) and quantile–quantile (QQ) plot (Fig. S2).

Communicating interaction effects using average predictive comparisons

To examine the effects of neighbourhood basal area and drought on tree diameter growth and mortality, we could look at their coefficients. However, the net effects of neighbourhood basal area and drought on growth and mortality may not be additive if their interaction effects are non-zero. To account for interactions, an option is to condition the main effect of one predictor on a fixed value of another interacting predictor. Following common practice, we could calculate the net effect of drought on diameter growth when the interacting predictor, neighbourhood basal area, is at its mean -1 SD, at the mean, and at mean $+1$ SD (Fig. S1). However, this implicitly assumes that any individual of a species is equally likely to be observed under the three arbitrary and counterfactual growth conditions. In reality, different tree species tend to be found under different combinations of neighbourhood basal area and drought due to life-history constraints. A more realistic way of examining the predictor effects is therefore to calculate the expected change in diameter growth and mortality using an average predictive comparison (Gelman & Pardoe, 2007).

Average predictive comparison (APC) is the weighted effect of a predictor when averaged (or integrated) over its joint distribution with other interacting predictors, *sensu lato*. We provide a brief explanation here and more illustrated detail in Appendix S2 and Fig. S1. For instance, the APC of drought reflects its *typical* effect under the neighbourhood basal areas that a species tends to be found. If a particular species is typically found under dense neighbourhood, then its drought APC will reflect the effect of drought interacting with higher-than-average neighbourhood basal area, and vice versa (Fig. S1). In the special case when (1) a species is typically found under an average neighbourhood or (2) the interaction term is zero, the APC of drought will be identical as the main coefficient of drought. In other words, when the APC of a predictor strongly deviates from its main coefficient, then it implies non-negligible interactions with other predictors and that the species' typical growing condition is far from average (Lai et al., 2024). In the *Results* section, we plotted each species' main drought coefficient against its APC as an intuitive illustration of which species experienced more or less severe drought impacts due to the typical neighbourhood basal area in its surroundings. The most important advantage of APC is that it is based on the empirical, and thus more probable and realistic, distribution of predictor values without the need to specify any counterfactual scenarios.

Community-level drought responses

To further understand how the species-level growth and mortality responses to drought aggregate to the community level, we calculated the community-weighted mean drought responses in growth, CWM^G, and mortality, CWM^M, as:

$$\begin{aligned}
\text{CWM}_{pt}^{G} &= \sum_{j} p_{jpt}\left(\beta_j + \gamma_j A_{pt}\right) && (5)\\
&= \sum_{j}\left(p_{jpt}\beta_j + p_{jpt}\gamma_j A_{pt}\right) && (6)\\
\text{CWM}_{pt}^{M} &= \sum_{j} p_{jpt}\left(\zeta_j + \theta_j A_{pt}\right) && (7)\\
&= \sum_{j}\left(p_{jpt}\zeta_j + p_{jpt}\theta_j A_{pt}\right)\ , && (8)
\end{aligned}$$

where p_{jpt} is the relative abundance of species j in plot p at census t. As in the CWM commonly calculated for functional traits, we treated species' density-dependent drought responses in diameter growth, $\beta_j + \gamma_j A_{pt}$ (i.e., the factor of drought, R, in Equation 2), and in mortality, $\zeta_j + \theta_j A_{pt}$ (i.e., the factor of drought, R, in Equation 4), as response "traits". Note that these CWMs implicitly assume intraspecific "trait" variations because the species-mean "trait" (β_j or ζ_j) could vary by populations that were subjected to different local neighbourhood basal areas (A_{pt}). This was also why we opted to calculate community-level drought responses using the actual coefficients here, instead of using APC as above for species-level responses, because at the community level each demographic response already does account for the local neighbourhood basal area.

We further rearranged Equation 5 as Equation 6 to decompose the CWM of total drought effect ($\beta_j + \gamma_j A_{pt}$) on diameter growth into the CWM of main drought effect (β_j) and the CWM of drought–neighbourhood interaction (γ_j). The purpose of this was to examine how much of the successional shift in CWM was due to the shift in species' relative abundance alone (i.e., p_{jpt} in the first term of Equation 6) and how much else was due to both relative abundance and local neighbourhood basal area (i.e., $p_{jpt}A_{pt}$ in the second term of Equation 8). The same decomposition was also performed on the CWM of total drought effect on mortality by rearranging Equation 7 as Equation 8. We then plotted the CWMs of total drought effect, main drought effect, and drought–neighbourhood interaction against total stand basal area to examine how community responses to drought changed during secondary succession.

Results

Overall, our models explained 18.9 and 13.5% of variation in diameter growth and mortality rate, respectively. Among the 60 species, this varied from 0.6 to 50.5% for diameter growth and 0.1 to 14.3% for mortality rates. Species also varied in size-dependent diameter growth and mortality rate (Fig. 1). Under the respective average condition under which each species was found, their maximum diameter growths ranged between 0.01 and 0.77 cm yr^{-1}, while minimum mortality rates ranged between 0.02 and 56.8% yr^{-1}.

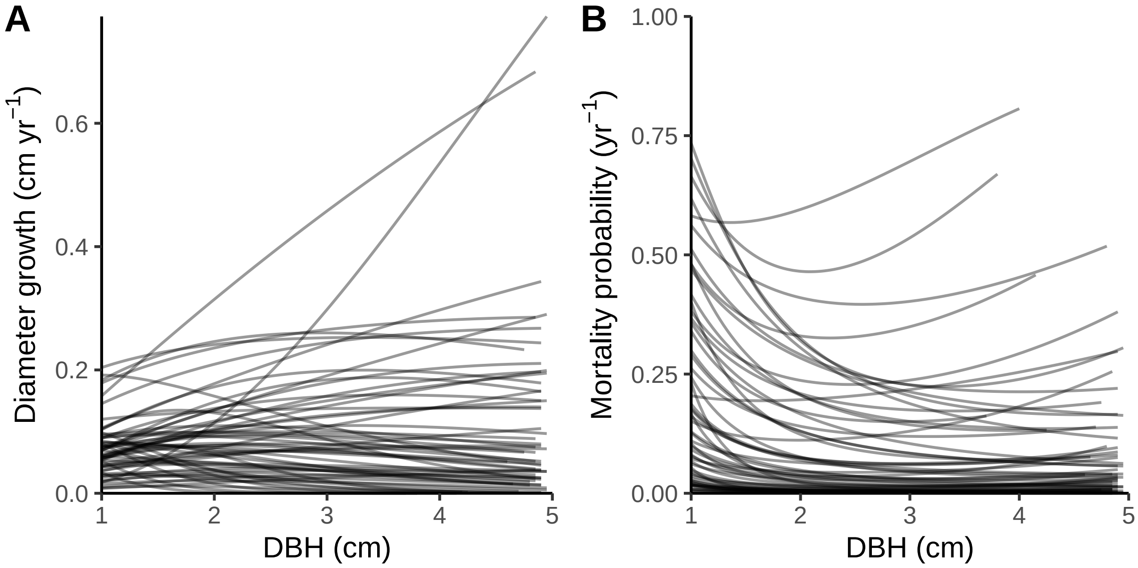

Figure 1: (A) Predicted diameter growth and (B) mortality rate across diameter for each of 60 tree species growing in our naturally regenerating Neotropical secondary forests. These predictions are conditioned on average neighbourhood basal area and drought values that each species experienced, and limited to the observed diameter range of each species.

The effects of drought on tree species performance were predominantly negative with some positive effects, with these being dependent on neighborhood basal area. Average predictive comparisons (APCs) show that the diameter growth of 25 species was negatively affected by drought, while the diameter growth of 11 species was positively affected by drought under their typical neighborhood basal area conditions (along Y-axis of Fig. 2A). Species' responses to drought in terms of mortality seemed independent of their responses in diameter growth (Fig. S3A). Under their typical neighbourhood basal area conditions, APCs show 28 species increased in mortality and none decreased in mortality with drought (credible intervals overlapped with zero along the Y-axis in Fig. 2B). We then compared species-specific APCs to their main drought coefficients to understand which species experienced stronger- or weaker-than-expected drought effects due to interactions with neighbourhood basal area. We found neighbourhood basal area typically ameliorated the effects of drought on the diameter growth of nine species (Fig. 2A), but exacerbated the effects of droughts on the diameter growth of eight species (Fig. 2A) and on the mortality of one species (Fig. 2B).

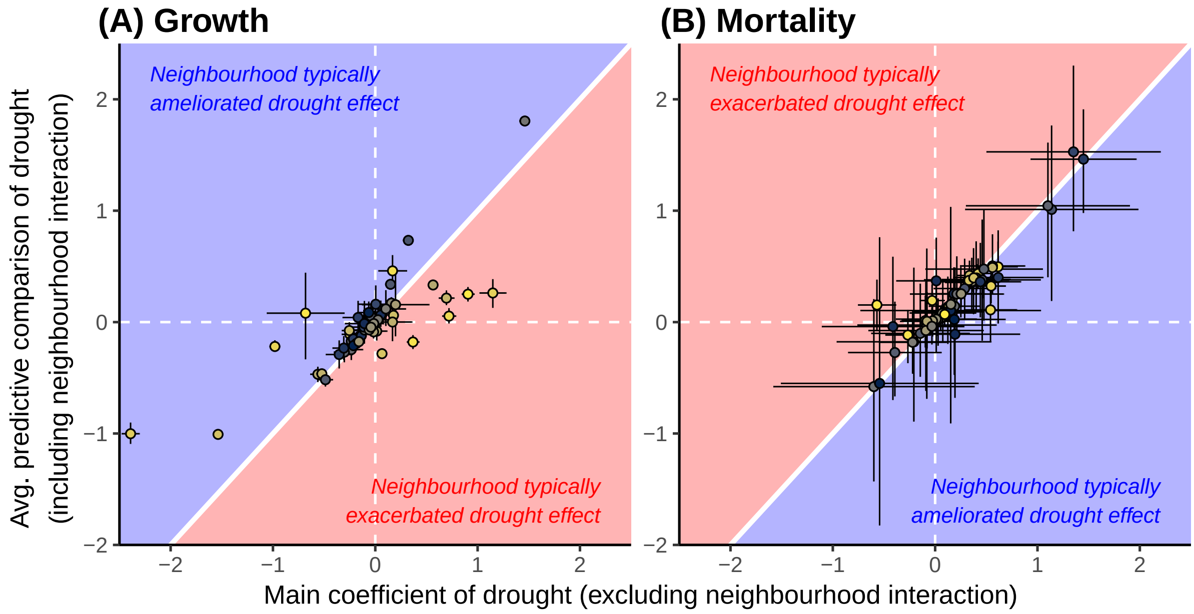

Figure 2: Average predictive comparisons of drought (integrated across empirical neighbourhood basal areas) plotted against the main effect of drought (neighbourhood basal area set at zero) on the log diameter growth (A) or mortality (B) of each species. Symbols close to the 1:1 white diagonal line are species with weak-to-zero interactions of drought × neighbourhood basal area; species in the blue shaded region achieved greater diameter growth or lower mortality when subjected to drought due to favorable neighbourhood basal area conditions, whereas species in the red shaded region performed worse under drought due to unfavorable neighbourhood basal area conditions. Filled dots and error bars are median estimates and 95% credible intervals. Colour of dots denote the successional status of each species (yellow = more associated with younger secondary forests; blue = more associated with older secondary forests).

We also compared demographic effects of drought and neighbourhood basal area to assess their relative importance. In terms of diameter growth, APC showed that the effects of neighbourhood basal area were greater in magnitude and were more consistently negative than drought (Fig. S3B). On the other hand, the effects of neighbourhood basal area on mortality showed mixed, weaker effects similar to those of drought (Fig. S3C). In contrast to drought, the effects of neighbourhood basal area were more related to the focal species' successional status: species that are associated with younger secondary forests tend to be more negatively impacted by neighbourhood basal area (i.e., slower diameter growths and higher mortality rates).

At the community level, community-weighted mean (CWM) growth response to total drought effect (main effect + context-dependent interaction with neighbourhood basal area) was overall negative and appeared mildly U-shaped in younger secondary forests with 0–10 m^2 ha^{-1} of total stand basal area, before increasing towards zero past 20 m^2 ha^{-1} of total stand basal area (Fig. 3A). Furthermore, CWM mortality response to total drought effect showed a hump-shaped trend during succession, reaching a maximum around 5 m^2 ha^{-1} of total stand basal area, and then decreased with succession (Fig. 3E). By partitioning the total drought effect into main drought effect and the interaction with neighbourhood basal area, we found that for diameter growth the increasingly negative main drought effect was opposed by the increasing positive interaction with neighbourhood basal area (Fig. 3B vs. 3C, see also Fig. 3D). In contrast, for mortality most of the total drought effect was directly contributed by the main drought effect (Fig. 3F), whereas the drought–neighbourhood interaction stayed close to zero (Fig. 3G, see also Fig. 3H).

Discussions

In this study, we quantified the demographic responses of the 60 most common tree species in a secondary forest chronosequence in central Panama to drought, after accounting for successional changes in neighbourhood basal area. Integrated across each species' empirical neighbourhoods, drought negatively impacted most species by either reducing diameter growth, increasing mortality, or both. The aggregated species-level responses was non-linear and indicate a community-level shift from the dominance of drought-susceptible saplings towards slightly more drought-tolerant saplings during secondary stand development. In

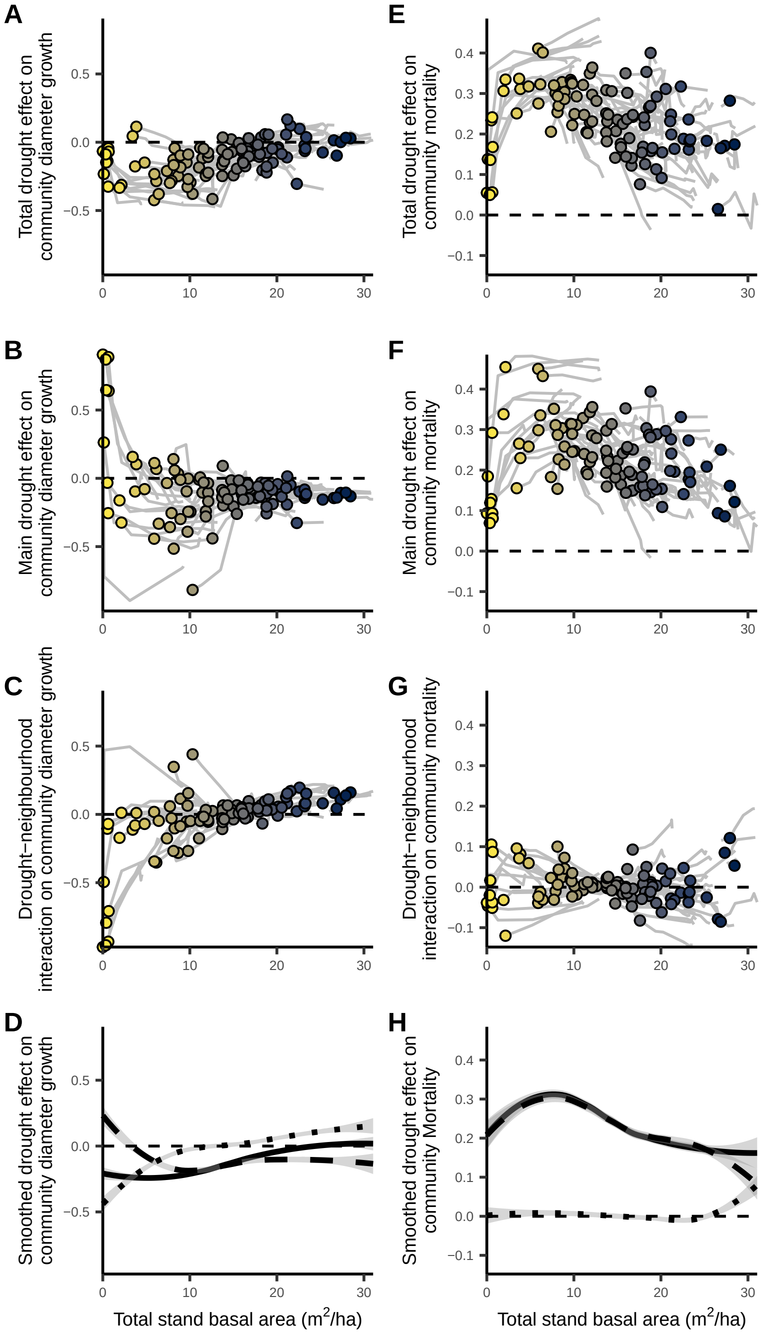

Figure 3: Community-level responses to drought during secondary succession, calculated as the community-weighted mean of species-level density-dependent drought responses in terms of log diameter growth (**left panels**) and log-odds of mortality (**right panels**). Circles are plots in their first census (coloured by total stand basal area), while grey lines are the annual successional trajectories of each plot. Horizontal dashed lines separate positive and negative community-level drought responses. Panel **A** (or **E**) is the total community growth (or mortality) response to drought, which is the sum of the main drought effect in Panel **B** (or **F**) and its interaction with neighbourhood density in Panel **C** (or **G**). The bottom panels **D** and **H** are smoothed splines to help visualise the total (solid lines), main (dashed lines) and interaction (dotted lines) effect components. Note that "community" here consists of a maximum of the 60 focal species and sapling individuals.

addition, the results suggest that the denser canopy later in succession had a facilitative effect, likely by reducing the evapotranspiration stress in the understory, that moderated drought stress of saplings later in succession.

Successional patterns at community level

High interspecific variations in demographic response to drought gave rise to emergent, nonlinear community-level shifts that varied over the course of succession. The drought-induced performance stress was highest around and decreased after reaching a total stand basal area of 10 m^2 ha^{-1}, which roughly corresponds to seven years of post-abandonment succession when self-thinning initiates and less than 20% of irradiance reaches the understory (Breugel et al., 2013). The results suggest that, as the forest continued to grow, the negative main drought effect on sapling growth (Fig. 3B) was alleviated by the increase in neighbourhood basal area over time (Fig. 3C), eventually leading to an absence of a community-level total drought effect later in succession (Fig. 3A). Combined, the results imply that successional communities were drought sensitive (based on main drought effect), but also that as succession proceeded, the negative drought impact on sapling growth was increasingly ameliorated by denser canopies, which created a buffered microclimate that retained soil water during drought and humidity in the understory (Lebrija-Trejos et al., 2011; Schwartz et al., 2022; Teixeira et al., 2020; Vinod et al., 2023). This successional process is also supported by Bretfeld et al. (2018), who found that soil water content was significantly higher in older than in younger forests in our study area during the 2015/16 El Niño event.

Variation in the sapling-community responses to lower rainfall seemed to be higher among the earliest successional communities (0–10 m^2 ha^{-1}), especially in terms of diameter growth (lighter points, Fig. 3). Each of these younger forests were generally dominated by a few early successional species, but the identity of the dominant pioneer species varied across plots likely due to dispersal limitations (Breugel et al., 2013, 2019; Craven et al., 2018). Variation in the community drought response among the earliest successional forests may thus reflect this high among-plot variation in the identity of the dominant species and their particular drought responses. The group of pioneers in our study site (see Supporting Information S14 in Lai et al., 2021) indeed include species that displayed very positive growth response to drought (e.g., *Conostegia speciosa* and *Vernonanthura patens*) as well as those that responded very negatively (e.g., *Banara guianensis* and *Vismia macrophylla*; Table S1). Community drought responses varied less among the later successional communities (darker points, Fig. 3), which could be due to a lower variation in drought response among the later successional species. However, our species-level results suggest that late-successional species were as varied in drought responses as the pioneers (Fig. 2). A more plausible reason is that older secondary forests were more diverse and less dominated by any species, therefore the contrasting species-specific responses have likely averaged out.

Together, the successional trajectory towards a more neutral and less variable sapling-community response to drought suggests that, as these secondary forests grow older, they become more resilient against climate change to some degree. As discussed above, such a resilience is likely to be partly the consequence of facilitative effects of an increasing canopy closure and shade provisioning that reduced evapotranspiration stress in the understory (Amissah et al., 2015; Holmgren et al., 2012; Vinod et al., 2023). However, our results suggest that the processes driving the trajectories in species and community growth and mortality may differ; while neighbourhood basal area seemed to have mediated the response of the sapling species and community to drought in terms of growth, we did not find a similar interaction in terms of mortality.

Despite a lack of amelioration from neighbourhood basal area, sapling mortality in late-successional communities showed signs of decrease; this suggests a greater resilience to drought among the sapling communities in older secondary forests. However, there is a caveat for interpreting such results from longitudinal data. The forests that were 18 years or older at the start of our study in 2009 would have gone through the previous 1997/98 drought bottleneck, which may have thinned out the drought-sensitive species and filtered for more drought-resilient species in these now-older forests. If that had been the case, the lower sensitivity of older successional forests to the stronger drought events over the course of this study would be a legacy of past drought events (Batllori et al. (2020), but see Anderegg et al. (2013)). This potential survivorship bias suggests that forests that survived previous droughts may be able to tolerate recurring drought events. Extreme drought events are predicted to become more frequent in many tropical regions (McDowell et al., 2022; Xu et al., 2019); to understand how recurring drought events will affect long-term forest dynamics, we need continuous monitoring over periods that cover multiple drought events.

Species strategies and life-history tradeoffs

Our findings provide evidence that early-successional communities consist of species with a diverse range of sapling growth responses to drought in terms of diameter growth and mortality, similar to Bretfeld et al. (2018)'s findings at the stand level. Furthermore, species' overall demographic responses to drought did not seem to be associated with their overall responses to neighbourhood competition (for light; Figs S3B and S3C). This contradicts the postulated trade-off between shade tolerance and drought tolerance (Kubiske et al., 1996; Sack, 2004; Smith & Huston, 1989) and the related hydraulic efficiency–safety trade-off (Tyree et al., 1994). The basis of these hypotheses is that adaptations that allow plants to tolerate drought stress, such as stomatal control and narrower, shorter vessels with thicker walls, come at the cost of lower hydraulic and photosynthetic efficiencies, and hence lower maximum growth rates (Anderegg et al., 2016; Choat et al., 2012). However, recent studies show that adaptation to shade and water stress can be complex (Puglielli et al., 2021). One study did find that while interspecific trait variation among tropical tree species corresponded to the hydraulic efficiency–safety trade-off, it resulted in coordinated drought- and shade-tolerance rather than the hypothesised trade-off (Markesteijn et al., 2011). Other studies found drought- and shade-tolerance to be largely independent from one another because drought and shade tolerance depend on different trait and physiological adaptations (Amissah et al., 2015; Holmgren et al., 2012; Markesteijn & Poorter, 2009; Sack, 2004). To maintain high photosynthetic rates during favourable periods, species may circumvent trade-offs between drought and shade tolerance by avoiding, rather than tolerating, droughts with alternative strategies such as deciduous leaf shedding, deep root system or internal water storage (Choat et al., 2005; Markesteijn et al., 2011; Paz, 2003).

Data on the demographic response of high numbers of cooccurring tropical tree species to drought in interaction with neighbourhood competition are still rare, especially in a successional context. Yet, this kind of data is crucial for identifying functional traits that coordinate interspecific growth strategies against drought (Anderegg et al., 2016; Radford Smith et al., 2024), which in turn could strengthen our inferences from chronosequence studies and forest inventories that are much more common in the Tropics (e.g., Poorter et al., 2021). Our results highlight that there is an important caveat to consider when linking demographic responses to traits. In successional tropical forests, the saplings of pioneer and late-successional tree species are typically associated with more open and closed conditions, respectively. Such a non-independence between species identity and habitat affiliation presents a conundrum: does interspecific variation in drought responses reflect variation in intrinsic traits, the extrinsic environment, or both? (O'Brien et al., 2017). Here we controlled for neighbourhood basal area and showed that the growth responses of several species to drought were not only species-specific but also influenced by site-specific successional contexts (Fig. 2A), whereas mortality responses were mostly species-specific (Fig. 2B).

The decoupled growth and mortality responses to drought across species makes interpreting the results in terms of species strategies challenging. Growth response may be more indicative of a species' *resilience* by maintaining growth during or recovering growth after a drought (DeSoto et al., 2020), whereas mortality response may be more indicative of *resistance* by surviving through a drought. Following a drought event, resilient species (e.g., *Inga* spp.) in our study may opportunistically grow in diameter when they are competitively released from less tolerant neighbours, but another resistant species (e.g., *Swartzia simplex*) known to have low growth rates may opt for a more conservative strategy to survive through drought. This further highlights that response traits conferring stress resilience may be very different to those that conferring stress resistance. We also showed that growth response to drought was more density dependent than mortality response, possibly because diameter growth under stress is more co-limited by resource competition whereas mortality is often more stochastic.

Implications and future directions

We have demonstrated the context dependence of the effects of interannual rainfall variability on the recovery of tropical forests facing increasing frequency and intensity of drought events. Going forward, we need to focus on the accumulating effects of repeated drought events on the population and community dynamics of trees in tropical secondary forests (DeSoto et al., 2020; O. L. Phillips et al., 2010), and potential dependencies on species interactions and other combined stressors. For example, direct effects of water deficit may be exacerbated by indirect effects, such as increased susceptibility to pests and pathogens (Batllori et al., 2020; Hossain et al., 2018; Tng et al., 2022). Interspecific variation in the drought responses of coexisting species (e.g., Peltier et al., 2016) implies that droughts will lead to shifts in competitive hierarchies (Batllori et al., 2020; Cavin et al., 2013; Lai et al., 2024), as species that are more strongly affected by a drought event may in a subsequent wetter period experience increased competition from species that were less affected by the drought. Similarly, species that are more drought-tolerant may benefit from reduced growth and enhanced mortality of their drought-sensitive competitors. Future studies need to better understand how the combined direct and indirect effects of shifts in competitive hierarchies will contributing to long-term (legacy) effects of droughts on secondary forests recovery (Anderegg et al., 2015; Batllori et al., 2020; Brodribb et al., 2020; Müller & Bahn, 2022).

The lack of correlation between growth and mortality responses to drought cautions against a simplistic use of growth response to infer drought tolerance. Drought-related mortality risks may lag more than the immediate growth response if trees have reduced capacities to recover pre-drought growth rates (DeSoto et al., 2020). While critical hydraulic failure may be the main cause of drought-induced mortality (Rowland et al., 2015), trees could prolong their short-term survivals with internal carbon reserves (O'Brien et al., 2014), but resource reallocation away from maintenance and defense may still eventually lead to post-drought tree mortality (Doughty et al., 2015). The potential lag in mortality response also prevented us from interpreting the decoupled growth and mortality responses to drought as a demographic compensation mechanism that may buffer populations from crashing (Doak & Morris, 2010);

even if insensitive mortality to drought may rescue a population from declined growth, this may only be a short-term process that does not help forest communities to persist in the long run. Future studies should evaluate the fate of tropical forests following drought events using multiple aspects of demography to achieve a more concrete understanding of species' and communities' responses to climate change (e.g., Matlaga et al., 2024; Sheth & Angert, 2018).

Predicting how increasing drought frequencies and intensities will influence successional dynamics and the potential to restore diverse tropical forest ecosystems through assisted or natural regeneration is an enormous challenge. One indispensable approach to accumulate the data needed for predictive modelling is the longitudinal study (Anderson-Teixeira et al., 2015; Baker et al., 2021; Lindenmayer et al., 2022). When combined with a chronosequence setup, the response of tree species and communities to drought events can be assessed along broader forest-age gradients. Ideally, such studies need to be maintained long enough to cover multiple periods of drought, include sufficient replication to include spatial variability across the landscape, and be of large-enough scale to obtain data for the modelling of demographic rates for more than a handful of species (Breugel et al., 2024; O. L. Phillips et al., 2010). Yet, despite their obvious importance, long-term secondary forest studies remain exceedingly rare. Currently, we are aware of fewer than 20 active long-term studies on secondary forest dynamics across the Tropics (van Breugel, unpublished data), most of which are substantially smaller than the current field study and vary in terms of land-use history, sampling protocol, spatial extent and age range (e.g., see supplementary information in Schorn et al., 2024).

While field studies such as the one presented here are mostly linked to the modelling of community and ecosystem-level dynamics, we argue that they have a role to play in active forest restoration. A lack of species-level data on demographic rates and how these vary in response to different environmental conditions constitute an important barrier to the successful implementation of active forest restoration initiatives in most tropical landscapes (Baker et al., 2021). Field experiment is an approach to address this data gap but is very expensive to set up (Gasparinetti et al., 2022; Sinacore et al., 2023) and generally include a limited number of species (Breugel et al., 2011; Mayoral et al., 2017). Our study demonstrates how data from long-term secondary forest studies can be leveraged to quantify species- and community-level demographic responses to drought across a range of neighbourhood conditions and then guide species selection in reforestation projects (e.g., Charles et al., 2018; Holl et al., 2020; Marshall et al., 2022; Prieto-Rodao et al., 2023). However, these demographic models are data-demanding; we were able to statistically model only 60 relatively common species out of hundreds of tree species found across our study area (Breugel et al., 2013). Moreover, financial limitations will always restrict the scope of long-term ecological monitoring programs (Caughlan & Oakley, 2001). One way to improve species coverage is to identify a set of functional traits that explain species' demographic responses to drought, and then extrapolate the predictions to new or data-sparse species (Umaña et al., 2023).

Conclusions

The capacity of naturally regenerating secondary forests to maintain primary productivity and act as carbon sinks is vulnerable to the drying climate as predicted for many tropical regions (Corlett, 2016). At the time of writing, we are in the midst of another El Niño event that has brought droughts to many tropical biodiversity hotspots, such as the Amazon basin (Jiang et al., 2024) and our study region. While extreme weather events are becoming increasingly frequent, our understanding of the response of forest ecosystems to these events remains mixed (Bennett et al., 2023; Wigneron et al., 2020) and requires more data. We show that the species dynamics of sapling communities in early successional forests were more strongly affected by annual variation in rainfall, especially during the first few years of succession. As the secondary forests grew older, the effect of drought on sapling communities weakened, possibly due to the ameliorative effect of denser canopies on evapotranspiration and/or a higher relative abundance of drought-tolerant species. Saplings in young secondary forests were on average more susceptible to drought, but their species- and community-level responses were also highly variable, suggesting that some young secondary forest communities are more tolerant to drought than others, pointing to possibilities for steering the forest landscape towards this type of more resilient communities in restoration. To extrapolate our findings to other species and sites, however, we would need better mechanistic links between drought stress response and hydraulic failure.

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Supplementary Information for

Species- and community-level demographic responses of saplings to drought during tropical secondary succession

1 Challenges in fitting size × environment interactions

In the main text, we described that we opted not to include the interactions between diameter, drought and neighbourhood basal area due to difficulties in model convergence and a lack of interpretability. Here we elaborate the latter reason using the diameter-growth model as an example. The same reasoning also applies to the mortality model because the two models shared a similar structure.

With the nonlinear[1] Zeide diameter-growth model

$$G = D^b \exp(a - cD),$$

where diameter growth rate G is a function of diameter D and the three growth parameters a, b, and c, we may wish to include the effect of an external factor X (in our case, drought) on G so that

$$G = D^b \exp(a' - cD + \beta X),$$

where β is the effect of covariate X. We note that $a = a' + \beta X$, meaning the main effect of X can be interpreted as moderating the overall diameter growth of a species.

We attempted to test if a tree's diameter mediates its growth response to X. For example, larger trees may respond to drought differently than smaller trees. We could test this hypothesis by including a statistical interaction term between D and X, such that:

$$G = D^b \exp(a' - c'D + \beta' X + \gamma DX),$$

where γ could be the diameter–drought interaction effect.

A model with such an interaction term could be rewritten in two ways. First as,

$$G = D^b \exp(a' - c'D + (\beta' + \gamma D)X),$$

where $\beta = \beta' + \gamma D$ so we emphasise how diameter moderate growth response to X, or equivalently:

$$G = D^b \exp(a' - (c' - \gamma X)D + \beta' X),$$

where $c = c' - \gamma X$ so we emphasise how X moderate the size-decline component of the Zeide growth model.

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[1] In the main text, we presented the right-hand-side in logarithmic form that appears linear due to the log-link in our generalised linear mixed-effect model.

However, to produce a humped diameter-growth curve, both growth parameters b and c need to be positive-constrained. This means that $c = c' - \gamma X > 0$ needs to be satisfied during statistical inference. Yet, it is non-trivial to ensure $c' - \gamma X > 0$ by constraining c' and γ separately, because there is a dependency on X (i.e., even if we enforce postive constrains on c' and γ, some values of X could still violate the $c' - \gamma X > 0$ requirement). Another way to think about this is that we need to satisfy $\frac{c'}{\gamma} > X$, which is difficult when most statistical software only allow one to constrain parameters separately.

Another solution that we considered is to let $c = e^{c' - \gamma X}$, such that c is always positive in the formulation:

$$G = D^b \exp(a' - e^{c' - \gamma X} D + \beta' X).$$

However, this formulation is hard to interpret biologically, even though it ensures the humped diameter-growth curve. It is awkward because X now acts on G in two different scales: X moderates a linearly, but moderates c in logarithmically. More crucially, this produces unintended nonlinearity in the effect of X on G even when diameter is fixed to a particular value. We can examine this undesired property by examining how growth rate varies with respect to X in the partial derivative:

$$\frac{\partial \log G}{\partial X} = D\gamma e^{c' - \gamma X} + \beta'.$$

We used $\log G$ because the partial derivative looks cleaner and it is easy to back-transform to G. To further simplify let's fix D and let $\theta = De^{c'}$ so that we can focus on the parameters that correspond to X, i.e., β' and γ:

$$\frac{\partial \log G}{\partial X} = \theta\gamma e^{-\gamma X} + \beta'.$$

From the partial derivative (i.e., slope of $\log G$ against X), we see that the effect of X on $\log G$ is nonlinear, as well as depending on X itself. Although a covariate such as drought could certainly affect log growth nonlinearly, we view the nonlinearity introduced by this model formulation as an unintended side effect in an attempt to constrain c, rather than a nonlinearity that is well-informed by biological mechanisms. This undesired property vanishes in the original formulation $G = D^b \exp(a' - (c' - \gamma X)D + \beta' X)$ because the partial derivative is simply $\frac{\partial \log G}{\partial X} = D\gamma + \beta$ (note the lack of dependency on X), but we cannot ensure that $c = c' - \gamma X > 0$ will be satisfied without more sophisticated parameter constrains. Given our limited mathematical abilities, we opted to simplify the model without the interactions between diameter, drought and neighbourhood basal area.

2 Average predictive comparisons

In Fig. S1 below, we provide a graphical explanation on the value of performing average predictive comparisons (Gelman & Pardoe, 2007) to summarise the typical effect of a predictor when there is another interacting covariate. The X- and Y-axes are the two predictors of tree diameter growth and mortality (Z-axis) in our analyses. The slopes (black solid lines) represent the interaction effect between drought and neighbourhood basal area on the response. In this example, the effect of drought changes from negative to positive with increasing neighbourhood basal area.

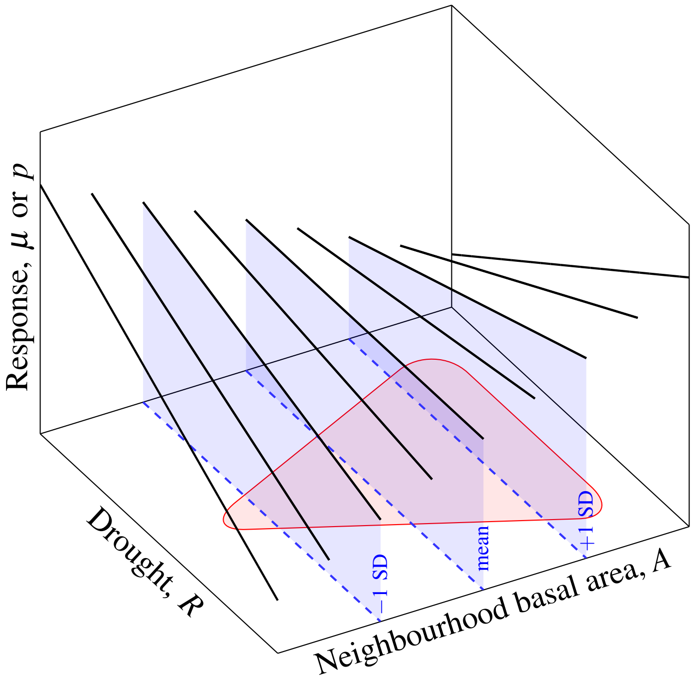
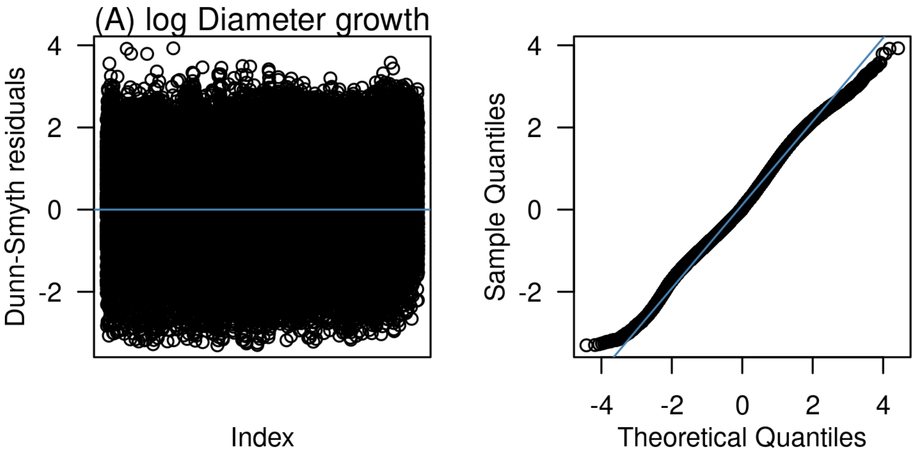


Figure S1: Conceptual diagram to illustrate average predictive comparisons, adapted from Lai et al. (2024) and tailored to our study context.

After fitting such an interaction effect in a model, a common way to illustrate the interaction is to plot three fitted lines of drought effect under three *counterfactual* neighbourhood basal area, e.g., mean, mean $+1$SD and mean -1SD (blue slices in Fig. S1). These neighbourhood basal area are counterfactual because they are hypothetical situations under which the modified drought effects may take place. In reality, however, these combined values of drought and neighbourhood basal areas may only rarely or not take place at all, thus rendering some counterfactual predictions unrealistic. For example, if most of the observed data points fall within the red zone of the joint predictor space, then the counterfactual fitted line at neighbourhood basal area of mean -1SD is hardly relevant. In other words, most of the realised drought effects are typically positive, because most empirical observations experience higher-than-average neighbourhood basal area.

Average predictive comparisons work by integrating the realised drought effects within the *empirical* joint predictor space, and then summarises the average (or "typical") effect of drought integrated over observations. We aim to keep explanations brief here; for more information, refer to the original work of Gelman & Pardoe (2007) and an ecological application in Lai et al. (2024).

3 Residual diagnostics



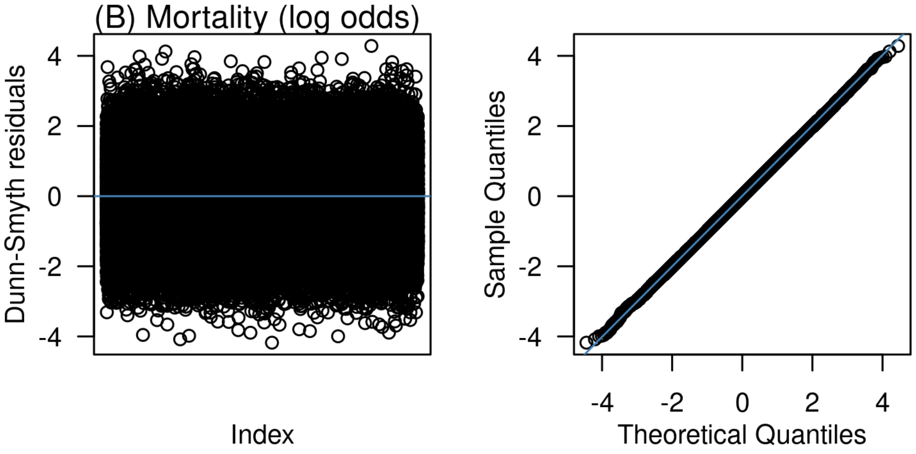


Figure S2: Dunn–Smyth residuals and quantile–quantile (QQ) plot used to diagnose model assumptions.

4 Species-specific coefficients

Table S1: Estimated species-specific coefficients and standard error (in parentheses). Diameter growth parameters include $\log a$, b, c, α, β, and γ, while mortality parameters include $\log v$, u, w, δ, ζ, and θ. See Equations 2 and 4 in the main text for their meanings. Bold numbers indicate coefficients of drought, neighbourhood basal area and their interactions that did not overlap with zero.

Species	log a	b	c	alpha	beta	gamma	log v	u	w	delta	zeta	theta
Acalypha diversifolia	-2.59 (0.06)	1.17 (0.1)	0.46 (0.03)	-0.03 (0.08)	**-0.23 (0.06)**	-0.03 (0.07)	-3.05 (0.13)	4.81 (0.26)	1.55 (0.08)	-0.07 (0.13)	0.19 (0.13)	-0.22 (0.13)
Adenaria floribunda	-2.86 (0.04)	4.67 (0.07)	2.95 (0.02)	**-3.4 (0.04)**	**0.17 (0.07)**	**-0.37 (0.06)**	0.01 (0.11)	2.41 (0.12)	0.95 (0.04)	**1.49 (0.14)**	**0.61 (0.1)**	0.16 (0.13)
Alchornea costaricensis	-4.17 (0.06)	2.03 (0.05)	0.6 (0.02)	**-1.72 (0.05)**	0 (0.05)	**0.2 (0.04)**	-1.87 (0.16)	2.26 (0.18)	0.48 (0.06)	0.22 (0.13)	**0.56 (0.16)**	**-0.37 (0.12)**
Alchornea latifolia	-0.99 (0.05)	2.13 (0.09)	1.22 (0.03)	**-0.34 (0.07)**	-0.04 (0.06)	**0.16 (0.07)**	-6.34 (0.46)	2.56 (0.5)	1.36 (0.17)	-0.68 (0.58)	**1.14 (0.43)**	-0.53 (0.54)
Amaioua corymbosa	-2.37 (0.04)	1.33 (0.05)	0.25 (0.02)	**-0.14 (0.04)**	-0.03 (0.04)	0.06 (0.04)	-4.11 (0.34)	4.09 (0.69)	0.64 (0.21)	-0.2 (0.21)	0.19 (0.33)	**-0.37 (0.18)**
Apeiba tibourbou	-1.96 (0.09)	1.49 (0.11)	0.89 (0.04)	**-0.5 (0.14)**	0 (0.09)	**0.28 (0.12)**	-1.44 (0.12)	3.64 (0.13)	0.93 (0.04)	**0.44 (0.1)**	**0.25 (0.13)**	0.02 (0.1)
Baccaris trinervis	-2.93 (0.05)	0.94 (0.12)	0.34 (0.03)	**-0.57 (0.06)**	**-0.25 (0.04)**	**-0.26 (0.05)**	-0.68 (0.07)	1.97 (0.13)	0.56 (0.04)	**0.47 (0.1)**	**0.42 (0.06)**	-0.03 (0.09)
Banara guianensis	-8.59 (0.05)	1.26 (0.04)	0.1 (0.01)	**-4.92 (0.04)**	**-2.39 (0.04)**	**-2.14 (0.05)**	1.29 (0.07)	2.31 (0.07)	0.29 (0.02)	**1.26 (0.1)**	**0.46 (0.07)**	0.15 (0.1)
Byrsonima crassifolia	-5.09 (0.02)	0.7 (0.02)	0.02 (0.01)	**-2.53 (0.02)**	**0.18 (0.02)**	**0.24 (0.01)**	-0.66 (0.07)	1.91 (0.07)	0.27 (0.02)	**0.54 (0.08)**	**0.13 (0.06)**	-0.01 (0.08)
Casearia commersoniana	-2.48 (0.06)	1.22 (0.06)	0.36 (0.02)	0.1 (0.06)	**-0.3 (0.05)**	**0.13 (0.05)**	-4.6 (0.42)	4.09 (0.71)	0.74 (0.23)	0.33 (0.27)	**1.1 (0.41)**	-0.24 (0.22)
Casearia sylvestris	-2.74 (0.03)	0.86 (0.02)	0.04 (0.01)	**-0.19 (0.03)**	**-0.15 (0.02)**	**0.09 (0.03)**	-3.56 (0.18)	3.43 (0.28)	0.5 (0.09)	0.25 (0.13)	-0.09 (0.17)	0.02 (0.13)
Cestrum megalophyllum	-1.48 (0.08)	1.07 (0.17)	0.89 (0.05)	**-0.36 (0.08)**	**-0.17 (0.08)**	**0.34 (0.07)**	-3.77 (0.17)	3.14 (0.26)	1.32 (0.09)	0.12 (0.12)	**0.4 (0.17)**	-0.04 (0.12)
Citrus aurantium	-3.25 (0.05)	2.11 (0.11)	1.65 (0.03)	**-2.44 (0.05)**	**-0.56 (0.04)**	**-0.23 (0.03)**	-1.15 (0.17)	4.35 (0.33)	0.45 (0.1)	**0.62 (0.16)**	**0.38 (0.18)**	0.02 (0.13)
Clibadium surinamense	-2.36 (0.04)	3.1 (0.16)	3.03 (0.03)	**-2.91 (0.03)**	**0.37 (0.03)**	**0.65 (0.02)**	-0.49 (0.1)	1.35 (0.16)	0.96 (0.05)	0.14 (0.11)	**-0.27 (0.11)**	-0.17 (0.12)
Cochlospermum vitifolium	-3.65 (0.05)	1.47 (0.04)	0.68 (0.01)	**-2.37 (0.04)**	**0.7 (0.04)**	**1 (0.03)**	0.6 (0.12)	3.34 (0.11)	0.7 (0.04)	**0.58 (0.18)**	-0.1 (0.12)	-0.2 (0.18)
Conostegia speciosa	-5.68 (0.1)	2.71 (0.22)	1.62 (0.06)	**-3.37 (0.08)**	**1.15 (0.07)**	**1.33 (0.06)**	-0.18 (0.08)	2.89 (0.15)	0.71 (0.05)	**0.61 (0.1)**	**0.55 (0.07)**	**0.33 (0.09)**
Conostegia xalapensis	-3.84 (0.01)	0.51 (0.02)	0.24 (0.01)	**-1.64 (0.01)**	**-0.52 (0.01)**	**-0.12 (0.01)**	-0.72 (0.03)	1.82 (0.04)	0.24 (0.01)	**0.7 (0.04)**	**0.56 (0.03)**	**0.15 (0.04)**
Cupania cinerea	-3.22 (0.03)	1.12 (0.03)	0.06 (0.01)	**-0.46 (0.03)**	**-0.24 (0.02)**	**0.24 (0.02)**	-3.65 (0.13)	3.4 (0.19)	1.06 (0.06)	**0.31 (0.1)**	**0.36 (0.13)**	0.03 (0.11)
Cupania rufescens	-2.62 (0.05)	1.4 (0.05)	0.24 (0.02)	**-0.15 (0.05)**	-0.09 (0.05)	**0.14 (0.04)**	-4.32 (0.29)	2.53 (0.44)	0.57 (0.14)	-0.04 (0.21)	**1.45 (0.26)**	-0.04 (0.19)
Cupania scrobiculata	-2.57 (0.03)	0.76 (0.03)	0.06 (0.01)	-0.01 (0.03)	**-0.21 (0.03)**	**0.11 (0.03)**	-4.24 (0.22)	3.05 (0.29)	0.79 (0.1)	-0.19 (0.19)	**0.62 (0.22)**	**-0.37 (0.18)**
Eugenia venezuelensis	-2.34 (0.05)	1.31 (0.07)	0.38 (0.02)	**-0.87 (0.06)**	0.01 (0.05)	**0.3 (0.06)**	-5.36 (0.32)	2.57 (0.38)	1.18 (0.13)	-0.4 (0.45)	-0.08 (0.35)	-0.22 (0.49)
Hampea appendiculata	-2.3 (0.03)	1.89 (0.04)	0.53 (0.01)	**-1.02 (0.03)**	**0.16 (0.03)**	**0.36 (0.03)**	-2.4 (0.17)	2.83 (0.23)	0.94 (0.07)	**0.41 (0.15)**	0.07 (0.17)	0.1 (0.13)
Inga cocleensis	-2.63 (0.03)	0.74 (0.04)	0.47 (0.01)	**-1.37 (0.02)**	**0.32 (0.02)**	**0.96 (0.02)**	-2.58 (0.15)	2.43 (0.16)	0.56 (0.05)	**0.54 (0.11)**	0.29 (0.15)	0.01 (0.12)
Inga thibaudiana	-3.09 (0.02)	1.51 (0.02)	0.72 (0.01)	**-2.73 (0.02)**	**1.46 (0.02)**	**1.43 (0.01)**	-1.61 (0.18)	2.77 (0.2)	0.54 (0.07)	0.16 (0.16)	0.12 (0.18)	-0.09 (0.16)
Isertia haenkeana	0.02 (0.11)	1.79 (0.42)	2.79 (0.09)	**-0.4 (0.1)**	0.17 (0.1)	**0.36 (0.08)**	-0.98 (0.09)	2.49 (0.14)	1.06 (0.05)	0.17 (0.09)	0.02 (0.08)	0.02 (0.08)
Lacistema aggregatum	-2.03 (0.02)	0.23 (0.02)	0.06 (0.01)	**-0.06 (0.02)**	**-0.14 (0.02)**	0.02 (0.02)	-4.42 (0.14)	3.22 (0.26)	0.57 (0.08)	-0.01 (0.09)	0.18 (0.14)	0.11 (0.1)
Lantana camara	-1.43 (0.22)	1.99 (1.07)	4.08 (0.19)	**-2.33 (0.19)**	**-0.68 (0.19)**	**-0.83 (0.16)**	0.31 (0.11)	3.83 (0.22)	1.78 (0.07)	**1.35 (0.12)**	**-0.57 (0.09)**	**-0.81 (0.1)**
Lozania pittieri	-1.41 (0.04)	0.83 (0.06)	0.27 (0.02)	-0.03 (0.05)	**-0.11 (0.05)**	**0.15 (0.06)**	-4.8 (0.46)	2.78 (0.59)	0.92 (0.2)	0.53 (0.39)	-0.6 (0.5)	0.04 (0.43)
Miconia affinis	-2.32 (0.03)	0.13 (0.05)	0.19 (0.02)	0.02 (0.04)	**-0.18 (0.03)**	-0.02 (0.04)	-3.26 (0.06)	1.79 (0.07)	0.72 (0.03)	**0.12 (0.05)**	**0.41 (0.07)**	-0.01 (0.05)
Miconia argentea	-3.24 (0.02)	0.82 (0.02)	0.19 (0.01)	**-1.15 (0.02)**	0 (0.01)	**0.35 (0.01)**	-1.8 (0.05)	1.71 (0.06)	0.3 (0.02)	**0.27 (0.05)**	**0.36 (0.05)**	**-0.12 (0.05)**
Miconia minutiflora	-2.29 (0.04)	0.17 (0.06)	0.42 (0.02)	**-0.63 (0.04)**	-0.02 (0.03)	**0.2 (0.04)**	-2.62 (0.07)	1.85 (0.09)	0.9 (0.03)	-0.08 (0.08)	0.05 (0.07)	0.06 (0.08)
Miconia prasina	-1.77 (0.04)	0.73 (0.04)	0.14 (0.01)	**-0.34 (0.05)**	-0.02 (0.04)	0.07 (0.04)	-3.57 (0.22)	2.37 (0.25)	0.88 (0.08)	0.15 (0.15)	0.21 (0.23)	0.09 (0.18)
Mosquitoxylum jamaicense	-1.55 (0.04)	0.55 (0.05)	0.1 (0.02)	**-0.28 (0.05)**	**-0.49 (0.04)**	**-0.09 (0.04)**	-3.23 (0.24)	3.77 (0.33)	1.1 (0.11)	0.28 (0.18)	-0.15 (0.24)	0.14 (0.18)
Myrciaria floribunda	-2.15 (0.08)	1.44 (0.11)	0.67 (0.04)	-0.05 (0.08)	-0.11 (0.08)	0.13 (0.09)	-4.67 (0.46)	4.32 (0.81)	0.57 (0.27)	0.19 (0.27)	**1.35 (0.43)**	0.35 (0.26)
Ochroma pyramidale	-5.58 (0.03)	3.14 (0.02)	0.31 (0.01)	**-2.08 (0.03)**	**-0.98 (0.02)**	**-1.07 (0.02)**	0.77 (0.14)	4.53 (0.15)	1.32 (0.05)	**1.16 (0.18)**	**0.54 (0.13)**	**0.6 (0.17)**
Palicourea guianensis	-2.25 (0.03)	0.27 (0.06)	0.15 (0.02)	**-0.39 (0.04)**	**-0.06 (0.03)**	**-0.07 (0.04)**	-1.71 (0.05)	0.63 (0.08)	0.37 (0.03)	0.03 (0.06)	0.07 (0.05)	0.06 (0.05)
Piper aduncum	-4.35 (0.04)	0.74 (0.06)	0.16 (0.02)	**-1.62 (0.04)**	**0.72 (0.03)**	**0.86 (0.03)**	0.3 (0.07)	2.11 (0.1)	0.51 (0.03)	**0.75 (0.08)**	-0.03 (0.06)	**-0.29 (0.08)**
Piper colonense	-1.96 (0.07)	1.51 (0.11)	0.65 (0.04)	**-0.17 (0.07)**	**-0.35 (0.07)**	0.11 (0.07)	-3.27 (0.37)	4.87 (0.92)	0.65 (0.26)	-0.09 (0.3)	-0.21 (0.38)	0.04 (0.33)
Pachira sessilis	-2.57 (0.06)	1.17 (0.06)	0.24 (0.02)	**-0.74 (0.08)**	-0.02 (0.05)	0.1 (0.06)	-4.14 (0.29)	2.55 (0.36)	0.93 (0.12)	-0.14 (0.22)	0.48 (0.29)	0.16 (0.21)
Protium panamense	-1.33 (0.03)	0.43 (0.05)	0.12 (0.01)	**-0.23 (0.03)**	**-0.09 (0.03)**	**0.09 (0.03)**	-5.61 (0.41)	2.77 (0.49)	1.2 (0.17)	-0.48 (0.43)	0.15 (0.45)	-0.05 (0.46)
Psychotria grandis	-2.61 (0.03)	0.62 (0.04)	0.06 (0.01)	**-0.32 (0.04)**	0.05 (0.03)	0.06 (0.04)	-2.99 (0.14)	2.75 (0.21)	0.62 (0.07)	-0.11 (0.13)	0.03 (0.13)	-0.07 (0.13)
Quassia amara	-3.13 (0.09)	1.39 (0.14)	0.51 (0.05)	-0.08 (0.07)	-0.11 (0.1)	0.14 (0.09)	-3.87 (0.21)	3.46 (0.41)	0.67 (0.13)	**-0.47 (0.18)**	0.01 (0.2)	**0.5 (0.16)**
Ryania speciosa	-2.28 (0.03)	0.37 (0.04)	0.15 (0.01)	0.02 (0.03)	**-0.21 (0.03)**	0 (0.03)	-5.72 (0.25)	2.86 (0.3)	1.16 (0.1)	-0.38 (0.23)	0.19 (0.25)	-0.17 (0.22)
Schefflera morototoni	-2.29 (0.02)	1.06 (0.02)	0.29 (0.01)	**-1.27 (0.02)**	**-0.04 (0.02)**	**0.13 (0.01)**	-2.33 (0.21)	2.85 (0.22)	0.9 (0.07)	-0.28 (0.22)	0.01 (0.2)	-0.2 (0.21)
Senna hayesiana	-2.15 (0.04)	0.71 (0.1)	1.09 (0.03)	**-0.9 (0.04)**	**-0.25 (0.04)**	**-0.31 (0.04)**	-1.22 (0.06)	2.05 (0.11)	0.62 (0.03)	**0.44 (0.08)**	**0.34 (0.06)**	**-0.15 (0.08)**
Siparuna guianensis	0.19 (0.17)	1.62 (0.69)	3.18 (0.14)	-0.32 (0.18)	0.2 (0.17)	**0.33 (0.14)**	-1.54 (0.1)	2.65 (0.18)	0.89 (0.06)	-0.17 (0.12)	-0.03 (0.09)	-0.19 (0.12)
Siparuna pauciflora	-2.17 (0.06)	0.98 (0.08)	0.41 (0.03)	**-0.23 (0.07)**	-0.04 (0.06)	**0.3 (0.06)**	-3.6 (0.24)	2.83 (0.35)	0.66 (0.11)	0.19 (0.19)	-0.39 (0.23)	**0.38 (0.19)**
Swartzia simplex	-1.99 (0.06)	0.77 (0.12)	0.58 (0.04)	-0.02 (0.05)	-0.06 (0.06)	**0.18 (0.05)**	-5.9 (0.57)	3.05 (1.13)	0.74 (0.36)	-1.19 (0.82)	-0.54 (0.49)	-0.01 (0.73)
Talisia nervosa	-0.58 (0.06)	1.09 (0.15)	1.66 (0.04)	-0.11 (0.06)	0.05 (0.06)	0.02 (0.05)	-6.3 (0.4)	2.28 (0.61)	0.92 (0.21)	0.01 (0.27)	-0.41 (0.35)	**0.53 (0.26)**
Terminalia amazonia	-2.34 (0.02)	0.8 (0.02)	0.02 (0.01)	**-0.47 (0.02)**	**-0.16 (0.02)**	**0.18 (0.02)**	-4.89 (0.28)	3.01 (0.34)	1 (0.12)	0.31 (0.26)	-0.09 (0.29)	0.13 (0.27)
Ternstroemia tepezapote	-2.07 (0.08)	0.54 (0.12)	0.35 (0.04)	**0.17 (0.05)**	0.03 (0.09)	-0.02 (0.06)	-2.94 (0.17)	2.38 (0.23)	0.71 (0.08)	-0.28 (0.18)	-0.22 (0.17)	0.24 (0.18)
Thevetia ahouai	-2.78 (0.02)	0.05 (0.03)	0.21 (0.01)	**-0.53 (0.03)**	-0.02 (0.02)	**-0.05 (0.02)**	-1.99 (0.04)	1.76 (0.07)	0.15 (0.02)	-0.01 (0.04)	**0.15 (0.04)**	**-0.1 (0.04)**
Trichospermum galeottii	-1.57 (0.03)	0.6 (0.06)	0.6 (0.02)	**-1.22 (0.02)**	**0.56 (0.02)**	**0.64 (0.01)**	-0.68 (0.15)	2.21 (0.14)	0.5 (0.05)	0.22 (0.21)	-0.08 (0.13)	-0.24 (0.19)
Vernonia patens	-3.82 (0.04)	0.4 (0.06)	0.45 (0.02)	**-1.37 (0.03)**	**0.91 (0.03)**	**0.7 (0.02)**	0.09 (0.05)	2.02 (0.07)	0.76 (0.02)	**0.5 (0.05)**	**0.09 (0.05)**	0.03 (0.04)
Vismia baccifera	-4.94 (0.02)	0.33 (0.02)	0.1 (0.01)	**-2.15 (0.01)**	**0.07 (0.01)**	**0.61 (0.01)**	0 (0.03)	1.46 (0.03)	0.2 (0.01)	**0.31 (0.03)**	**0.33 (0.03)**	**-0.07 (0.03)**
Vismia billbergiana	-3.04 (0.09)	2.22 (0.14)	0.96 (0.05)	0.15 (0.09)	0.1 (0.1)	0.06 (0.09)	-2.66 (0.11)	1.74 (0.16)	0.6 (0.05)	0.02 (0.11)	-0.03 (0.09)	-0.02 (0.1)
Vismia macrophylla	-5.66 (0.01)	2.14 (0.02)	1.17 (0.01)	**-4.15 (0.01)**	**-1.54 (0.01)**	**-0.99 (0.01)**	-0.31 (0.05)	1.71 (0.06)	0.15 (0.02)	**0.48 (0.06)**	**0.38 (0.06)**	-0.05 (0.06)
Vochysia ferruginea	-1.62 (0.02)	1.09 (0.02)	0.06 (0.01)	**-0.79 (0.02)**	**0.15 (0.01)**	**0.45 (0.02)**	-4.24 (0.27)	2.76 (0.5)	0.72 (0.16)	0 (0.26)	0.46 (0.29)	-0.19 (0.27)
Xylopia frutescens	-2.74 (0.01)	0.86 (0.01)	0.01 (0)	**-0.67 (0.01)**	**-0.04 (0.01)**	**0.07 (0.01)**	-2.28 (0.05)	1.74 (0.08)	0.18 (0.02)	**0.22 (0.05)**	**0.25 (0.06)**	-0.08 (0.05)
Zanthoxylum acuminatum	-2.01 (0.06)	0.79 (0.08)	0.37 (0.03)	-0.05 (0.05)	**-0.31 (0.06)**	**0.13 (0.05)**	-4.1 (0.19)	2.96 (0.28)	0.95 (0.09)	0.13 (0.14)	**0.44 (0.2)**	-0.12 (0.14)

5 Comparing the effects of drought and neighbourhood basal area

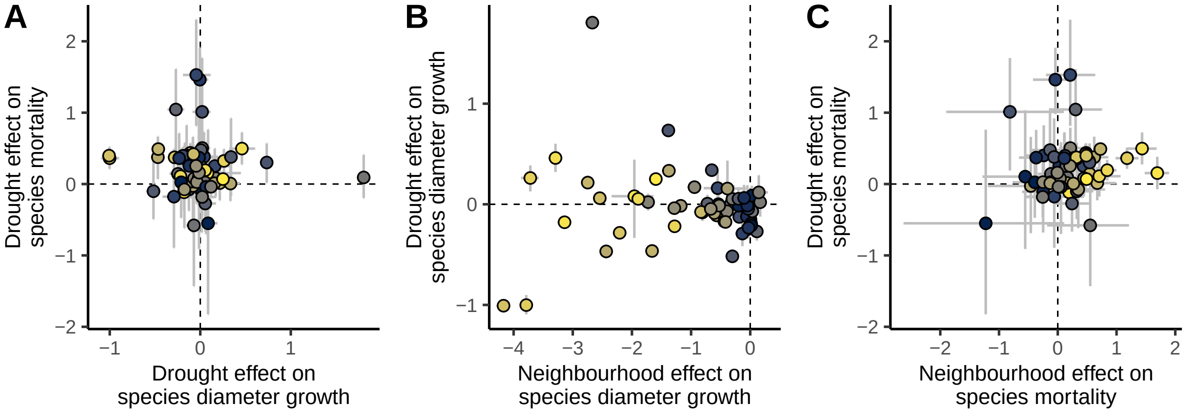


Figure S3: Average predictive comparisons for the typical effects of drought or neighbourhood basal area on the log diameter growth or mortality across species, plotted in pairwise combinations. Filled circles and error bars are median estimates and 95% credible intervals. Colours denote the successional status of each species (yellow = more associated with younger secondary forests; blue = more associated with older secondary forests).

6 Correlation between model parameters

Table S2: Spearman's rank correlation between pairs of parameters from the growth and mortality models. Diameter growth parameters include $\log a$, b, c, α, β, and γ, while mortality parameters include $\log v$, u, w, δ, ζ, and θ. See Equations 2 and 4 in the main text for their meanings.

	a	**b**	**c**	**alpha**	**beta**	**gamma**	**v**	**u**	**w**	**delta**	**zeta**	**theta**
a	1.00	-0.12	0.19	0.52	-0.04	0.01	-0.53	0.23	0.53	-0.47	-0.35	-0.06
b	-0.12	1.00	0.64	-0.28	0.05	0.07	0.19	0.30	0.22	0.19	0.15	-0.04
c	0.19	0.64	1.00	-0.20	0.20	0.13	0.25	0.07	0.23	0.10	-0.09	-0.06
alpha	0.52	-0.28	-0.20	1.00	-0.26	-0.18	-0.76	0.31	0.25	-0.62	-0.14	0.06
beta	-0.04	0.05	0.20	-0.26	1.00	0.70	0.21	-0.37	-0.09	-0.04	-0.24	-0.11
gamma	0.01	0.07	0.13	-0.18	0.70	1.00	0.00	-0.04	0.04	-0.02	-0.16	-0.20
v	-0.53	0.19	0.25	-0.76	0.21	0.00	1.00	-0.33	-0.34	0.68	0.02	-0.03
u	0.23	0.30	0.07	0.31	-0.37	-0.04	-0.33	1.00	0.45	-0.08	-0.04	0.06
w	0.53	0.22	0.23	0.25	-0.09	0.04	-0.34	0.45	1.00	-0.24	-0.15	-0.01
delta	-0.47	0.19	0.10	-0.62	-0.04	-0.02	0.68	-0.08	-0.24	1.00	0.16	0.19
zeta	-0.35	0.15	-0.09	-0.14	-0.24	-0.16	0.02	-0.04	-0.15	0.16	1.00	-0.05
theta	-0.06	-0.04	-0.06	0.06	-0.11	-0.20	-0.03	0.06	-0.01	0.19	-0.05	1.00

References

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