

DEMOGRAPHY BEYOND THE POPULATION

A trait-mediated, neighbourhood approach to quantify climate impacts on successional dynamics of tropical rainforests

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Summary

1. Second-growth forests account for 40% of the terrestrial forest carbon sink and represent the dominant forest cover in tropical regions. Uncertainties in predicting responses of these ecosystems to climate change arise from high tree species diversity, complex links between eco-physiology and demography, and the role of ontogeny and competition in mediating individual tree responses to climate. The dynamic nature of second-growth forests adds further uncertainty to our ability to quantify the relative importance of climate in mediating successional trajectories.

2. To address these uncertainties, we develop a hierarchical Bayesian neighbourhood modelling approach that quantifies how the joint response of two key functional axes, wood density and specific leaf area (SLA), modulate impacts of inter-annual variation in seasonal water stress (number of days during dry season > 1 kPa vapour pressure deficit) and night-time temperature on growth and survival of small (5–10 cm dbh) and large (≥ 10 cm dbh) trees for 171 rainforest species in 6 s-growth and 2 old-growth 1-ha mapped stands. We use model results to examine potential climate impacts on the successional trajectories of these stands.

3. High water stress reduced large tree growth but favoured growth of small trees. Drought also reduced tree survival for both large and small trees. Tree species with high wood density suffered lower growth reductions and had higher survival under water stress. High SLA magnified the negative effects of water stress on tree growth and survival. Across all tree sizes, high night-time temperatures did not influence growth or survival. Simulated successional trajectories under different climate scenarios using these results suggest that multi-annual droughts will have substantial impacts on the successional trajectories of tropical forests, leading to lower stem numbers, basal area and biomass. Sustained drought will also shift functional composition of second-growth forest by favouring species with low SLA which tend to dominate in late stages of succession.

4. By incorporating trait-mediated effects on key drivers of tree demography and successional dynamics, our approach provides an integrated perspective on interspecific variation in vulnerability to drought and consequences for successional trajectories in tropical rainforests. Our results suggest that multi-annual drought stress will significantly alter structure, composition and dynamics of second-growth forests and, from a functional perspective, accelerate succession. However, this effect may be hampered by dispersal limitation of old-growth species into second-growth forests.

Key-words: drought, functional traits, secondary tropical forests, second-growth forests, successional trajectories, Tree demography, warming

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Introduction

Climate-change models project rapidly increasing surface temperature in tropical regions (Diffenbaugh & Scherer 2011), and precipitation is expected to decline as much as

50% in some regions and seasons (Christensen *et al.* 2007; Mora *et al.* 2013; Sherwood & Fu 2014). The responses of tropical rainforest trees to higher temperatures and decreased rainfall are still poorly understood (Zhou *et al.* 2013). Observations from long-term forest-monitoring networks and manipulative drought experiments in tropical forests have shown that high temperatures or extreme drought events can result in lower tree growth (Feeley *et al.* 2007; Clark, Clark & Oberbauer 2010) and elevated mortality (Chazdon, Brenes & Alvarado 2005; da Costa *et al.* 2010; Phillips *et al.* 2010). The associations between climate and tropical tree performance, however, remain understudied, especially with respect to the factors (i.e. species, tree size and competition) that mediate individual tree responses to climate (Zuidema *et al.* 2013).

To date, most research on climate impacts on tropical tree growth and survival has been conducted in old-growth forests (e.g. Feeley *et al.* 2007; Phillips *et al.* 2010). Research examining the impacts of climate change on second-growth tropical forests lags far behind (Anderson-Teixeira *et al.* 2013). Beyond quantifying the effects of climate change on tree physiology, it is essential to understand the importance of climate relative to other factors (e.g. competition during stand thinning) in mediating successional trajectories (i.e. changes in forest structure and composition), since second-growth forests are not only widespread today but are also likely to increase in extent in the future (Malhi *et al.* 2014).

Second-growth forests may be particularly vulnerable to climate variability and change for several reasons. High stem turnover and low basal area in second-growth stands result in high light and temperature environments, particularly in early successional stages, making these stands susceptible to climate extremes (Nicotra, Chazdon & Iriarte 1999; Lebrija-Trejos *et al.* 2011). Competition for soil nutrients and water resources, which may intensify under drought, may also be acutely severe in young second-growth forests, where high stem densities interact with high resource demands to lead to high stand dynamism (Lasky *et al.* 2014). At the community scale, second-growth forests contain a high proportion of short- and long-lived pioneer tree species whose physiological characteristics may make them highly vulnerable to drought and higher temperatures (Bazzaz & Pickett 1980; Lohbeck *et al.* 2013).

Large uncertainties in predicting second-growth tropical forest responses to climate arise from the exceptional diversity of tropical tree species, a majority of which are locally rare. Functional traits may provide a useful way to reduce the massive diversity of tropical tree species into manageable dimensions for analysis and, at the same time they provide a framework for generating hypotheses about the mechanisms underlying tree species' responses to climate change (Fauset *et al.* 2012). Identifying the functional traits that are most closely related to the effects of climatic stressors on tree performance is an important step towards forecasting the future of tropical forests and scaling organismal

responses to regional and global patterns of ecosystem functioning (e.g. carbon and water fluxes) (Fisher *et al.* 2010).

An additional challenge is to determine the importance of ontogeny and competition in mediating tree responses to climate change (Clark *et al.* 2014). Large trees experience a markedly different competitive environment compared to small trees or saplings in the shaded understorey. Larger individuals are generally thought to be more susceptible to drought because of their greater hydraulic constraints (Niklas & Spatz 2004; Phillips *et al.* 2010) and elevated evapotranspiration rates. Below the canopy, tree crowns are exposed to lower irradiance, temperature and vapour pressure deficit, and may therefore exhibit weaker growth or mortality responses to warming or drought with respect to carbon loss and hydraulic function (Saatchi *et al.* 2013).

Here, we address these knowledge gaps with annual growth and mortality data from six successional and 2 old-growth 1-ha mapped forest plots in the Caribbean lowlands (50–220 m asl) of Costa Rica collected between 1997 and 2012 (Table 1). We combine 14 years of data on annual tree growth and survival and neighbourhood crowding with local climate records to evaluate tree responses to inter-annual differences in night-time temperature and dry-season water-stress (here defined as the proportion of daytime hours during the dry season (Jan–Apr) with vapour pressure deficit [VPD] > 1 kPa). This metric of water stress has been shown to most accurately capture drought effects on tree performance in old-growth stands in the study region (Clark, Clark & Oberbauer 2013). Similarly, a strong negative association between night-time temperature and a variety of forest productivity metrics was identified by Clark, Clark & Oberbauer (2013). The dataset contains a total of 69 507 individual tree-year growth observations (8801 unique individuals) and 68 256 tree-year survival observations (9540 unique individuals). Using these data, we address the following three goals:

1. Evaluate the degree to which climate impacts on small (5–10 cm dbh) and large (≥ 10 cm dbh) tree growth and survival differ.
2. Characterize how interspecific variation in functional traits modulate impacts of inter-annual variation in night-time temperature and water stress on tree growth and survival.
3. Use results from growth and survival models to simulate how the frequency and intensity of extreme climate extremes may alter successional trajectories in the structure and functional composition of these forests.

We analyzed the data within a hierarchical Bayesian framework that allowed us to evaluate the importance of interspecific variation in two key functional traits that have been implicated in tree species' climatic responses: specific leaf area (SLA: $\text{mm}^2 \text{ area mg}^{-1} \text{ mass}$) and wood specific gravity (WSG, also referred to as wood density: $[\text{g dry wood cm}^{-3} \text{ green wood}]/\text{density of water}$). We focused on these two traits because they exhibit strong links to plant eco-physiology and ecosystem-level carbon storage, and

Table 1. Information on eight 1-ha study plots in northeastern Costa Rica

Plot name (abbrev.)	Year abandoned	Year sampling initiated	Location	Latitude	Longitude
El Bejuco (EB)	1995	2005	Chilamate	10-46°N	84-06°W
Juan Enriquez (JE)	1995	2005	Chilamate	10-46°N	84-07°W
Lindero Sur (LSUR)	1985	1997	La Selva	10-41°N	84-03°W
Tirimbina (TIR)	1982	1997	La Virgen	10-40°N	84-11°W
Lindero El Peje second-growth (LEPS)	1977	1997	La Selva	10-43°N	84-03°W
Cuatro Rios (CR)	1972	1997	La Virgen	10-39°N	84-13°W
Lindero El Peje primary (LEPP)	Old-growth	2005	La Selva	10-42°N	84-04°W
Selva Verde (SV)	Old-growth	2005	Chilamate	10-44°N	84-07°W

can vary greatly among species (Lasky *et al.* 2014). For example, photosynthesis and leaf respiration both increase with greater SLA (Reich *et al.* 1998; Wright *et al.* 2004), thus potentially affecting whole-tree carbon balance and growth. WSG is closely associated with whole-plant hydraulic function; trees with denser wood have a lower risk of cavitation, but tend to have slower growth rates (Chave *et al.* 2009; Poorter *et al.* 2010). In an effort to understand the role of tree size in mediating climate responses, the relationship between functional traits and climatic responses was allowed to differ for trees between 5 and 10 cm dbh (small trees) and large trees (≥ 10 cm in dbh). These two size classes reflect understorey vs. subcanopy and canopy individuals.

Materials and methods

TREE DATA

Between 1997 and 2012 we annually monitored woody vegetation in six early and intermediate aged successional plots and two old-growth forest plots in Sarapiquí County, Heredia Province, in the Caribbean lowlands (50–220 m asl) of Costa Rica (Chazdon *et al.* 2010; Table 1). All plots were 1 ha in size (50 × 200 m). Three plots were located at La Selva Biological Station, three in Chilamate, about 7 km to the west of La Selva, and two near La Virgen, c. 20 km west of La Selva. The regional life-zone is tropical wet forest with annual temperature and rainfall averaging 26 °C and ~3800 mm, respectively, between 1963 and 1991 (Sanford *et al.* 1994). Soils in the study areas are derived from weathered basalt and are primarily classified as ultisols (Sollins *et al.* 1994). All plots had been cleared and grazed lightly for several years before abandonment and had closed canopies from the initiation of vegetation monitoring, but varied in the abundance of remnant trees and surrounding vegetation (Redondo, Vilchez & Chazdon 2001). All stems ≥ 5 cm diameter at breast height (dbh) were identified to species, tagged, mapped and measured for growth and assessed for survival (see Appendix S1, Supporting information for details of census methods). In total, we analysed data for 9540 individual trees and 171 species.

FUNCTIONAL TRAIT DATA

Functional trait data for the study species were collected from trees in or directly outside of the eight study plots. We used standardized, published protocols for all functional trait measurements (Cornelissen *et al.* 2003; Williamson & Wiemann 2010). SLA measurements were made on 1–62 individuals per species (median = 5 indiv). We collected two leaves per individual (bulk prior to analysis), and sampled fully expanded sun-lit leaves with low levels

of herbivory or epiphyll cover whenever possible. Leaves were scanned to determined leaf area and oven-dried for ~72 h at 60 °C and weighed. SLA was calculated by dividing fresh leaf area by dry weight, including petioles since these represent an important component of light capture and photosynthetic structure (Cornelissen *et al.* 2003). We measured bulk WSG on 1–52 individuals per species (median = 5 indiv.). We used a 5.15 mm increment borer (Suunto, Finland) to core each tree from the bark to the pith. After removing the bark, we measured core volume with the water displacement method and recorded dry weight after drying for ~72 h at 105 °C (Williamson & Wiemann 2010). For each species, we used mean trait values calculated using all sampled individuals regardless of size. Sample sizes for each species are provided in Table S1. For our species, SLA and WSG represent relatively independent trait axes (e.g. Pearson's r between SLA and WSG values for the 171 study species is $r = -0.03$).

LOCAL CLIMATIC DATA

The Organization for Tropical Studies has operated an automated meteorological station at La Selva Biological Station since June 1992, providing nearly continuous 30-min records of rainfall, air temperature and relative humidity. Our analyses span the period 1997–2012 (Fig. S1). For each census interval over which annual diameter growth and survival was assessed for each individual tree, we calculated means of the daily values for minimum temperature (°C) (T_{min} , henceforth referred to as “night-time temperature” for simplicity) and of the proportion of dry-season (Jan–Apr) daytime hours with vapour pressure deficit > 1 kPa (which we use as an index of “water stress” or VPD).

STATISTICAL ANALYSES

We used these data to parameterize a hierarchical Bayesian model of annual diameter growth and survival across all tree species. The covariates were tree size, neighbourhood crowding, mean night-time temperature and water stress (dry-season high VPD) over each annual census interval. Survival analyses also included antecedent growth in the previous year. Analyses were conducted separately for small and large trees. We excluded species with unsampled traits, though their effects on focal stems were included in the calculations of neighbourhood crowding.

Our goal was to use functional trait data to help constrain the estimated growth and survival response of tree species to climatic variability. Functional traits such as SLA and WSG are likely to influence tree performance in multiple ways, including mean demographic rates and competitive interactions between species (e.g. Poorter *et al.* 2008; Uriarte *et al.* 2010; Lasky *et al.* 2014). To the degree that traits correspond to specific functions, it should be possible to link tree species variation in functional traits to physiological responses to climate variability, including differences among species in response to climate variation in the context of competition. To capture these multiple effects, we considered each

of these factors in hierarchical Bayesian models of growth and survival. Based on an exploration of the growth data, we assumed that observed log-transformed diameter growth (g , mm year⁻¹) was normally distributed, and we specified the following model for the expected (or mean) log-scale diameter growth:

$$E(\log(g_{tsi})) = \beta_{1s} + \beta_2 \log(\text{dbh}_{tsi}) + \beta_{3s} \log(\text{NCI}_{tsi}) + \beta_{4s} \text{Tmin}_t + \beta_{5s} \text{VPD}_t + \gamma_i \quad \text{eqn 1}$$

where g_{tsi} is the growth of stem i of species s in census interval t , dbh_{tsi} is stem i 's diameter at 1.3 m height at the start of the census interval, and NCI_{tsi} is an index of neighbourhood crowding for stem i . Tree-level random effects are denoted as γ_i . NCI is calculated for each focal stem i based on the size and distance (d) of its neighbours ($j = 1 \dots J$) within a 10 m radius at the start of census interval t :

$$\text{NCI}_{tsi} = \sum_{j=1, i \neq j}^J \frac{\text{DBH}_j^2}{d_{ij}^2} \quad \text{eqn 2}$$

We lacked information on neighbour trees outside the mapped area which may influence tree growth and survival of trees within 10 m of the plot edge. Excluding these trees would have significantly reduced sample sizes. To avoid this loss but incorporate a measure of neighbourhood crowding, we created a 10 m buffer zone around each plot that contained a population of trees with identical composition and size distribution to that of the trees within a 10 m edge of each plot (Uriarte *et al.* 2005). Location of individuals within this buffer zone was determined at random.

Expected probability of survival was estimated using a logistic model with the same covariates as for growth plus the effect of each stem antecedent year's growth (i.e. in year $t-1$, g_{t-1si}). For stem i in census year t , the model takes the form:

$$\log_{it}(s_{tsi}) = \beta_{1s} + \beta_2 \log(\text{dbh}_{tsi}) + \beta_{3s} \log(\text{NCI}_{tsi}) + \beta_{4s} \text{Tmin}_t + \beta_{5s} \text{VPD}_t + \beta_{6s} g_{t-1, si} + \gamma_i \quad \text{eqn 3}$$

To capture the ways in which inter-specific trait variation may mediate tree growth and survival responses to these covariates, each of the species-specific regression coefficients (except dbh) was modelled in a second-level regression as a function of species mean wood specific gravity (WSG) and specific leaf area (SLA). Variation in these functional traits among the focal trees may mediate species-specific average growth rates (β_{1s}), sensitivity to neighbourhood crowding (β_{3s}), and direct climate effects (β_{4s} , β_{5s}). Because we modelled small and large trees separately, we did not include a hierarchical trait-mediated effect for tree size. For a tree of species s , the value of the regression coefficient β for covariate k in eqns 1 and 3 (e.g. $k = 1$ represents the intercept, $k = 5$ the effect of antecedent growth, etc.) is modelled as follows:

$$\beta_{ks} = b_k + b_{k1} \text{WSG}_s + b_{k2} \text{SLA}_s \quad \text{eqn 4}$$

where b_k represents the mean value (across all species) for covariate k in eqns 1 and 3 (e.g. effect of VPD on growth for $k = 4$ in eqn 1), and b_{k1} and b_{k2} represent the departure from the mean effect with one standard deviation change in the value of WSG and SLA respectively from the average value of the trait across all species in the community. Because trait values are standardized to have mean = 0, parameter β_{ks} equals b_k at mean community trait values.

To prevent confounding of species-specific effects with inter-specific variation in mean diameter or neighbourhood crowding, we also standardized the covariates in eqns 1 and 3 by subtracting their species-specific means from their original values and dividing by their standard deviations. All other covariates were standardized by subtracting means and standard deviations computed across the whole dataset (all species) prior to analyses. All parameters (i.e. β s, b 's, and variance terms associated with the

log-normal g observation errors and the tree-level random effects) were given vague priors, and their posteriors were estimated via Markov chain Monte Carlo routines implemented in JAGS (Plummer 2007). Chains generally converged within 30 000 iterations.

We calculated several metrics of model fit including deviance information criteria (DIC) (Spiegelhalter *et al.* 2002), posterior predictive loss (D_{∞}) (Gelfand & Ghosh 1998), and R^2 between observed data and predicted values. To assess the overall importance of climate for understanding tree growth and survival, we fitted a model that excluded the two climate variables (i.e. night-time temperature and water stress) and compared this reduced model's performance—with respect to DIC, D_{∞} , and R^2 —to the full models described in eqns 1 and 3.

SIMULATIONS

To assess the impacts of climate on forest dynamics and to evaluate model performance, we used results from the fitted models for simulating stand dynamics. We used random draws from the simulated posteriors' Markov chains for parameters in eqns 1 and 3 as parameter values in each simulation run. Simulated individual random effects for both growth and survival were assumed to be constant for the life span of each tree. In order to maintain realistic stand dynamics, we simulated trees recruiting to the 5 cm size class. Simulated recruitment was based on a statistical model, where the observed number of recruits in each 2.5×2.5 m sub-quadrat was modelled as a function of NCI calculated from the centre of each sub-quadrat (See Appendix S1 for greater detail on simulation procedures).

We first evaluated model performance by comparing a number of stand metrics, including the number of stems in each size class per hectare, total basal area, total estimated biomass, and average WSG and SLA, between actual (i.e. observed over the length of the study period) and simulated conditions using observed climate data for the study period (Table 1). We also compared size distributions of simulated and observed data in the last year of the simulations. We used published allometric scaling equations to calculate above-ground biomass (AGB) for each stem and calculated stand biomass for each year (see Appendix S1 for details).

We then simulated dynamics under a series of climate scenarios from infrequent to sustained drought. We first simulated stand dynamics for the first 8 years of the period in which survival and antecedent growth data were collected (1998–2005) using minimum temperature and dry season VPD values randomly sampled from the observed values of these covariates but excluding the most extreme drought year (2006, Fig. S1). In the subsequent 6 years of the simulation, we imposed extreme drought conditions (i.e. 2006 conditions) at a range of frequencies, from 2 to 6 out of the six subsequent years. Within those final 6 years, drought years were chosen randomly under each scenario. We then compared drought scenarios using the same stand metrics used in evaluation between simulated baseline and extreme drought conditions. All analyses and simulations were conducted using R statistical software (R Development Team 2013).

Results

There was considerable variation across study years in night-time temperature, dry season VPD, and average tree growth and survival rates (Fig. 1, Fig. S1). Our trait-based models (eqns 1 and 3) captured inter-annual variation in growth and survival across our 171 study species (Table S2). Across all study species, greater tree size (β_2 in eqn 1) was associated with lower diameter growth for both small and large trees (Fig. 2). Greater neighbourhood crowding also

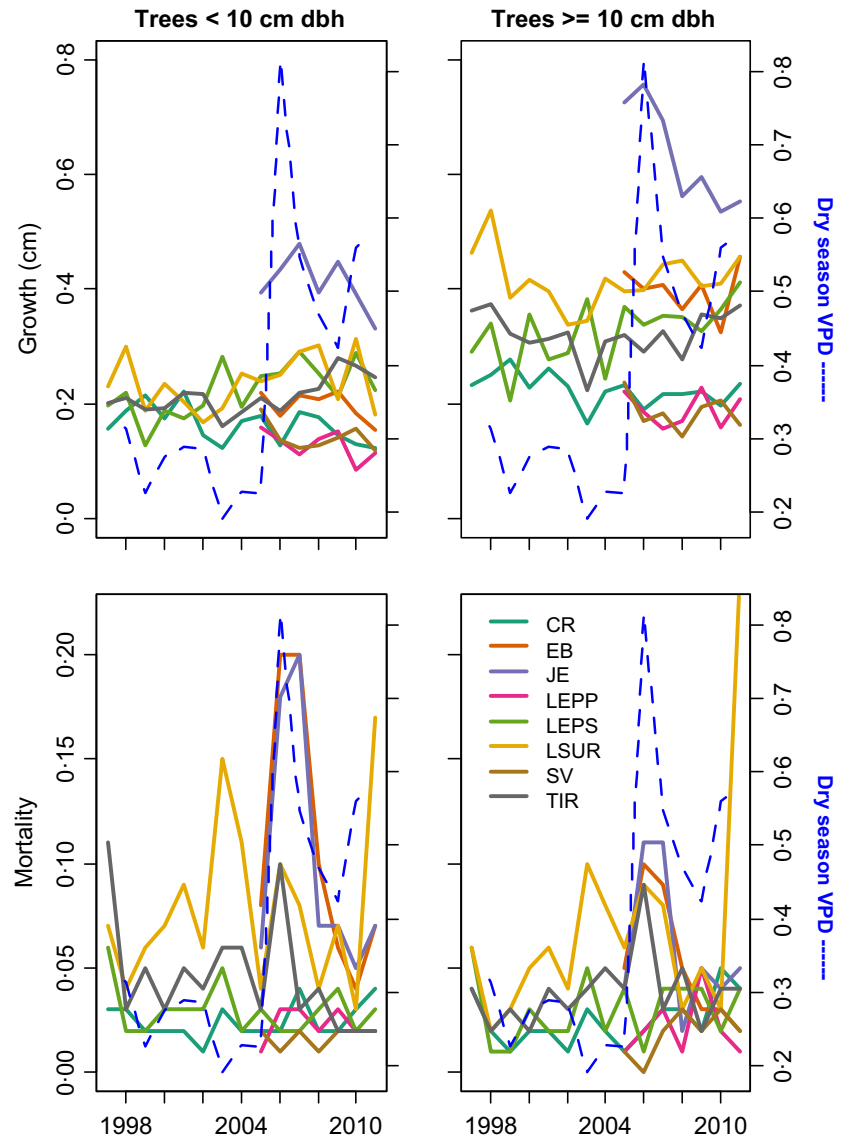


Fig. 1. Observed annual dry season VPD (proportion of days > 1 kPa during the dry season) and mean growth and mortality rates for small and large trees during the study period. Each solid line represents a different 1-ha plot (see codes in Table 1). Note that the length of the study period differs across plots (Table 1). Average growth was calculated by taking the mean for all trees measured in each plot-year. Mortality rates were calculated by dividing the number of individuals that died in each plot-year by the total number of stems measured in each plot-year.

resulted in lower growth for all size classes although this effect was more marked for smaller individuals (β_3 in eqn 1, Fig. 2). For both small and large trees, the most important predictor of survival was growth in the antecedent year (β_6 in eqn 3, Fig. 2). Across size classes, high antecedent growth increased survival. Larger trees had greater survival rates than smaller ones but only in the small tree size class (i.e. < 10 cm dbh). Tree diameter, however, did not influence survival of large individuals (i.e. ≥ 10 cm dbh). In contrast with the results for growth, neighbourhood crowding did not influence either small or large tree survival (Fig. 2).

The posterior estimates for the climate effects (β_4 and β_5 in eqn 1) across all species revealed associations of small and large tree growth with high water-stress (Fig. 2). Consistent with our expectation that larger trees would be more susceptible to hydraulic stress, the growth response of these individuals to high VPD was negative whereas small trees showed enhanced growth under drier conditions (Fig. 2). Despite the beneficial effect of drought on growth of small trees, high dry-season VPD was associated with lower sur-

vival of both small and large individuals (Fig. 2). Metrics of model comparison (DIC and posterior predictive loss) also demonstrated significant effects of dry-season VPD on growth and survival of trees of all sizes (Table S2). Finally, night-time temperature did not influence either growth or survival of small or large trees (Table S2, Fig. 2).

INTERSPECIFIC VARIATION IN FUNCTIONAL TRAITS AND TREE PERFORMANCE

Functional traits influenced tree performance via multiple pathways including effects on average growth and survival rates and in mediating effects of neighbourhood crowding, climatic factors, and antecedent growth on demography (Table 2). Higher wood density and SLA were associated with lower average growth rates for both small and large trees (parameters b_{11} and b_{12} in eqn 4, Table 2). Denser wood also altered the negative effects of neighbourhood crowding on growth, exacerbating the effect of crowding for small trees but buffering it for large individuals (parameter

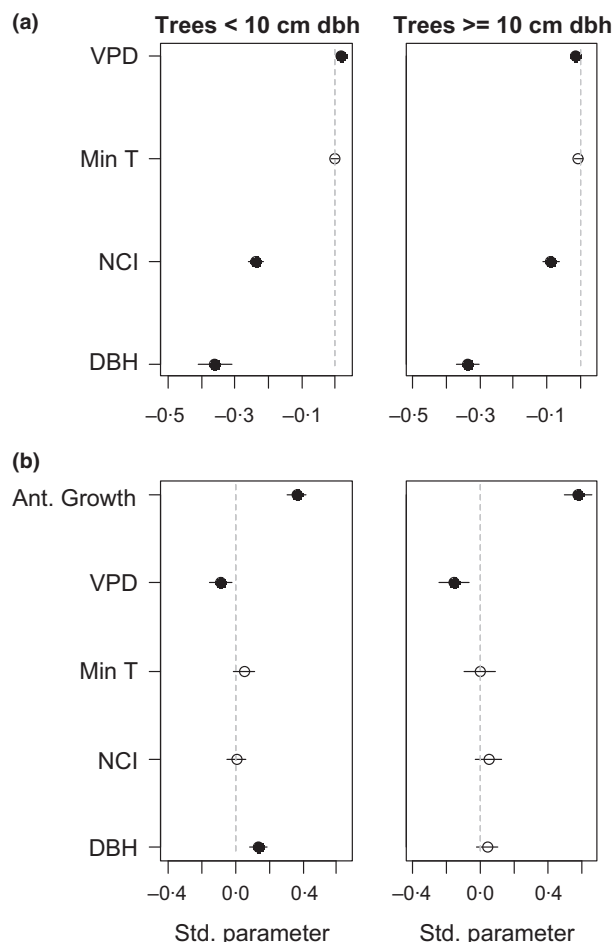


Fig. 2. Standardized regression coefficients for growth (A, eqn 1) and survival (B, eqn 3) models for small and large trees. Circles show posterior medians of β coefficients and lines indicate 95% CIs. Filled circles indicate significant results (i.e. CIs do not overlap 0). Open circles indicate non-significant results. Positive β indicates greater survival with increasing values of the covariate.

b_{21} in eqn 4, Table 2). For both large and small trees, high SLA intensified the negative effects of neighbourhood crowding on growth (parameter b_{22} in eqn 4, Table 2). High wood density and SLA were also associated with lower average survival rates for small trees (parameters b_{11} and b_{12} in eqn 4, Table 2). Interspecific variation in these two traits, however, did not influence average survival of large trees. Finally, high antecedent growth in the previous year was more beneficial for the survival of tree species with low SLA and wood density (parameter b_{51} and b_{52} , Table 2).

Interspecific variation in WSG and SLA influenced responses to drought for small and large trees. Across the 171 study species, growth of species with high SLA exhibited greater declines from water stress for both small and large tree growth (parameter b_{42} in eqn 4, Table 2). As expected, species with denser wood suffered lower reductions in growth under drought conditions (parameter b_{41} in eqn 4, Table 2). High SLA and low wood density also increased the risk of drought-induced large tree mortality (parameters b_{41} and b_{42} in eqn 4, Table 2) whereas neither of the two traits influenced drought-induced mortality for small trees (Table 2). Since night-time temperature did not influence either tree growth or survival for either size class (Fig. 2), we do not discuss this effect.

EFFECTS OF CLIMATE VARIATION ON SUCCESSIONAL DYNAMICS

We evaluated the ability of the growth and survival models to capture observed changes in composition and structure over the study period by comparing simulated and observed stand metrics over succession. These simulations used individuals that were present in the first year of the study, recruits over the study period, and observed climate data. In general, basal area and biomass increased across succession (Fig. 3). When comparing across plots, average

Table 2. Standardized regression coefficients for effect of interspecific variation in SLA and WSG on predictors of small and large tree growth

Covariate in log(g) model	WSG	Small tree growth	Large tree growth	Small tree survival	Large tree survival
Intercept, β_1	b_{11}	-0.480 (-0.507, -0.446)†	-0.385 (-0.411, -0.355)†	-0.407 (-0.476, -0.334)†	-0.005 (-0.085, 0.092)
Neighbour (NCI), β_3	b_{21}	-0.051 (-0.072, -0.033)†	0.053 (0.039, 0.074)†	NA	NA
Water stress (VPD), β_5	b_{41}	0.017 (0.006, 0.028)†	0.010 (0.000, 0.022)†	-0.051 (-0.125, 0.025)	0.201 (0.107, 0.291)†
Antecedent growth, β_6	b_{51}	NA	NA	-0.200 (-0.269, -0.129)†	-0.091 (-0.183, -0.001)†
SLA					
Intercept, β_1	b_{12}	-0.457 (-0.503, -0.415)†	-0.058 (-0.084, -0.029)†	-0.166 (-0.236, -0.096)†	0.035 (-0.038, 0.114)
Neighbour (NCI), β_3	b_{22}	-0.055 (-0.079, -0.033)†	-0.047 (-0.065, -0.031)†	NA	NA
Water stress (VPD), β_5	b_{42}	-0.019 (-0.030, -0.007)†	-0.041 (-0.050, -0.034)†	-0.036 (-0.113, 0.046)	-0.124 (-0.208, -0.046)†
Antecedent growth, β_6	b_{52}	NA	NA	-0.128 (-0.195, -0.059)†	-0.132 (-0.211, -0.047)†

Values for 2.5% and 97.5% quantiles are provided in parentheses.

†Denotes 95% CI does not overlap zero. We only show parameters for which the main effect of the covariate (Fig. 2) was significant (i.e. 95% CIs did not overlap 0).

stand level wood density decreased in early successional stands and then jumped up considerably between mid-successional and old growth stands (Fig. 3). For most of the plots, simulations closely captured successional trajectories in basal area, biomass, number of stems, and average SLA and wood density (Fig. 3) as well as size distributions at the end of the simulations (Fig. S2). One notable exception was the Lindero Sur plot for which observed successional trajectories in stem numbers, particularly for small trees, and in average wood density were considerably lower than simulated ones. Comparison of observed and simulated size class distributions also showed considerable differences for stems between 5 and 10 cm in dbh (Fig. S2).

Although initial conditions were substantially different among individual plots, comparison of a range of drought scenarios showed that an increasing frequency of drought over the final 6 years of the study period leads to lower stem density for both small and large trees coupled with lower basal area and stand biomass (Fig. 4). Multi-annual drought also resulted in lower SLA in most plots while the effect of drought on mean WSG was less clear (Fig. 4). These differences in plot-scale functional characteristics between dry and baseline conditions resulted, in part, from the effects of drought on growth and mortality of species that differ in SLA (Fig. 2, Table 2).

Discussion

Understanding how tropical forests will respond to a changing climate is critical for predicting global climate, preserving biodiversity and sustaining human livelihoods (Zuidema *et al.* 2013). Second-growth forests represent the prevalent tropical forest cover today and are expected to increase in extent worldwide (Chazdon 2014). Predicting the impacts of climate on these ecosystems is a critical research question (Anderson-Teixeira *et al.* 2013). The dynamic nature of second-growth stands, however, makes it difficult to disentangle climate impacts from other factors that affect variability in successional trajectories. By explicitly incorporating effects of ontogeny and competition during succession, the modelling approach presented here shows that two functional traits, wood specific gravity and specific leaf area, mediate demographic impacts of climate on rainforest trees. Our findings also demonstrate that trait-mediated variation in species responses to sustained drought is likely to alter composition, structure, biomass, and successional trajectories of second-growth tropical forests.

Of the two climate metrics considered in our analyses, only high dry season VPD significantly influenced tree growth and survival. High dry season VPD reduced tree

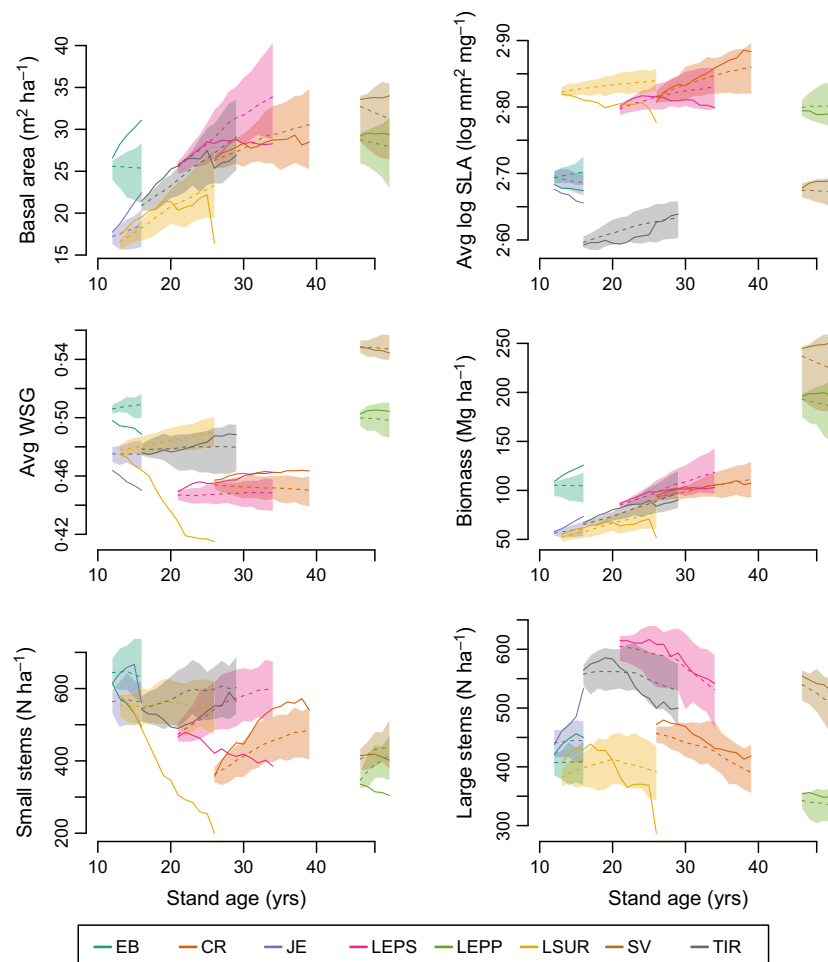


Fig. 3. Comparisons of plot characteristics between observed and simulated dynamics for each of eight 1 ha plots, where simulations used the observed time series of temperature and VPD conditions. Each solid coloured line shows observed data from a separate 1 ha plot. Dashed lines show the average result from simulations, and coloured regions indicate the range of results from 100 independent simulations.

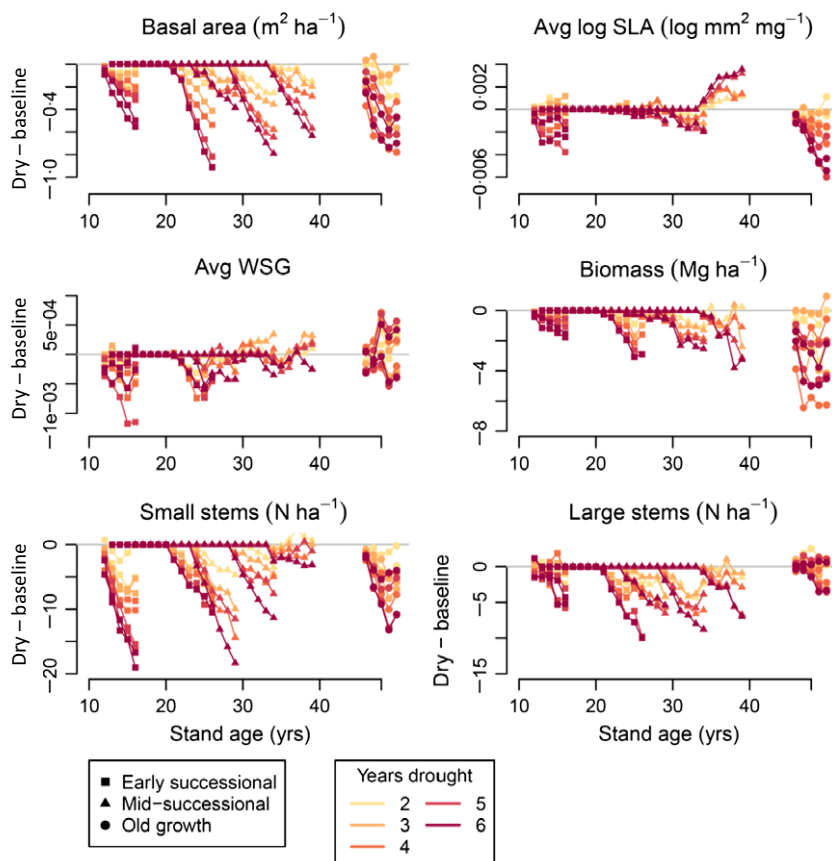


Fig. 4. Comparison of stand metrics over succession between climate scenarios for each of eight 1 ha plots. The baseline scenario used 14 (for plots in which census started in 1997) or 6 (for plots in which census started in 2005) years of climate by randomly sampling from the distribution of observed yearly values but excluding the driest year (2006). For the second scenario (dry), we simulated 8 years of dynamics for plots in which measurements started in 1997 using minimum temperature and dry season VPD values randomly sampled from the observed values of these covariates but excluding the most extreme drought year (2006). For the last 6 years and across all plots, we imposed extreme drought conditions (i.e. 2006 conditions) at a range of frequencies, from 1 to 6 of the six subsequent years. Within those final 6 years, drought years were chosen randomly under each scenario. Each line represents the mean outcome of 100 simulations for a different 1-ha plot over the 14 simulated years.

survival, supporting results elsewhere that link drought with elevated rates of tree mortality (Slik 2004; van Nieuwstadt & Sheil 2005; Chazdon, Brenes & Alvarado 2005; Brando *et al.* 2008; Phillips *et al.* 2010; da Costa *et al.* 2010). Although we hypothesized that larger individuals would be more susceptible to drought-induced mortality because of their greater hydraulic constraints and exposure, the magnitude of drought impacts on tree survival was similar for small and large trees. This finding contrasts with those from studies in old-growth stands (e.g. Phillips *et al.* 2010) and may result from harsher environmental conditions and stronger competition for soil nutrients and water resources in second-growth relative to old-growth stands.

The effects of drought on tree growth, however, differed for small and large trees. Large trees grew less during years with high dry-season VPD, suggesting that water limits whole-tree carbon assimilation and growth for large tropical trees, making these individuals more vulnerable to drought (Phillips *et al.* 2010). Their position higher in the canopy may also lead to greater evapotranspiration during dry periods and thus, lower growth. In contrast to large trees, small individuals grew more under high dry-season VPD conditions. Although the mechanisms that underlie the positive growth response of small trees to water stress remain unclear, it seems plausible that reduced water uptake by large canopy trees under drought conditions leaves more water available for smaller individuals. These

differential responses of small and large trees to dry season VPD highlight the importance of considering ontogeny and competition as key factors mediating tropical forest tree responses to climate (Phillips *et al.* 2010; Clark *et al.* 2014).

Trait-mediated variation in species responses to drought and neighbourhood crowding can offer insights into the mechanisms that underlie differential responses of small and large tree growth to drought. Our finding that over annual intervals the growth of large trees of species with higher wood density is less sensitive to daily water stress supports results elsewhere linking greater wood density with resistance to drought (e.g. Santiago *et al.* 2004; Phillips *et al.* 2010; Poorter *et al.* 2010). That small trees of species with high WSG exhibit stronger positive growth responses to high season VPD than species with low WSG may be explained by the well-known trade-off between hydraulic efficiency and hydraulic safety (O'Brien, Oberbauer & Clark 2004; Santiago *et al.* 2004; Markesteijn *et al.* 2011; McCulloh *et al.* 2011). Species with denser wood tend to have low hydraulic capacitance (Goldstein *et al.* 1998), which may limit their ability to compete for water under average climate conditions (Meinzer 2003). Our finding that across all years (i.e. under average climate conditions), high wood density exacerbates the negative effects of neighbourhood crowding on small but not on large tree growth supports this interpretation. Under drought conditions, however, high

WSG may reduce evaporative loss and lessen risk of partial xylem cavitation allowing small trees with high WSG to compete more effectively for water. In a pan-tropical analysis, Phillips *et al.* (2010) found that high WSG protected small trees from drought-induced mortality although a small sample size precluded any conclusion about large tree mortality. Nevertheless, the mechanisms that underlie links between wood density and drought vulnerability remain uncertain, because vessel width and pit pore width may vary substantially for a given wood density (Zanne & Falster 2010).

Among species, high SLA amplified the negative effects of drought on large tree growth. This effect may result from increases in evaporative water loss or decreases in photosynthesis due to stomatal closure under high VPD conditions (Meinzer 2003; O'Brien, Oberbauer & Clark 2004). In parallel, small trees from species with high SLA exhibited weaker positive growth responses to high dry-season VPD than those with lower SLA. This result is consistent with studies in an Amazonian rainforest where experimentally imposed drought led to community-wide declines in SLA (Metcalf *et al.* 2010). This is an important finding in the context of succession because species with high SLA are expected to dominate early successional stands when light levels in the subcanopy and understorey are high (Chazdon 2008; Lohbeck *et al.* 2013). Under a multi-annual drought scenario, these forest stands may become particularly vulnerable to drought.

Trait-mediated effects of climate on tree growth and survival, however, must be considered in tandem with inter-specific variation in other factors that drive tree demography. In our analyses, species with high wood density had lower average growth rates for both small and large trees and lower survival. Although high wood density has been associated with conservative resource acquisition strategies and low tree growth rates (e.g. Chazdon 2008), denser wood has also been associated with lower average mortality rates (Poorter *et al.* 2008; Lasky *et al.* 2014). However, these studies did not account for all the factors included in our model and the association between wood density and average mortality rates was noisy (e.g. $r = -0.22$ in Poorter *et al.* 2008). In our study, high SLA was associated with lower average growth for all trees and with low survival of small trees. A number of studies have uncovered correlations between high SLA and low survival (Poorter *et al.* 2008; Lasky *et al.* 2014). The association between SLA and growth rate, however, is less clear. For example, in a study of 5 neotropical forests Poorter *et al.* (2008) found a correlation of $r = -0.20$ between SLA and RGR, supporting our findings. However, Poorter *et al.*'s results may be driven in part by variation in neighbourhood crowding which could covary with SLA and influence average RGR. In our study, high SLA intensified the negative effects of neighbourhood crowding suggesting that growth of these species may be particularly sensitive to neighbourhood competition.

Our simulations demonstrate that more frequent droughts will lead to substantial changes in forest structure, composition and successional trajectories, favouring species with low SLA which tend to dominate late stages of succession. A recent review of climate impacts on forest regrowth concluded that drought reduces growth in forests of all ages but that within a community, species exhibit differential responses to climate (Anderson-Teixeira *et al.* 2013). Taken together, these findings suggest that climate change will lead to altered successional dynamics. A number of studies have uncovered shifts in the functional community composition of forests towards drought- and shade-tolerant species in response to climatic drivers (e.g. Feeley *et al.* 2011; Fauset *et al.* 2012). One limitation of these studies, however, is that other disturbance events or shifts in the factors that drive successional dynamics (e.g. neighbourhood crowding, functional characteristics) may underlie observed responses. For example, community-level wood density is expected to increase over succession in wet forests independent of climatic stress (Chazdon 2008; Lohbeck *et al.* 2013). By explicitly incorporating trait-mediated effects on the key factors that influence successional dynamics (e.g. average demographic rates, neighbourhood crowding), our study identifies multi-annual drought as an important driver of successional change and suggests an accelerated functional shift towards species that dominate late stages of succession. However, dispersal limitation is common for late successional species (Chazdon 2008). If dispersal does not keep pace, second-growth stands subject to repeated drought may functionally resemble older stands but will be missing lots of late-successional species that have not yet colonized.

The expected unprecedented warming across the tropics in coming decades (Diffenbaugh & Scherer 2011), combined with the likelihood of increased vapour pressure deficit due to increasing temperatures (Christensen *et al.* 2007; Sherwood & Fu 2014), presage intensifying negative climate impacts on tree growth and survival, and on biomass accumulation in the world's tropical rainforests. Our findings suggest that these effects will be particularly marked for tree species with high SLA. Because tropical forests contain the world's greatest diversity of tree species and life histories, identifying the functional traits that best predict tree responses to changing climatic drivers for a broad range of species will be an important step in building accurate models of tropical forest dynamics. Although wood density and SLA are coarse proxies for the physiological mechanisms that underlie tree species responses to climate, models that incorporate a greater range of inter-specific variation in functional traits and physiology as well as ontogenetic changes in tree species responses to climate will likely improve our ability to predict the responses of the tropical forest biome to the future climate and the resulting feedbacks to the atmosphere (Scheiter, Langan & Higgins 2009). A focus on understanding the effects of a changing climate on successional trajectories is needed if we are to accurately forecast the response of second-growth forests to future climates.

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Data accessibility

Tree plot data are available at http://esapubs.org/archive/appl/A025/029/Chazdon_data.txt

Functional trait data are available at <http://dx.doi.org/10.5061/dryad.d87v7> (Letcher et al. 2015).

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Fig. S1. Observed climate at La Selva, Costa Rica over the study period.

Fig. S2. Observed vs. simulated size distributions.

Table S1. Trait sampling sizes by species and size class.

Table S2. Model comparison statistics.

Appendix S1. Detailed description of data collection and simulation procedures.