



Tree competition in West African tropical forests mediated by the functional attributes of species and variation in soil moisture



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ABSTRACT

Understanding the ecological processes shaping competitive interactions among forest trees is crucial for predicting ecosystem productivity and climate change resilience. However, few studies have investigated how the biological attributes of tropical species may affect competitive outcomes under varying resource conditions. We collected and analysed a 10-year dataset of radial growth rates in canopy trees from a network of forest inventory plots located in divergent forest types over an extensive meteorological gradient in Ghana, West Africa. We used nonlinear models to estimate the relative reduction in potential growth (basal area increment) of individual target trees of a given species as a consequence of the combined effects of (1) target tree size, (2) variation in crowding levels by neighbouring trees, (3) the functional attributes of those neighbours (wood density and shade tolerance), and (4) local soil moisture levels. Analyses were conducted separately for the 15 most common species in the inventory network. In opposition to neutral theory, our findings indicate that the strength of interactions among competing species was distinctly asymmetric and dynamic. Wood density was an important characteristic that modified competitive outcomes for most species, particularly under varying levels of resource availability. Specifically, dense wood was an attribute that conferred comparatively stronger competitive ability in moisture-limited conditions. Larger individuals were notably less sensitive to the effects of moisture-dependent competition. Our results suggest that attributes such as wood density may reflect divergent life history strategies that differentiate species' fitness and competitive ability in varying environments. The dynamic nature of competition, influenced by a complex interplay of biological and abiotic factors, implies that more prevalent dry periods, which have been forecast for tropical Africa, may impact the physiognomy and function of future forest communities in the region.

1. Introduction

Anticipating the consequences of climate change for the organisation and function of tropical forests is a research imperative given their global importance as reservoirs of biodiversity and carbon (Hubau et al., 2020; Malhi, 2012; Sullivan et al., 2017). For the African continent, climate models forecast monotonic warming trends and changes in precipitation regimes, including potentially more severe dry season water deficits (Almazroui et al., 2020; James et al., 2013). These environmental changes are expected to impact the ecosystem services

provided by tropical ecosystems. Regional-scale analyses across West and Central Africa have documented a persistent decline in annual precipitation since the 1970s, based on multi-decadal climate datasets (Asefi-Najafabady and Saatchi, 2013). At a more localised scale, plot-level studies in Ghana have similarly reported long-term reductions in rainfall over the late 20th century (Fauset et al., 2012). These local drought trends have been linked to shifts in forest composition and function, including the abundance of tree taxa having phenotypic traits associated with drought tolerance, such as deciduous leaf phenology (Aguirre-Gutiérrez et al., 2019; Fauset et al., 2012). However, the

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potential demographic responses of tropical communities to climate variability are not well understood, due in part to the high species richness of tropical forests (>100 species·ha⁻¹ in this study) and the associated wide range of trait attributes and resource use strategies that may differentiate component taxa (De Guzman et al., 2021; Muller-Landau et al., 2021).

The role of competition in the assembly and persistence of species along environmental gradients has been a long-standing research theme (Canham et al., 2006; Kraft et al., 2015). Neutral theory is a parsimonious or null model that considers the effects of species differences in competitive ability as unimportant at broad scales (Hubbell, 2006). Instead, stochastic processes such as random dispersal and local extinction are assumed to generate general predictable patterns in the aggregation of taxa (Azaele et al., 2016; Leibold and McPeck, 2006). Empirical studies in diverse tropical forests have shown contrasting evidence regarding the equivalence of competitive effects among interacting species (e.g., Fortunel et al., 2016; Uriarte et al., 2004a, 2004b). For instance, Uriarte et al. (2004b) found that for more than half of the species studied, neighbouring individuals had similar effects on sapling growth, consistent with the assumptions of neutral theory. In contrast, Uriarte et al. (2004a) demonstrated that competitive effects varied significantly among species, with sensitivity to neighbourhood crowding differing across taxa. More broadly, neutral theory may not adequately account for the directional changes in the composition and function of tropical forests observed in Africa and elsewhere (Enquist and Enquist, 2011). An alternate and more mainstream hypothesis is that asymmetrical competitive interactions are ubiquitous, dynamic, and underpin niche-based pathways of community assembly (Leibold and McPeck, 2006; Silvertown, 2004). According to life history theory, natural selection has differentially shaped the physiological and anatomical attributes of species to optimise their resource use under particular conditions (Herms and Mattson, 1992). Contrasting resource strategies lead to genotype-by-environment interactions, which, in turn, generate trade-offs in plant performance and competitive ability (Pacala et al., 1996; Tilman, 1985). For example, species may be differentiated by attributes that confer either a potential for rapid growth in productive environments or, alternately, a physiological stress tolerance under low resource conditions (Angert et al., 2009; Pacala and Tilman, 1994). A comparatively high intrinsic growth potential, as a competitive strategy, may be underlain by elevated metabolic rates and carbon allocation to the construction of tissues (foliage, roots and stems) that enhance resource acquisition from the environment (Herms and Mattson, 1992; Poorter et al., 2010). Stress tolerance, in contrast, may depend on relatively greater investments of photosynthate to herbivory defences, mechanical stability, and storage, which have costs in terms of growth capacity (Grime, 1977; Kobe, 1997).

Variation in moisture availability has been identified as a primary factor that separates species in terms of competitive performance and fitness (Clark et al., 1999; Condit, 1998; Enquist and Enquist, 2011). Consequently, soil water supply has been identified as a structuring driver of community richness patterns in tropical forests (Ibrahim et al., 2025). Characteristics that may separate species in their water relations include a stem architecture that facilitates either a high water transport capacity (wide xylem vessels) or, alternately, enhanced stress and cavitation resistance under moisture limitation (narrow conduits) (De Guzman et al., 2021; Poorter et al., 2010; Sperry et al., 2006). Associated experimental research conducted in a variety of biomes has identified relationships between soil water and the differential competitive ability of plants (e.g., Angert et al., 2009; Lebrija-Trejos et al., 2023; Pérez-Ramos et al., 2019). Most studies have focused on juvenile life stages. In contrast, analyses of the relations between resource variation and interspecific competitive differences for canopy trees in tropical forests widely distributed across environmental gradients are presently limited (but see Rozendaal et al., 2020).

This study examined factors mediating competitive interactions among adult trees in diverse tropical communities under natural

conditions. We compiled and analysed a comprehensive 10-year dataset of individual tree annual growth rates from a network of forest monitoring plots spanning a broad climatic gradient in West Africa, ranging from humid wet to drier semi-deciduous forests. All plots were randomly located within intact unmanaged forests. We developed nonlinear, spatially explicit models at a neighbourhood scale to understand the effects of competition on the fitness of individual trees. Fitness responses, quantified for multiple focal species, were defined as an estimated reduction in the magnitude of potential stem growth (basal area increment). Our analyses explicitly quantified the effects of variation in the abundance, size, and proximity of neighbouring trees, the functional attributes of those neighbours (wood density and shade tolerance), and soil moisture levels. Wood density was assumed to be at least partly correlated with various phenotypic characters, such as hydraulic function, that may underpin potentially divergent competitive strategies among species (i.e., rapid growth versus stress tolerance) (Poorter et al., 2010). Similarly, we tested the efficacy of using a shade tolerance classification to discriminate plant strategies. Our simplest model examined evidence supporting neutral theory, specifically that species are effectively equivalent in competitive ability. However, we expected that the attributes and resource strategies of trees influence competitive outcomes, particularly under varying levels of resource availability. We therefore fit competing, more complex models with competition functions that were scaled by species-specific values of either wood density or shade tolerance, as well as an index of soil moisture supply. We specifically hypothesised that dense wood or high shade tolerance reflects a conservative, stress-tolerant plant strategy (De Guzman et al., 2021; Poorter and Markesteijn, 2008), which confers strong competitive ability in resource-limited conditions.

2. Materials and methods

2.1. Study sites

We used forest inventory data collected under the auspices of the Global Ecosystem Monitoring Network (<https://www.globalecosystemmonitoring.com/>). Associated field survey plots in Ghana were established using a stratified random sampling design within protected forest reserves. We collected data in nine 1-ha plots in three reserves: Ankasa Conservation Area (ACA), Bobiri Forest Reserve (BFR), and Kogyae Strict Nature Reserve (KSNR). Each reserve encompassed three plots: ACA (ANK1, ANK2, and ANK3), BFR (BOB1, BOB2, and BOB3), and KSNR (KO2, KO3, and KO4). The sampled sites span a latitudinal and environmental gradient ranging from wet coastal areas in the southwest to the drier interior regions of central Ghana. Based on a gridded reanalysis of climate data (Karger et al., 2017) for the decade since 2010, mean annual precipitation ranged from ~2,057 mm at coastal sites (ACA) to ~1,095 mm for northern interior plots (KSNR). Mean annual temperatures ranged from 25.4 °C in the south to 27.2 °C at northern locations (Table S1). All sites experience a prominent dry season from ~December to March, when total monthly precipitation falls below 100 mm (Hall and Swaine, 1981). Based on plant community composition, the ACA, BFR, and KSNR forests are classified as wet evergreen, moist semi-deciduous, and dry semi-deciduous types, respectively (Hall and Swaine, 1981).

Surveys were conducted annually from 2012, although the three moist forest plots were not censused in 2014, 2019, and 2021. The specific month of data collection was consistent between years but varied across forest types: surveys were conducted in March, June, and September in wet, moist, and dry forests, respectively. All trees with diameters ≥ 10 cm were identified to the species level, tagged, and mapped relative to a reference location (southwest plot corner). Stem diameters were measured to the nearest millimetre (0.1 cm) at 1.3 m above ground level. However, the point of measurement (POM) of the diameter was adjusted for some individual trees to account for swelling or buttressing in the basal portions of the bole. Specifically, POMs were

raised by fixed increments of 0.5 m up to a maximum level of 4.5 m for individuals when evidence of buttress formation was observed. POM levels were painted and documented to ensure measurement consistency across censuses.

2.2. Growth data

We compiled field survey data for a 10-year analysis period (2012–2021). We removed records with missing measurements ($N = 310$) and excluded data for trees that died ($N = 705$ stems). We excluded records for swamp trees ($N = 21$) and lianas ($N = 16$). The final dataset comprised diameter measurements for 4,234 trees belonging to 221 species, 182 genera, and 53 families. We analysed growth dynamics separately for the 15 most common tree species, based on sample size ($N > 150$ trees per species; Table 1). We derived a time series of annual basal increment (BAI, $\text{cm}^2 \cdot \text{year}^{-1}$) from stem diameter data for each tree, assuming circular cross sections. For non-census years in moist forests, we computed the average annual BAI using field data from the start and end of the two-year census interval.

2.3. Species guilds and wood density classification

We used a prior classification of the regeneration guild of forest taxa in Ghana (Hawthorne, 1995, 1996) as a proxy for shade tolerance. Hawthorne's semi-quantitative classification was based on a floristic inventory and qualitative observations of the environmental correlates of species occurrence (Sheil et al., 2006). Three guild categories were described: (1) a gap-specialist (pioneer) class comprised of light-demanding, shade-intolerant taxa, (2) a shade-tolerant (shade-bearer) class associated with

resource-limited closed canopy environments, and (3) a non-pioneer light-demanders (NPLD) category, consisting of species with an intermediate capacity for shade-tolerance (Hawthorne and Abu-Juam, 1995).

We obtained wood density values from the Global Wood Density database (Zanne et al., 2009). For species with missing density data ($N = 133$), mean values at the genus or family level were substituted (Baker et al., 2004). For each focal species ($N = 15$), we grouped all neighbour taxa into two or three distinct wood density classes (e.g., low, medium, high) using k -means clustering (Hartigan and Wong, 1979). We then ran preliminary regression models comparing the performance of the two-class and three-class groupings and selected the classification that provided the more parsimonious fit based on Akaike information criterion (AIC) for use in subsequent analyses.

2.4. Soil moisture

We used gridded ERA5-Land climate reanalysis data from the European Centre for Medium-Range Weather Forecasting (ECMWF). The ERA5-Land dataset has global coverage, a ~ 9.0 km pixel size, and an hourly temporal resolution (Muñoz-Sabater et al., 2021). Specifically, we acquired data for soil moisture content to a depth of 1.0 m. Hourly data were aggregated to monthly and then annual composites. Annual values were formulated to correspond with the different data collection periods of each site, as previously described. Thus, annual mean soil moisture content estimates were generated for the 12 months from March to February for the wet forest, from June to May for the moist forest, and from September to August for the dry forest. We then downscaled the 12-month aggregated soil moisture values from 9.0 km to ~ 900 m (30 arc-second) spatial resolution for each plot using kriging.

Table 1
Mean biological and environmental attributes of the 15 focal tree species (5th and 95th percentiles in brackets).

Species (acronym)	Family	^a Forest type			Biological attribute			Diameter (cm)	Neighbour density (trees-ha ⁻¹)	Rainfall (mm-year ⁻¹)
		Dry (%)	Moist (%)	Wet (%)	^b Guild	^c Leaf phenology	Wood density (g-cm ⁻³)			
<i>Carapa procera</i> (CARAP PROC)	Meliaceae	0	3.8	96.2	ST	E	0.604	14.8 (10.4, 58.3)	439 (212, 736)	2064 (1755, 2484)
<i>Celtis mildbraedii</i> (CELT MILD)	Ulmaceae	0	100	0	ST	E	0.594	21.3 (11, 58.4)	594 (368, 835)	1238 (932, 1486)
<i>Celtis zenkeri</i> (CELT ZENK)	Ulmaceae	0	100	0	NPLD	D	0.609	18.8 (11.1, 33.4)	707 (368, 905)	1238 (943, 1500)
<i>Cynometra ananta</i> (CYNOM ANAN)	Leguminosae	0	0	100	ST	E	0.830	51.8 (12.3, 72.2)	460 (297, 665)	2069 (1823, 2511)
<i>Erythrophleum suaveolens</i> (ERYTH SUAV)	Leguminosae	100	0	0	NPLD	D	0.873	41.7 (19.0, 69.1)	156 (71, 255)	1099 (855, 1426)
<i>Funtumia elastica</i> (FUNTU ELAS)	Apocynaceae	0	100	0	NPLD	D	0.424	14.2 (10.4, 25.7)	651 (354, 849)	1196 (943, 1500)
<i>Heritiera utilis</i> (HERIT UTIL)	Malvaceae	0	0	100	NPLD	E	0.480	20.7 (11.2, 71.8)	439 (293, 764)	2008 (1070, 2484)
<i>Nesogordonia papaverifera</i> (NESOG PAPA)	Sterculiaceae	0	100	0	ST	E	0.645	21.6 (11.6, 50.4)	622 (368, 863)	1217 (932, 1486)
<i>Pouteria alnifolia</i> (POUTE ALNI)	Sapotaceae	100	0	0	P	D	0.555	19.6 (11.9, 40.1)	226 (113, 354)	1078 (855, 1426)
<i>Protomegabaria macrophylla</i> (PROTO MACR)	Euphorbiaceae	0	0	100	ST	E	0.602	17.9 (10.9, 44.7)	439 (297, 693)	2064 (1823, 2484)
<i>Pterocarpus erinaceus</i> (PTERO ERIN)	Leguminosae	100	0	0	P	D	0.740	25.3 (12.6, 50.9)	184 (85, 325)	1140 (871, 1436)
<i>Sterculia rhinopetala</i> (STERC RHIN)	Sterculiaceae	0	100	0	NPLD	D	0.673	15.1 (10.6, 40.3)	665 (424, 877)	1238 (926, 1471)
<i>Sterculia tragacantha</i> (STERC TRAG)	Sterculiaceae	85.8	14.2	0	P	D	0.514	20.5 (11.6, 45.9)	283 (127, 736)	1140 (871, 1436)
<i>Strephonema pseudocola</i> (STREP PSEU)	Combretaceae	0	0	100	ST	E	0.633	27.4 (11, 58.0)	424 (297, 653)	2065 (1823, 2484)
<i>Triplochiton scleroxylon</i> (TRIPL SCLE)	Sterculiaceae	0	100	0	P	D	0.335	38.1 (12.7, 109.7)	608 (354, 874)	1238 (932, 1485)

Notes.

^a Dry, moist, and wet show the proportional distribution (%) of trees by species across forest types.

^b Guild classes reflect shade tolerance: NPLD = Non-pioneer light demanders; P = Pioneer species; ST = shade-tolerant (see Hawthorne, 1995).

^c D and E denote deciduous and evergreen species, respectively. Diameter, neighbour density and rainfall are mean values with 5th and 95th percentiles in brackets.

Given this resolution, all trees within a 1-ha plot were assigned the same soil moisture value for each census year. A USGS digital elevation model (https://topotools.cr.usgs.gov/gmted_viewer/gmted2010_global_grids.php) and soil hydraulic and thermal parameters (Dai et al., 2013) having ~900 m spatial resolution were used as covariates for the kriging-based interpolation. To assess the accuracy of the kriging interpolation, we performed cross-validation at each ERA5-Land grid cell. We calculated the root mean square error (RMSE) for each plot and year as the difference between observed and predicted soil moisture values. Mean RMSE values ranged from 0.021 to 0.039 across plots and years (Table S2), indicating that the spatial interpolation effectively captured soil moisture variability at the plot level. The entire workflow was performed using R functions from the package ‘KrigR’ (Kusch and Davy, 2022).

After downscaling, the 12-month soil moisture values were standardised to generate a soil moisture index (SMI; Gao et al., 2016). SMI accounts for low soil water content (wilting point) that is potentially unavailable for root absorption:

$$SMI = \frac{Q_{soil} - \min(Q_{soil})}{\max(Q_{soil}) - \min(Q_{soil})} \quad (1)$$

where Q_{soil} is the downscaled, 12-month, volumetric soil moisture fraction ($m_{H_2O}^3 m_{soil}^{-3}$), and min and max represent the corresponding minimum and maximum moisture levels observed for the period of our analyses for each tree location.

2.5. Statistical analyses

Our goal was to evaluate the potential role of biotic and abiotic factors in modulating the intensity of competition for resources among neighbouring trees. As competition is a local neighbourhood phenomenon, we investigated the magnitude of neighbour effects at the level of individual trees. Although the spatial extent of these interactions varies with species and tree size (Stoll and Newbery, 2005; Uriarte et al., 2010), we defined the neighbourhood as all trees within a fixed 15 m radius of each focal tree. This threshold is consistent with prior studies demonstrating that competitive interactions among trees predominantly occur within 10–20 m and decline sharply beyond this range (Canham et al., 2004, 2006; Coates et al., 2009; Muscarella et al., 2018; Uriarte et al., 2004b, 2005). Our preliminary analysis (Fig. S1) further confirms that neighbour influence is negligible beyond 15 m for most focal species. While we acknowledge variability in competitive interactions across spatial scales and species, the 15 m radius captures a biologically meaningful and computationally feasible scale for our analyses.

Based on an implicit assumption that tree taxa are differentiated in terms of their life-history and resource allocation strategies, and therefore respond uniquely to competition from neighbours, we formulated separate sets of nonlinear regression models for each of the 15 focal tree species (Table 1). We build on a tradition of neighbourhood modelling approaches in which the demographic performance of an individual tree is analysed in terms of the fine-scale spatial distribution of proximate trees and heterogeneity in the physical environment (Canham et al., 2004). The statistical framework is based on the application of maximum-likelihood principles to estimate model parameters (Edwards, 1992), contrasting the traditional null hypothesis testing paradigm that prevails in the dendrochronological literature (Canham and Uriarte, 2006). As in prior studies (e.g., Buechling et al., 2017; Canham et al., 2006; Coates et al., 2013; Gómez-Aparicio et al., 2011; Korolyova et al., 2022; Uriarte et al., 2004a, b; Valor et al., 2024), we assumed that each focal tree species has an innate maximum growth potential (i.e., in the absence of neighbours) that is reduced by competitive interactions with neighbouring trees:

$$BAI = PG \times s(\text{diameter}) \times \nu(NCI) \quad (2)$$

where BAI is annual basal area increment ($\text{cm}^2 \cdot \text{year}^{-1}$) at the POM of a given target tree, PG is maximum potential growth rate in the absence of size or competition effects. The functions s and ν are nonlinear modifiers that scale PG according to stem diameter and neighbourhood crowding, respectively. PG was treated as a plot-level fixed effect, with a unique PG estimate for each of the nine survey plots to account for site-specific variation in growth potential. We adopted this fixed-effects approach because our likelihood-based modelling framework estimates separate parameters for each plot and does not incorporate hierarchical random components. This approach is consistent with prior neighbourhood modelling frameworks (e.g., Canham et al., 2006; Buechling et al., 2017), where plot-specific growth potential is estimated to capture ecological heterogeneity among sites. Size and competitive effects were scalar variables (values from 0 to 1) that fractionally reduced potential growth.

2.5.1. Size effects

To quantify the effect of tree size on PG in Eq. 2, we used a lognormal function:

$$\text{Size} = \exp \left(-0.5 \times \left(\frac{\ln \left(\frac{\text{diameter} + X_p}{X_0} \right)}{X_b} \right)^2 \right) \quad (3)$$

where diameter is an annual time series of stem diameter measurements (cm), X_0 and X_b define the mode and breadth of the function, and X_p is a shift parameter that allows for positive intercepts when stem diameter is zero (Canham and Murphy, 2016). The lognormal generates a unimodal, asymmetrical curve that can fit monotonically increasing, decreasing, or unimodal data distributions (Canham et al., 2004). For those species ($N = 6$, Table 2) where the POM of diameter varied across individual trees due to stem buttressing, we allowed the mode and variance of Eq. 3 to vary as separate Gaussian functions of POM:

$$X_0 = X_h^\dagger \times \exp \left(-0.5 \times \left(\frac{\text{POM} - X_0^\dagger}{X_b^\dagger} \right)^2 \right) \quad (4)$$

and

$$X_b = X_h^* \times \exp \left(-0.5 \times \left(\frac{\text{POM} - X_0^*}{X_b^*} \right)^2 \right) \quad (5)$$

where POM is the point of measurement of diameter for a given sample tree. The parameters X_h^\dagger , X_0^\dagger and X_b^\dagger , and X_h^* , X_0^* and X_b^* determine the height, mode and breadth of a given equation, respectively.

2.5.2. Competition effects

We modelled competition effects using a nonlinear exponential decay function (ν in Eq. 2):

$$\nu = \exp(-C \times BA_{ratio}^\gamma \times NCI^\delta) \quad (6)$$

where NCI is a neighbourhood crowding index, which estimates the strength of competitive effects on a target tree based on the configuration and density of trees (Eq. 8). The parameters C and δ determine the shape of the response in a target tree to variation in NCI. The basal area ratio (BA_{ratio}) quantifies the relative size of a target tree compared to its neighbours and is used to adjust the crowding effect in the growth model (Eq. 7). It is defined as the ratio of the mean basal area of all neighbouring trees (within 15 m) to the basal area of the target tree:

$$BA_{ratio}^{\text{target}} = \frac{\frac{1}{n} \sum_j BA_j}{BA_{\text{target}}} \quad (7)$$

Table 2

Model selection criteria based on AIC scores (penalised for model complexity). Shown are differences in the AIC of a candidate model (i) relative to the minimum AIC in a species-specific set of models ($\Delta_i = AIC_i - AIC_{\min}$).

Species	Sample size	Δ AIC for alternate models							Best model statistics		
		Null	Size	Bigger tree	Neutral	Taxonomy	Guild	Density	^b NP	Bias	R ²
^a <i>Protomegabaria macrophylla</i>	1162	1288.1	166.2	0	80.2	72.9	202.4	52.4	16	1.12	33.1
<i>Strephonema pseudocola</i>	478	543.5	40.3	0	28.1	21.3	14.4	30.2	12	1.04	27.4
^a <i>Celtis mildbraedii</i>	2144	3449.4	155.9	106.3	118.6	22	0	75.1	22	1.08	54.1
<i>Erythrophleum suaveolens</i>	190	158.4	41.2	3	19.1	0	0	11.2	18	1.03	44.3
<i>Sterculia rhinopetala</i>	1444	1771.6	116.6	79.9	1.6	6.2	0	4.9	18	1.12	44.3
<i>Sterculia tragacantha</i>	984	444.8	131.3	85.6	14.9	4.7	0	19	21	0.99	24.7
<i>Carapa procera</i>	523	431.4	53.8	31.3	28.1	0	24.6	1.9	19	1.1	36.0
<i>Celtis zenkeri</i>	805	526.8	127.7	152	92.6	0	76.3	54.3	18	1.03	27.4
^a <i>Cynometra ananta</i>	546	644.7	27	17.5	6.9	10.4	6.9	0	21	1.01	36.4
<i>Funtumia elastica</i>	3031	1479.7	434.7	365.8	262.4	158	110.8	0	17	0.98	17.5
^a <i>Heritiera utilis</i>	515	916.5	155.8	55	21.5	26.1	8	0	24	1.19	63.8
^a <i>Nesogordonia papaverifera</i>	876	928.4	111.5	54.4	53.7	30.3	38.4	0	21	1.02	43.5
<i>Pouteria alnifolia</i>	546	245.2	56	32.7	29.6	11.3	15.3	0	18	0.99	16.3
<i>Pterocarpus erinaceus</i>	236	320.1	43.2	4.4	4.1	10.7	10.9	0	16	0.97	40.6
^a <i>Triplochiton scleroxylon</i>	585	1331	272	222.2	109	110.2	127.5	0	22	1.08	68.1

Notes.

^a Models account for differences in the height of diameter measurements (POM, see methods). Sample size refers to the model fitting datasets (trees \times years). Δ AIC for the best model is zero (bolded). Covariates in alternate models: Null = fit with a single mean value, Size = neighbour diameter only, Bigger tree = competition index based on a simple count of larger neighbour trees, Neutral = equivalent competitors, Taxonomy = competitors classified by taxonomic identity (3 classes: conspecifics, within family and others), Guild = competitors classified by shade tolerance (3 classes), Density = competitors classified by wood density (2 or 3 classes depending on focal species).

^b NP is the number of model parameters. Bias is derived from the slope of observed vs predicted growth.

where $BA_{\text{ratio}}^{\text{target}}$ is the basal area ratio for the target tree, n is the number of neighbouring trees within 15 m of the target tree, BA_j denotes the basal area of neighbouring tree j , and BA_{target} is the basal area of the target tree.

The neighbourhood crowding index (NCI) in Eq. 6 accounts for both the stem diameter and proximity of neighbouring trees relative to a target tree:

$$NCI_{\text{target}} = \sum_{i=1}^K \lambda_i \left(\sum_{j=1}^{n_i} \frac{(\text{diameter}_{ij})^\alpha}{(\text{distance}_{ij})^\beta} \right) \quad (8)$$

where NCI_{target} is the neighbourhood crowding index for the target tree, K is the total number of neighbour groups (e.g., wood density, shade tolerance, taxonomic classes), n_i is the number of neighbours in group i located within 15 m of the target tree, diameter_{ij} (m) is the stem size of neighbour tree j in group i , and distance_{ij} (m) is the horizontal distance between the target tree and neighbour j in group i . The exponents α and β adjust the shape of the effects of neighbour diameter and distance, respectively.

The competition coefficient (λ_i) in Eq. 8 scales the aggregated effect of neighbour group i on the target tree, reflecting differences in competitive ability associated with specific functional or taxonomic attributes. In prior studies, unique values of λ_i were estimated based on the taxonomic identity of the neighbours (Buechling et al., 2017; Canham et al., 2004). Here, to test whether resource allocation strategies of neighbours influence their competitive ability, rather than their identity per se, we assigned individual neighbour taxa to homogeneous attribute classes and computed unique λ_i for each class. We formulated and evaluated independent models fitted with alternate attribute classes. Specifically, we compared models using (1) separate λ_i for K categories of wood density ($K = 2$ or $K = 3$, depending on the focal species), (2) unique λ_i for different guild (shade tolerance) classes ($K = 3$), and (3) separate λ_i values for conspecifics, neighbours of the same family as the target tree, and nonfamilial neighbours ($K = 3$ groups). We additionally fit simpler alternate models that treated all neighbour species as equivalent in terms of their competition potential (i.e., $\lambda = 1$).

To capture the full effects of competition on target trees located near plot edges, we simulated neighbourhood conditions outside of plot boundaries (since those trees were not measured during field surveys).

Adopting methods from Uriarte et al. (2005, 2016), we generated a hypothetical population of trees within 20 m buffer regions surrounding all plot edges. The simulated buffer populations had a size distribution and species composition equivalent to the structure and composition of the surveyed trees that were located inside and within 20 m of plot boundaries. The simulated trees were randomly located within the buffers.

2.5.3. Water supply effects

To test whether variation in soil moisture influences the strength of crowding effects from neighbours, we modelled the competition-shape parameter C in Eq. 6 as a Gaussian function of soil moisture:

$$C = Q_h \times \exp \left[-0.5 \times \left(\frac{\text{SMI} - Q_0}{Q_b} \right)^2 \right] \quad (9)$$

where SMI is a dimensionless soil moisture index describing mean 12-month soil moisture availability (Eq. 1), and Q_0 , Q_b , and Q_h describe the mode, breadth, and height of the function, respectively. This formulation was chosen a priori based on biological expectations and ecological theory: competition is expected to peak at intermediate moisture levels, where water availability supports physiological activity and resource uptake, and to decline under drought or saturated soil conditions, as stress reduces growth and resource demand (Maestre et al., 2009). Such unimodal responses align with stress gradient theory, which predicts shifts in plant-plant interactions along environmental gradients (Maestre et al., 2009). By allowing the C parameter to vary unimodally with soil moisture, we explicitly test for a nonlinear interaction between competition and water availability.

2.5.4. Model specification and selection

Model parameters were estimated using maximum likelihood. A global optimisation algorithm (simulated annealing, Goffe et al., 1994) was used to determine parameter values that maximised the log-likelihood of predicting the observed growth rates for a focal species, given a particular model form (Uriarte et al., 2004b). To quantify uncertainty in parameter estimates, we computed support intervals for each parameter (Edwards, 1992) (Table S3). These intervals define the range of parameter values around the maximum likelihood estimates for which the log likelihood decreases by no more than 2 units. We used a

normal probability density function (PDF) to calculate the likelihood. The PDF was modified to account for heteroscedasticity in the model residuals by allowing the standard deviation (SD) to vary as a power function of the mean:

$$SD = a + G^b \tag{10}$$

where a and b are estimated parameters and G is a vector of predicted growth rates (BAI).

Akaike's information criterion (AIC), penalised for model complexity, was computed to compare the performance of alternate models (Johnson and Omland, 2004). Model fit was assessed based on the proportion of variation explained (R^2) and prediction bias (slope of the regression of observed vs. predicted BAI). Analyses were conducted in R statistical software (version 4.1.1; R Core Team, 2021) using the 'likelihood' package (version 1.7; Murphy, 2015).

3. Results

We tested seven alternative growth models for the 15 most common tree species in the survey plots. The models explained 16%–68% of observed growth variation, depending on species (Table 2 and Fig. S3). All models produced unbiased estimates of growth. Based on information theory, the best-supported models for all focal species accounted for the independent effects of target tree size and neighbour competition. In

general, growth potential in all focal species increased nonlinearly with increasing stem diameter (Fig. S2). Thus, larger individual trees had a higher maximum growth potential, controlling for other factors. For three species, this relationship was unimodal, whereby growth increased rapidly with size and then declined beyond a threshold diameter level. Growth in the other species increased monotonically with size but did not reach a threshold within the range of our field data (Fig. S2).

3.1. Effects of wood density and shade tolerance

Our findings generally reject the hypothesis of equivalent neighbour effects on competition dynamics. By model selection (Table 2), competition outcomes for most focal species (13 of 15) were influenced by biological attributes related to the life-history or resource allocation strategies of their neighbours, such as wood density, shade tolerance, or their taxonomic identity. Only two focal taxa (*Protomegabaria macrophylla* and *Strephonema pseudocola*) were insensitive to any of the modelled attributes of their neighbours, and only responded, in terms of a growth reduction, to the density of larger neighbour trees in their vicinity (within 15 m). The wood density of neighbouring trees modulated competitive interactions for almost half of the focal taxa (7 of 15), controlling for other factors (Table 2). In most cases, neighbour trees with comparatively dense wood were stronger competitors than neighbours with softer or lower wood density (Fig. 1a and b). There were two

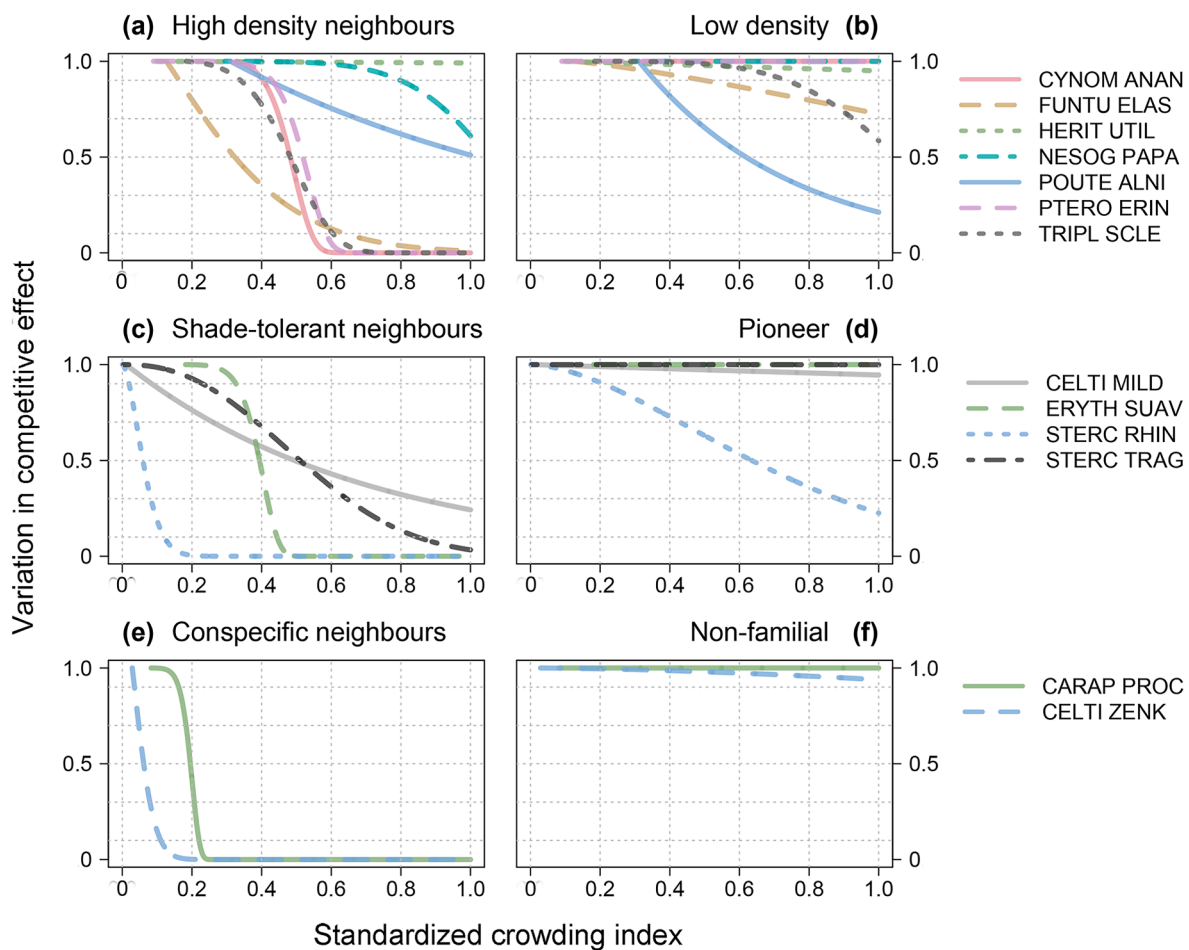


Fig. 1. Predicted stem growth in a 30 cm tree for 13 focal species that were sensitive to the biological attributes (i.e. resource allocation strategies) or taxonomy of their neighbours. The best-supported species-specific models (Table 2) were used in these analyses. The response variable is the proportional reduction in maximum potential growth. A standardized crowding index accounts for observed variation in the configuration, density and biological attributes of the neighbouring trees. We predicted growth reductions for each species under two alternate neighbourhood scenarios: (1) neighbours with dense vs. soft wood (a and b); (2) shade-tolerant vs. light-demanding neighbours (c and d); and (3) conspecific vs. neighbours from other families (e and f). Soil moisture was fixed at the observed mean level for a species.

exceptions, as *Nesogordonia papaverifera* and *Pouteria alnifolia* were relatively more sensitive to neighbours with low-density wood. Competition in four of the focal species was influenced by the shade tolerance ability of neighbours. Shade-tolerant neighbours were consistently stronger competitors relative to light-demanding species (pioneers, Fig. 1c and d). Competition outcomes for the remaining two focal species were influenced by the taxonomy, but not the resource allocation strategies of the neighbours. For these focal taxa, conspecific neighbours were stronger competitors relative to trees from other species or families (Fig. 1e and f).

3.2. Moisture, size and wood density interactions

Competitive outcomes were regulated by a composite of factors. The strength and shape of these relationships were highly species-specific. For some species ($N = 6$), moisture limitation independently amplified crowding effects from neighbours, controlling for tree size and trait variation. For example, for a constant density and configuration of neighbours (Crowding index, Eq. 8), potential growth in a 30-cm target tree was progressively reduced along a gradient of decreasing moisture supply and minimised in dense stands and xeric soils (Fig. S4). Responses in a target tree to neighbourhood crowding effects also depended on tree size. For most focal species ($N = 9$), 10 cm trees were more sensitive to increasing levels of crowding relative to 50 cm individuals, regardless of moisture availability or trait effects (Fig. 2a vs. 2d and Fig. 2c vs. 2f).

More generally, however, competitive outcomes were determined by the nonadditive effects of target tree size, levels of neighbourhood crowding, the resource allocation strategies of neighbours, and moisture conditions. For example, size-dependent variation in a target tree's response to crowding was modified by soil moisture supply. For most focal species ($N = 10$), 10 cm target trees in xeric environments were substantially more sensitive to elevated crowding levels relative to 50 cm trees in mesic soils (Fig. 2b vs. 2f). However, for a few species (e.g., *Sterculia tragacantha* and *Funtumia elastica*), 50 cm trees showed greater sensitivity to neighbourhood crowding than 10 cm trees under xeric conditions (Fig. 2a vs 2d). Notably, for these same species, larger trees in wetter conditions were more sensitive to crowding increases relative to smaller trees in xeric sites (Fig. 2a vs. 2f). Variations in plant strategies additionally mediated the shape of these relationships. Neighbours having attributes that enhanced their competitive ability (high wood density, shade-tolerance, or conspecifics), magnified the negative effects of crowding on small trees in moisture-limited environments (Fig. 2a vs. 2f). Again, the shape and magnitude of these responses varied substantially among focal species.

4. Discussion

Our findings reveal that growth generally increased nonlinearly with stem diameter, although the strength and shape of this relationship varied by species. Most taxa showed increasing growth with size, but *Funtumia elastica*, *Celtis zenkerii*, and *Pouteria alnifolia* followed peak-and-decline trends, consistent with ontogenetic constraints or size-

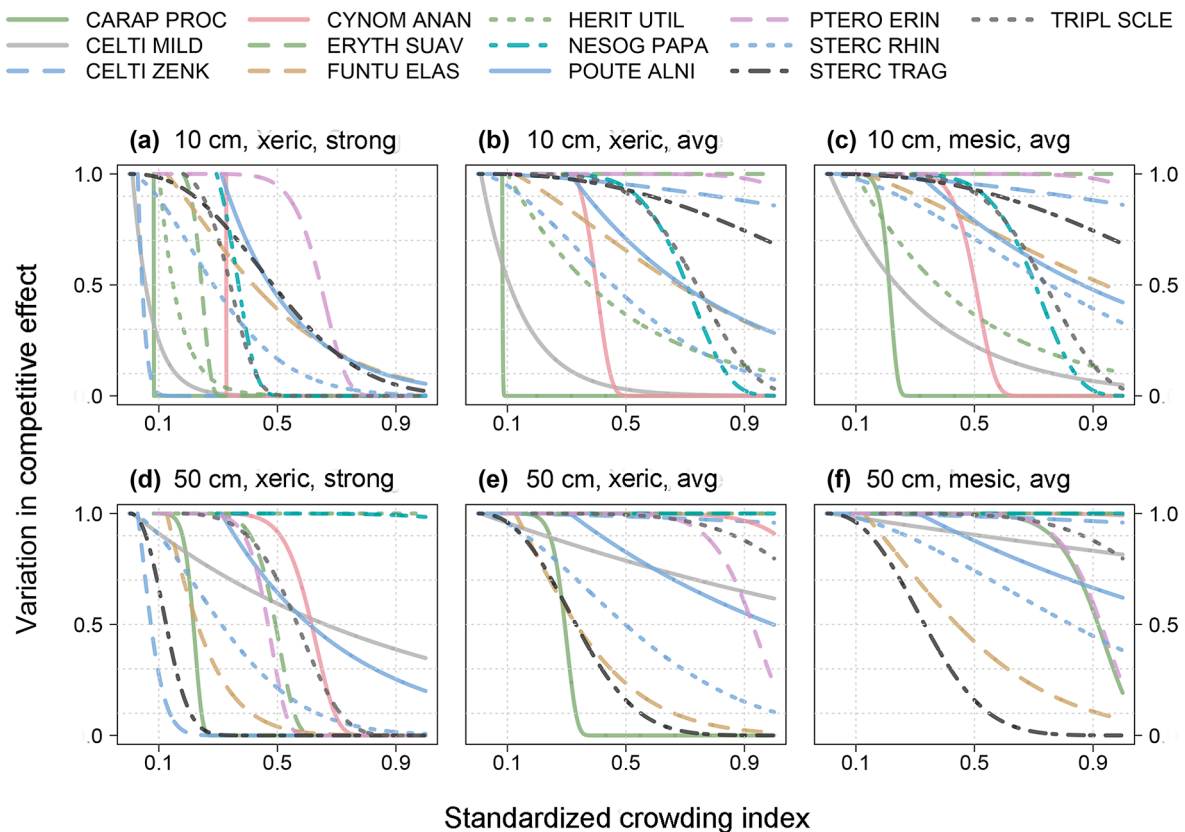


Fig. 2. Predicted competitive effects on growth for 13 focal species as a function of tree size, soil moisture conditions, and the allocation strategies of the neighbours. The competitive effect (y-axis), calculated from Eqs. 6–9, represents the expected proportional reduction in maximum potential growth in a target tree (10 or 50 cm diameter) due to observed variation in the density and configuration of neighbour trees (crowding index) under three alternate soil moisture and neighbour trait scenarios: (1) xeric sites and strong competitors (a and d), (2) xeric sites and average strength competitors (b and e), and (3) mesic sites and average strength competitors (c and f). The crowding index (x-axis) was scaled by the maximum observed value for a species to facilitate species comparisons. Moisture conditions were set using percentiles: xeric and mesic were defined by the 5th and 95th percentiles of observed soil moisture. Competitor strength was set by trait level (e.g., average vs. high wood density class).

related physiological limitations (Mencuccini et al., 2005). These patterns align with the life-history strategies of *F. elastica* and *C. zenkeri*, both classified as non-pioneer light-demanding species (Table 1). Such species often exhibit broader environmental tolerance and higher landscape frequency than pioneers or shade-tolerant taxa, reflecting traits shared with both successional groups (Bayu et al., 2017). While this ecological flexibility may promote rapid early growth, it may also come with trade-offs, such as increased investment in reproduction or structural maintenance, that limit sustained diameter growth at larger sizes. *P. alnifolia*, a pioneer species, follows a different successional pathway but similarly shows fast growth that slows as structural demands increase. Future trait-based studies could elucidate whether these declines reflect ontogenetic transitions, species-specific allocation strategies, or anatomical limitations.

We also found that wood density and shade tolerance of neighbouring trees significantly influenced focal tree growth. Neighbours with denser wood and greater shade tolerance exerted stronger competitive effects, particularly under drier conditions. These effects were most pronounced for smaller trees, suggesting that both functional attributes and moisture availability mediate competition outcomes. Together, these findings highlight the complex interactions between biotic and environmental factors in shaping species-specific growth responses in tropical forests.

4.1. Effects of wood density and shade tolerance

Our findings highlight the importance of functional strategy divergence among species and the role of ecological context in shaping neighbourhood processes. Consistent with previous studies in tropical forests (Fortunel et al., 2016; Rozendaal et al., 2020), we found that species with a higher wood density exert stronger competitive effects relative to taxa with comparatively soft wood (Fig. 1a). The competitive advantage associated with high wood densities may be attributed to a conservative resource-use strategy (Chave et al., 2009; Kunstler et al., 2016; Lasky et al., 2014). Species with dense wood typically have a reduced innate growth potential, allocating a greater proportion of their resources to structural support and defence functions (Chave et al., 2009; Poorter and Markesteijn, 2008; Rüger et al., 2012). This allocation strategy enhances their ability to withstand mechanical damage, herbivory and other biotic pressures, while also improving tolerance to resource limitation (Kitajima and Poorter, 2010; Poorter et al., 2014).

Our results show that, for most focal species, high wood density confers strong competitive advantages under conditions of low water availability (Fig. 2a, b, 2d, and 2e). In general, despite variation among taxa, tree species with dense wood have a stress-resistant hydraulic architecture characterised by comparatively narrow xylem vessels (Sperry et al., 2006). Smaller vessels, in terms of both cross-sectional area and length, have a lower transport capacity but are considered to be more resistant to drought-associated low water potentials that can cause wall collapse and dysfunction (Chave et al., 2009; Markesteijn et al., 2011; Poorter and Markesteijn, 2008; Santiago et al., 2018). In contrast, species characterised by a wood structure that is relatively less dense may have wider and longer vessel conduits that facilitate a greater transport capacity, but that are concurrently more vulnerable to embolism and loss of function under water stress (Hacke et al., 2001). Thus, in xeric conditions, this trade-off can favour species with dense wood and a stable xylem architecture, as hydraulic safety facilitates a continuity of water supply to support essential physiological functions, including resource allocation to growth processes (Chen et al., 2019; De Guzman et al., 2021).

However, some studies have shown that wood density, as a species trait, is not always a reliable predictor of competitive ability (Fajardo, 2016), which is also consistent with our results (Fig. 1e and f). Wood density variation within species, driven by divergent adaptations to specific ecological niches (Swenson and Enquist, 2007), may obfuscate the relevance of this trait as a predictor of competitive ability. While wood density is often correlated with hydraulic traits linked to drought

resistance, it does not capture the full range of strategies species use to survive in competitive environments. For instance, species with similar wood density may exhibit different drought responses due to variations in vessel size, pit membrane properties, and water storage capacity (Delzon et al., 2010; Wheeler et al., 2005). Some species compensate for low embolism resistance through high water storage capacity, buffering against temporary water deficits (Meinzer et al., 2008; Pineda-García et al., 2013). Additionally, the relatively weak evidence for a universal relationship between xylem efficiency and safety identified in a prior meta-analysis (Gleason et al., 2016) suggests that wood density alone may not consistently determine species' competitive advantage in all environmental contexts. Since competitive ability depends on multiple interacting factors, including resource acquisition, growth rate, and stress tolerance, a quantification of anatomical traits such as leaf morphology and root architecture could contribute to a more complete or general understanding of competitive dynamics.

For a minority of species, a capacity for shade tolerance was more important than wood density as a predictor of competitive outcomes. Our results demonstrate that shade-tolerant neighbours exert a stronger competitive effect on focal species relative to pioneer species (Fig. 1c and d), corroborating previous studies (Kunstler et al., 2016; Uriarte et al., 2004b). Shade-tolerant species typically invest in traits such as high specific leaf area, which improves light capture efficiency and reduces respiration costs, thereby enhancing photosynthetic performance and net carbon gain under low-light conditions (Chave et al., 2009; Poorter and Markesteijn, 2008). Additionally, these species allocate more resources towards structural support, promoting canopy dominance. Consequently, they create deeper shade and competitively suppress pioneer species, which depend strongly on high light availability for growth (Hu et al., 2020; Rahman et al., 2021).

While wood density and shade tolerance were generally stronger predictors of neighbour effects, two focal species deviated from this pattern. *Protomegabaria macrophylla* and *Strephonema pseudocola*, both shade-tolerant evergreens found in wet forests, were insensitive to these traits and responded only to neighbour size. In environments with persistently low light and relatively stable conditions, trait-mediated interactions may be less ecologically relevant (Kraft et al., 2015). For these species, growth appears to be more constrained by architectural suppression, such as crowding from large neighbours, than by variation in neighbour function (Uriarte et al., 2004b). This suggests that under conditions of light limitation and low trait contrast, competitive effects may be governed by spatial structure than by functional divergence.

The stronger effects of conspecific neighbours on focal species identified in this study can be explained by their shared occupancy of ecological niches (Guo et al., 2021). This observation aligns with the resource partitioning hypothesis, which predicts more intense competition among conspecific individuals due to matching resource dependency (Lebrija-Trejos et al., 2014; Liu et al., 2016, 2021; Tilman, 1982). As conspecifics share similar growth requirements and phenotypic traits, they are more prone to experience direct competition for limited critical resources, leading to more intense intraspecific competition compared to heterospecifics (Goldberg and Barton, 1992). We note that only two species were more sensitive to the taxonomic identity of neighbours relative to neighbour trait variation. We suggest that trait-mediated competitive dynamics are likely prevalent in plant communities in general, but that additional axes of functional variation not explored in this study (e.g., leaf, hydraulic, or root traits) may influence the competitive responses of *Carapa procera* or *Celtis zenkeri* in this study (Fig. 1e and f) (Laughlin, 2014).

4.2. Moisture, size, and wood density interactions

Our study advances an understanding of how competitive outcomes among tree species are shaped by complex interactions between the individual effects of moisture availability, tree size, and wood density. We found that larger trees of a given species are less sensitive to

competition than their smaller counterparts and demonstrate comparatively lower sensitivity to water stress (Fig. 2). These findings underscore the greater capacity of larger trees to maintain growth and survival under water-limited conditions, a trend observed across divergent forested ecosystems (Chen et al., 2022; Germain et al., 2018; Gómez-Aparicio et al., 2011).

Consistent with resource-limitation theory, competitive pressures intensify under moisture scarcity, constraining tree physiological processes essential for growth and survival, such as photosynthesis and nutrient transport (Chen et al., 2019; Dale and Frank, 2022; Tilman, 1988). Under low-moisture conditions, larger trees gain competitive advantages through their structural and physiological adaptations. They typically have extensive root systems that access deeper soil layers, tapping into stable water reserves beyond the reach of smaller trees (Canadell et al., 1996; Li et al., 2019; Schwinning, 2010). Additionally, the broad canopies of larger trees intercept a disproportionate share of rainwater, which via stemflow is concentrated in soil reservoirs proximate to their root systems (Crockford and Richardson, 2000; Schume et al., 2004). This resource redistribution may reduce moisture availability for smaller trees, potentially elevating associated physiological and competitive stress (Magalhães et al., 2021). A size-based competitive advantage may also be underlain by a higher photosynthetic capacity associated with a more extensive leaf area, which allows for greater carbon assimilation and storage, supporting growth and survival under competitive and moisture-limited conditions (Hérault et al., 2011; Stephenson et al., 2014). However, it is important to recognise that under severe and prolonged drought conditions, larger trees may experience increased susceptibility to hydraulic constraints, such as higher embolism risks and flow limitations associated with greater tree height. For instance, Stovall et al. (2019) demonstrated that taller trees exhibit elevated mortality risks during intense drought episodes, suggesting that extreme and persistent drought conditions could potentially reverse or significantly alter the patterns observed in our study. Our findings are also consistent with aspects of biodiversity research (Lebrija-Trejos et al., 2023), where species-specific responses to temporal variation in the environment, such as fluctuating soil moisture storage, may lead to shifting competitive outcomes. More specifically, variability in resource supply may favour distinct taxa at different times, depending on the functional strategies of the coexisting species (Chesson, 1994; Kelly and Bowler, 2002).

We focused our analyses on the growth potential of trees at a local neighbourhood scale (i.e. within 15 m). Our approach was partly pragmatic, facilitating an investigation of the fine-scale biological and abiotic factors shaping competitive interactions between individual trees. We show that annual growth capacity declined exponentially for most species at this scale. However, we also acknowledge that interactions between individuals and environmental effects may encompass larger areas (Uriarte et al., 2010). A recent study has revealed a significant spatial structure in the composition of tropical forests at distances approaching ~100 m (Kalyuzhny et al., 2023). The authors attributed the non-random overdispersion of adult trees of a given species to the strong effects of conspecific negative density dependence (CNDD), such as host-specific pathogen infection or herbivory, that limited the survival of progeny near parent trees. The effects of CNDD acting on juveniles at local scales (<20 m) apparently propagated over extensive spatial and temporal gradients to influence the distribution of adult trees and composition of extant forests (Kalyuzhny et al., 2023). We suggest that these seemingly contrasting research outcomes are complementary and underscore the importance of different analytical approaches for understanding the complexity of demographic and species assembly processes in tropical forests.

5. Conclusions

Our neighbourhood analyses elucidate the nuanced dynamics of competitive interactions among tree species, demonstrating that

variation in species fitness strategies significantly influences competitive outcomes. For most focal species, high wood density was associated with stronger competitive ability. This aligns with theoretical expectations that investment in dense wood reflects a resource allocation strategy that prioritises the construction of xylem architectures resistant to dysfunction from vessel embolism during periods of water stress (Chave et al., 2009). Supporting this hypothesis, we found that the competitive advantage of dense wooded species was particularly pronounced under water-limited conditions. These findings suggest that climate-driven declines in water availability could reshape tropical forest communities by modifying competitive relationships and ensuing survivorship patterns, potentially promoting denser-wooded species. In this study, we used wood density data as a proxy to understand how the life history and functional strategies of species may scale their competitive effects. Investigating the specific anatomical traits underlying patterns identified by our analyses represents an important direction for future research.

CRedit authorship contribution statement

Forzia Ibrahim: Writing – review & editing, Writing – original draft, Visualization, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Arne Buechling:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Formal analysis, Conceptualization. **Stephen Adu-Bredu:** Writing – review & editing, Methodology, Conceptualization. **Shalom Addo-Danso:** Writing – review & editing, Methodology. **Akwasi Duah-Gyamfi:** Writing – review & editing, Methodology. **Yadvinder Malhi:** Writing – review & editing, Methodology. **Martin Svátek:** Writing – review & editing. **Radim Matula:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Data availability

Data will be made available on request.

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fecs.2025.100377>.

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