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TRAÇOS FUNCIONAIS DE PLANTAS DIRECIONAM O FUNCIONAMENTO E A DINÂMICA DE COMUNIDADES FLORESTAIS

PLANT FUNCTIONAL TRAITS DRIVE FOREST COMMUNITY FUNCTIONING AND DYNAMIC

JAMIR AFONSO DO PRADO JÚNIOR

UBERLÂNDIA - MG
FEVEREIRO / 2016

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Tese apresentada à Universidade Federal de Uberlândia como parte dos requisitos para a obtenção do título de Doutor em Ecologia e Conservação de Recursos Naturais.

Dr. Ivan Schiavini
(orientador)

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RESUMO

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O objetivo desta tese foi avaliar como os traços funcionais de plantas direcionam o funcionamento e a dinâmica de florestas estacionais tropicais em diferentes níveis ecológicos: comunidades, populações e indivíduos arbóreos. Foi testado como diferentes hipóteses ecológicas (fertilidade do solo, complementariedade de nichos, distribuição dos traços funcionais ou simplesmente a quantidade de vegetação inicial) atuam simultaneamente na produtividade das florestas estacionais tropicais. Nossos resultados mostraram que a produtividade de biomassa destas florestas é impulsionada principalmente pela quantidade de vegetação inicial (sendo maior em florestas com maior biomassa inicial) e pela distribuição dos traços funcionais entre as espécies (maior produtividade em florestas com traços funcionais conservativos). Surpreendentemente, a produtividade não esteve ligada à complementariedade de nichos, e negativamente à fertilidade solo. Estes resultados realçam que, de um ponto de vista funcional, existe um paradoxo na produtividade de florestas estacionais e florestas úmidas. Também foi avaliado como o crescimento e a mortalidade das espécies é direcionada pelos seus traços funcionais, e como estas relações mudam com sua ontogenia. Foi observado que, em indivíduos de estatura menor, traços funcionais relacionados ao aumento da captura de luz, como maior área foliar e área de copa, aumentam as taxas de crescimento e/ou reduzem as taxas de mortalidade. Em indivíduos maiores, traços funcionais que aumentam a tolerância à seca, como maior densidade de madeira, reduzem as taxas de mortalidade. Finalmente, foi avaliado como as interações entre indivíduos arbóreos vizinhos, mediadas pelos seus traços funcionais, determinam o crescimento, sobrevivência e/ou recrutamento de uma determinada árvore focal. Foi encontrado que o efeito direto dos traços da árvore focal, independente de seus vizinhos, é o principal componente que influencia os processos demográficos. Mesmo assim, a influência da "quantidade" e da "qualidade" dos vizinhos também foi suportada, sendo que alguns traços funcionais aumentaram a competição e outros aumentaram a tolerância à maior concentração de árvores vizinhas. Estes resultados indicam que os traços interespecíficos podem promover simultaneamente a dominância local por um grupo de espécies com alto crescimento e sobrevivência, ao mesmo tempo em que outros traços aumentam a tolerância à competição e o recrutamento, o que permite estabilizar as diferenças entre os nichos e promover a diversidade local.

Palavras-chave: biomassa florestal, diferenciação de nichos, diversidade funcional, florestas estacionais tropicais, taxas demográficas.

INTRODUÇÃO GERAL

As florestais tropicais sustentam grande parte do equilíbrio e produtividade dos ecossistemas globais (FAO 2015). Estima-se que mais de um bilhão de pessoas dependam diretamente de atividades relacionadas à exploração destas florestas (Kamanga et al. 2009), e são inúmeros os serviços ecossistêmicos diretos e indiretos que estas florestas provêm, como estoque e sequestro de carbono, estabilidade climática, proteção e manutenção dos regimes hídricos, abrigo e recursos para a fauna, produção de alimentos, remédios e combustíveis (Diaz et al. 2011). Compreender os padrões estruturais e os processos dinâmicos destas florestas é fundamental para o entendimento do funcionamento de todos os sistemas biológicos, além de permitir o estabelecimento de predições sobre como os ambientes naturais responderão às crescentes intervenções antrópicas (Chazdon 2014).

Embora estudos indiquem que existe um padrão na dinâmica e funcionamento das florestas tropicais (Lewis et al. 2009), a alta diversidade alfa e a baixa densidade apresentada pela maioria das espécies dificultam a compreensão e determinação destes padrões ecológicos (Gourlet-Fleury et al. 2005). Além disso, a baixa similaridade florística entre os fragmentos florestais, fortemente influenciada pela distância entre eles, restringe os estudos a uma escala regional de comparação (Nekola & White 1999; Condit et al. 2002).

Avaliar as mudanças espaciais e temporais nas comunidades e populações de plantas com base em suas características (traços) funcionais tem se mostrado um caminho promissor para a compreensão dos padrões e processos que regem as florestas tropicais (Poorter et al. 2008). Um traço funcional pode ser definido como um atributo com influência potencialmente significativa no estabelecimento, sobrevivência ou *fitness* de uma espécie em seu ambiente natural (Reich et al. 2003). Os estudos dos traços funcionais avaliam a função que cada espécie, e até mesmo indivíduo, exerce na comunidade, e por serem independentes de classificações taxonômicas, permitem a comparação dos resultados em uma dimensão global (Pérez-Harguindeguy et al. 2013).

Grande parte do conhecimento sobre os traços funcionais em florestas tropicais provém de estudos em florestas úmidas (pluviais ou ombrófilas), sendo comum a extrapolação das informações para outra as florestas estacionais (Lohbeck et al. 2015). Estas, no entanto, apresentam processos estruturais, funcionais e sucessionais muito distintos, principalmente por estarem condicionadas à estacionalidade climática (dois a seis meses de seca) (Murphy & Lugo 1986). As florestas estacionais tropicais estão entre os ecossistemas mais fragmentados e ameaçados no mundo (Miles et al. 2006) e, esta complexidade de sua estrutura funcional, que envolvem deciduidade e restrição aos períodos de crescimento e reprodução de muitas espécies no período seco, aumentam sua suscetibilidade à perturbação (Kalacska et al. 2004). Conhecer os padrões e processos funcionais das florestas estacionais tropicais permitirá subsidiar políticas de manejo sustentável e conservação destas florestas.

Esta tese foi dividida em três capítulos complementares, que buscaram avaliar como os traços funcionais de plantas direcionam o funcionamento e a dinâmica de florestas estacionais tropicais. O primeiro capítulo, em uma abordagem de comunidades, objetivou determinar como diferentes hipóteses ecológicas direcionam a produtividade destas florestas. O segundo capítulo, em uma abordagem de populações, objetivou determinar como o crescimento e a mortalidade das espécies é influenciada pelos seus traços funcionais, e como essa influência varia de acordo com sua ontogenia. O terceiro capítulo, em uma abordagem de indivíduos, objetivou avaliar como as interações entre os indivíduos vizinhos, mediadas por seus traços funcionais, determinam a competição, coexistência e distribuição das espécies. Para isso, foram avaliados dados de dinâmica de oito florestas estacionais tropicais, ao longo de um período de cinco anos, e traços funcionais de mais de 170 espécies.

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CAPÍTULO 1

CONSERVATIVE SPECIES DRIVE BIOMASS PRODUCTIVITY IN TROPICAL DRY FORESTS

Conservative species drive biomass productivity in tropical dry forests[1]

SUMMARY

1. Forests account for a substantial part of the terrestrial biomass storage and productivity. To better understand forest productivity we need to disentangle the processes underlying net biomass change.
2. We tested how above-ground net biomass change and its underlying biomass dynamics (biomass recruitment, growth, and mortality) can be explained by four alterative and contested hypotheses; the soil fertility, biomass ratio, niche complementarity and vegetation quantity hypotheses.
3. Above-ground biomass dynamics was evaluated over a five-year period in 200 permanent sample plots in 8 tropical dry forests in Brazil, and related to soil fertility, community-weighted mean (CWM) traits that are important for carbon storage and sequestration (wood density, specific leaf area, maximum stem diameter and deciduousness), species richness, functional diversity, and initial stand biomass.
4. Initial stand biomass was the best predictor of all three processes of biomass dynamics, providing strong support for the vegetation quantity hypothesis. In these dry forests the dominance of conservative species, rather than of acquisitive species, is associated with high biomass growth and storage, probably because their low specific leaf area and high wood density allows them to keep on functioning during drought stress.
5. Paradoxically, high soil fertility (Ca) led to low biomass productivity, probably because of nutrient imbalance.
6. In contrast to what is shown for controlled experiments, we found no support for niche complementarity (in terms of functional diversity or species richness) for forest

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productivity. Biomass storage was favoured by low- rather than high trait diversity, as most of the biomass is concentrated in species with large stem diameter and high wood density.

7. *Synthesis*: Biomass dynamics is mainly shaped by vegetation quantity, and then by vegetation quality, in line with the mass ratio hypothesis. Dry forests show different trait-productivity relationships than wet forests, as stands with “slow” trait values are “fast” in terms of productivity. Diversity matters, but in a different way than expected; high trait diversity does not enhance productivity, but instead, does low trait diversity enhance carbon storage.

Keywords: biodiversity-ecosystem functioning, biomass ratio hypothesis, carbon stocks and sequestration, community weighted mean traits, functional diversity, green soup hypothesis, niche complementarity, plant population and community dynamics, soil fertility.

INTRODUCTION

Forests account for 70– 90% of terrestrial above and below-ground biomass (Houghton, Hall & Goetz 2009) and they present therefore a major global carbon sink (Brienen *et al.* 2015). To better understand forest productivity, we need to disentangle the processes underlying net biomass change. Net changes in forest above-ground biomass are the result of three processes of biomass dynamics: biomass gain from recruiting trees, biomass growth of surviving trees, and biomass loss from mortality (Brienen *et al.* 2015; Rozendaal & Chazdon 2015). Yet, most biomass productivity studies have focused on total biomass change over time, disregarding how the underlying processes are shaped by different drivers. Different dynamic processes are shaped by different drivers acting simultaneously, such as soil nutrient availability (Quesada *et al.* 2012), vegetation quantity (i.e., the initial stand biomass) and vegetation quality (i.e. species richness and their functional attributes; Finegan *et al.* 2015; Lohbeck *et al.* 2015). Furthermore, these differences can vary among vegetation types and with spatial and temporal scales (Malhi 2012).

Four main hypotheses have been put forward how species diversity can contribute to vegetation productivity: the soil fertility hypothesis (Pastor *et al.* 1984), the biomass ratio hypothesis (Grime 1998), the niche complementarity hypothesis (Tilman 1999), and the green soup (or vegetation quantity) hypothesis (Finegan *et al.* 2015; Lohbeck *et al.* 2015). The *soil fertility hypothesis* predicts that increases in soil nutrient availability has a positive effect on biomass productivity (growth and recruitment) since plants can grow faster when resource availability is high (Wright *et al.* 2011; Quesada *et al.* 2012), but it may also intensify competition, leading to higher mortality and turnover rates (Malhi *et al.* 2006). However, it is uncertain to what extent forests are nutrient limited (Vieira *et al.* 2004; Baraloto *et al.* 2011), since many forest species tolerate low nutrient levels, nutrients are quickly recycled through litter decomposition (Wright *et al.* 2011), and high productivity in tropical forests is often found on very infertile soils (Malhi 2012).

The *biomass ratio hypothesis* predicts that ecosystem processes are driven by the (traits of the) most abundant species in the community (Grime 1998). If the biomass ratio hypothesis plays a role, then productivity should be closely related to the community-weighted mean trait values (CWM), a community metric that weights species trait values by the relative basal area of the species in the community (Garnier *et al.* 2004). Higher biomass productivity is expected for communities dominated by fast-growing acquisitive species, having higher specific leaf area resulting in higher light capture, photosynthetic rates and net carbon gain (Poorter & Bongers 2006), and also have lower wood density resulting in high stem hydraulic conductivity and photosynthetic carbon gain (Santiago *et al.* 2004) and lower construction costs per wood volume (Chave *et al.* 2009). Conversely, these trait values may also result in higher biomass mortality of the community because acquisitive species have higher respiratory rates, and suffer more from herbivory, stem breakage and pathogen attack (Reich *et al.* 2003; Wright *et al.* 2010).

The *niche complementarity hypothesis* predicts that communities with a higher diversity of species (Tilman 1999) or functional traits (Díaz *et al.* 2011) use available resources more efficiently because of higher niche differentiation and interspecific facilitation, thus increasing biomass productivity of the community (Zhang, Chen & Reich 2012). Moreover, higher niche complementarity can reduce (indirectly, though lower likelihood of growing near a conspecific individuals) the negative effect of host-specific pathogens and herbivores, thereby reducing biomass mortality and increasing growth (Schnitzer *et al.* 2011). However, in forest communities, an increasing number of coexisting species can not only lead to niche differentiation but also to niche overlap and, hence, species redundancy (i.e., species that are functionally similar and make use of the same resources (Walker 1992).

Consequently, studies have found no relationship or even a negative relationship between taxonomic diversity and productivity (Vilà *et al.* 2003; Cavard *et al.* 2010). Functional traits provide a mechanistic link between species identity and ecosystem functioning, and productivity could therefore be more closely related to the variation in trait values in the community (i.e. functional trait diversity, Díaz *et al.* 2011) than to species richness. For example, higher functional diversity can indicate a pool of coexisting species with different life histories and ecological traits, e.g. multilayered canopies, roots at different depths and different light requirements, optimizing resources use (Vilà *et al.* 2013). An increasing number of studies have tested whether and how functional trait diversity contributes to productivity and many of them found no support for the contribution of niche complementarity hypothesis promoting ecosystem productivity (Conti & Díaz 2013; Finegan *et al.* 2015; Lohbeck *et al.* 2015).

The *green soup hypothesis* predicts that productivity is mainly driven by vegetation biomass, suggesting that vegetation “quantity” is more important than vegetation “quality” (sensu Lohbeck *et al.* 2015). A tight positive relationship between productivity and vegetation biomass is especially found early in succession (Lohbeck *et al.* 2015), where higher leaf area index results in higher light capture and total carbon gain. Later in succession, forest stands are closed and the light availability is reduced, leading to a negative relation between productivity and vegetation biomass (Peña-Claros *et al.* 2008; Toledo *et al.* 2011; Finegan *et al.* 2015; Rozendaal & Chazdon 2015).

Most of our knowledge on the relationships between different drivers and biomass storage and productivity in the tropics were conducted in moist and wet forests (Brienen *et al.* 2015; Finegan *et al.* 2015; Rozendaal & Chazdon 2015). However, the relationships between drivers and biomass dynamics may be fundamentally different between wet and dry forests, since different resources limit plant performance in these forest types. For example, water availability limits forest growth in dry forests whereas light availability does so in wet forest (Lohbeck *et al.* 2013). Thus, conservative trait values that enhance drought tolerance, such as dense wood (implying less hydraulic failure, Pineda-García, Paz & Meinzer 2013) and lower specific leaf area (implying less transpiration, Poorter & Bongers 2006), may enhance species performance and hence, productivity in dry forests, whereas these conservative trait values are found to *reduce* biomass productivity in wet forests (Malhi *et al.* 2004; Finegan *et al.* 2015). Similarly, the niche complementarity effect has been found to be stronger in more stressful environments (Paquette & Messier 2011) and should, therefore, be more apparent in dry forests compared to wet forests.

The aim of this study is to evaluate how net above-ground biomass change and its underlying processes of biomass dynamics (biomass recruitment, growth, and mortality) are driven by soil nutrient availability (soil fertility hypothesis), community-weighted mean trait values (biomass ratio hypothesis), taxonomic and functional diversity (niche complementarity hypothesis) and by the initial stand biomass (green soup hypothesis). We present data of above-ground biomass dynamics over a five-year period in tropical dry forests in Brazil, and evaluate whether the relationships reported for moist and wet forests also hold for dry forests. We evaluated four key functional traits that are important for biomass stocks and productivity (maximum stem diameter, wood density, specific leaf area and deciduousness). We addressed the following questions: 1) What is the relative importance of each biomass dynamic process (growth, recruitment, and mortality) for net biomass change?; 2) How do soil nutrient availability, taxonomic and functional diversity, CWM traits and initial stand biomass affect these biomass dynamics? We predict higher biomass growth, recruitment and mortality on fertile soils and for communities that are dominated by fast-growing acquisitive species; that higher niche complementarity increases recruitment and growth and reduces mortality; and that higher stand biomass reduces recruitment and increases growth and mortality (see conceptual framework in Fig. 1); 3) Which of these ecological hypotheses (soil fertility, biomass ratio, niche complementarity or green soup) best explains variation in each driver of net biomass change?

METHODS

Research sites, species and soil sampling

This study was conducted in eight seasonal tropical dry forests (18º29’ to 19º40’ S and 47º30’ to 48º24’ W), in Minas Gerais state, Southeastern Brazil (Appendix S1). The region experiences a tropical savanna climate (Aw Megathermic climate of Köppen), characterized by rainy summers (October to March) and dry winters (April to September). Annual rainfall ranges from 1123 to 1547 mm, dry season length from four to six months of drought (with less than 100 mm rainfall during the dry season) and mean annual temperature of 21-22º C (Appendix S1). The study areas are located in conservation units or legal reserves and are surrounded by an agricultural or urban matrix (Lopes *et al.* 2012). The forests were slightly disturbed (up to 2004) by cattle grazing and/or very light selective logging (maximum one or two trees per hectare). Plots were established, in the core areas in each site, where we did not find any sign of tree stumps or logging. Based on the forest structure (e.g., high basal area) and the observed low growth rates, we consider the forests as mature. Since the disturbance was light or absent in our plots, we expect that it had minimal effects on our results. Soil type in studied areas is primarily red latosols that vary from moderately to strongly acidic (Embrapa 1982).

In each forest, 25 contiguous permanent sample plots (20 × 20 m) were established totaling one ha per site. In the first census, which was carried out at different time periods for each forest (t_0, 2006-2009), all trees with stem diameter at breast height (DBH, 1.30 m) ≥ 5 cm were tagged, their diameter was measured, height estimated, and identified to species level. In the second census, after five years for each forest (t_1, 2011–2014), all trees were re-measured and growth, mortality and recruitment rates were evaluated. A total of 8701 individuals were measured, belonging to 237 species, 161 genera and 58 families.

To determine soil nutrient availability, soil samples were collected from 0-20 cm soil depth at three fixed locations distributed in each plot. The three samples were pooled, sieved with a 2-mm sieve to remove roots and stones and air-dried for 24 hours. Soil analyses were conducted at the Soil Laboratory of Agricultural Sciences Institute of the Federal University of Uberlandia, Brazil for the following soil variables: pH (distilled water solution), phosphorus and potassium (Mehlich III extraction method, P and K in mg.dm^{-3}), calcium (Ca), magnesium (Mg), aluminum (Al) and cation exchange capacity (CEC, the sum of all exchangeable cations K, Ca, Mg, Al and acidity, in KCl 1mol.L^{-1} solution, in cmol.dm^{-3}). Additional information on soil nutrients values can be found in Appendix S2.We did not measure soil nitrogen, which tends to have a positive effect on forest productivity, although soil P is more often found to be limiting in tropical forests that occur on highly weathered soils (i.e. our study areas, Quesada et al 2012).

Forest structural and species diversity variables

To describe forest structure and diversity, we evaluated at t_0 four structural and species diversity variables per plot: tree density (ha^{-1}), rarefied species richness (S, from a random sampling of 30 individuals as this number of individuals is found in most plots), Shannon-Wiener index (H’) and Pielou’s index (J’). These two last diversity measures take also the relative abundance of each species into account, and are therefore better indicators of species diversity and species evenness than species richness. We used rarefied species richness instead of species richness to correct for the confounding positive effect of tree density in species richness. These variables were calculated in R 3.1.2 (R Development Core Team 2013), using the “vegan” package (Oksanen *et al*. 2014). Additional information on structural and species diversity variables values can be found in Appendix S2.

Functional traits

We evaluated four key functional traits that are important for biomass productivity: a whole plant trait (maximum stem diameter D_{max}), a stem trait (wood density WD), and two leaf traits (specific leaf area SLA; and deciduousness Dec, whether a species is deciduous or evergreen). Traits were evaluated for most species (171 for D_{max}, WD and Dec, and 106 species for SLA), and these species covered together 89% (range 79-93%) of the initial basal area of each forest. Traits were measured according to standard measurement protocols (D_{max} and SLA, Pérez-Harguindeguy *et al.* 2013), obtained from the global wood density database (WD, g.cm-3, Zanne *et al.* 2009, *available online*), or obtained from previous studies in the area (Dec, Lopes *et al.* 2014). Species maximum stem diameter (cm) is a potential indicator of tree longevity and life history strategy, and was calculated as the upper 95-percentile stem diameter for those trees whose diameter was equal to or greater than 10% of the observed maximum diameter of a population (King, Davies & Noor 2006). We used the DBH dataset of the first census to calculate species D_{max}. Specific leaf area (leaf area divided by leaf dry mass, $mm^2. mg^{-1}$) is an indicator of light interception efficiency and transpiration rates (Poorter & Bongers 2006). SLA was measured from fully expanded sun and shade leaves, with no obvious symptoms of pathogen or herbivore damage. Ten leaves were collected from 5-10 (average 7.8) adult trees (with DBH near to D_{max}) for each species. Wood density is an indicator of the volumetric wood construction costs, and species resistance to stem breakage, pathogen attack, and drought (Chave *et al.* 2009). Deciduousness is an important trait that enhances drought survival (Poorter & Markesteijn 2008). It also reduces the length of the growing season for species, whereas a deciduous canopy may increase light availability in understory that could enhance understory productivity during the dry season. Additional information on species functional trait values can be found in Appendix S3.

Community weighted mean traits and functional diversity indices

Community weighted mean (CWM) trait values and functional diversity (FD) indices were calculated per plot for the initial census. Traits were weighted by species' relative basal area in the plot t_0. We used species basal area as a weighting-factor because basal area reflects relative biomass which is a better indicator of plant performance than abundance. For functional diversity we excluded deciduousness because it is a binary trait (evergreen or deciduous). We used three complementary indices to measure FD (Mason *et al.* 2005; Villéger, Mason & Mouillot 2008): functional richness (F_{ric}) as the amount of multivariate-trait space filled by the community; functional evenness (F_{eve}) that indicates how species' basal area is spread over multivariate-trait space (F_{eve} is higher when basal area distribution is homogeneous across the multivariate-trait space); and functional divergence (F_{div}) as the degree of divergence from the center that most dominant species occupy in multivariate-trait space (F_{div} is higher when most of basal area is concentrated in the extremes of the multivariate-trait space). These functional diversity indices are orthogonal, i.e. there is no dependence between them *a priori* (Mason *et al.* 2005). All CWM and FD indices were calculated using the "FD" package in R (Laliberté & Legendre 2010). Additional information on community weighted mean (CWM) trait and functional diversity (FD) values can be found in Appendix S2.

Estimation of forest aboveground biomass components

We calculated aboveground biomass (AGB) for each tree based on tree DBH (cm), height (H, m) and species' wood density (WD, g.cm^{-3}): $AGB = 0.0673\times(WD\times DBH^2\times H)^{0.976}$ (Chave *et al.* 2014).

For each plot we estimated five different AGB components, and for the rate variables we divided the values by the census length (five years):

Initial biomass (AGB_i, Mg.ha^{-1}) – initial biomass of sampled trees in the first census (t_0);

Biomass increment of survivors (AGB_{surv}, Mg.ha^{-1}.yr^{-1}) – annual biomass increment produced by the growth of all trees that survived from t_0 to t_1;

Biomass increment of recruits (AGB_{recr}, Mg.ha^{-1}.yr^{-1}) – annual biomass increment obtained from the trees that attained at least 5 cm DBH in t_1 and that were not sampled in t_0. AGB_{recr} was calculated as the biomass of the recruit minus the biomass of the same individual with a DBH of 5 cm. Thus, we assume that the tree was recruited immediately after the first census and avoid biomass overestimation assuming that recruits had initial DBH of 0 cm in the initial census (Talbot *et al.* 2014).

Biomass mortality (AGB_{mort}, Mg.ha^{-1}.yr^{-1}) – annual biomass loss obtained from the trees that died between t_0 and t_1. To be able to compare biomass loss (i.e., mortality) with biomass gain (i.e., recruitment and growth), the biomass mortality was calculated as the biomass of the tree in the initial census, minus the biomass of the same individual with a DBH of 5 cm (Talbot *et al.* 2014).

Net biomass change (AGB_{net}, Mg.ha^{-1}.year^{-1}) – is the net annual change in biomass during the census period ($t_1 – t_0$), calculated as $AGB_{net} = AGB_{surv} + AGB_{recr} - AGB_{mort.}$

Statistical analyses

To evaluate how net above-ground biomass change is determined by underlying biomass dynamic processes (biomass recruitment, growth, and mortality) we performed linear mixed models including sites as random effects (to account for the nestedness of the plots within sites). Biomass dynamics was not significantly related to differences in rainfall amount and rainfall seasonality (number of months with less than 100 mm and 50 mm of precipitation) across sites (Appendix S1), and was therefore not further included in the analyses. To test how biomass dynamics was driven by different predictors we related each process of biomass dynamics (AGB_{surv}, AGB_{recr} and AGB_{dead}) to soil nutrients (pH, P, K, Ca, Mg, Al and CEC), community weighted mean trait values (CWM_{dmax}, CWM_{wd}, CWM_{sla}, CWM_{dec}), taxonomic diversity (S, H', J'), functional diversity indices (F_{ric}, F_{eve}, F_{div}) and vegetation "quantity" (initial biomass and tree density) using linear mixed models, including sites as a random effect. We used all subsets regression analysis and selected the models that had lowest Akaike Information Criterion (AIC). Models were considered to be equally supported if the difference in AIC was less than two units (Burnham & Anderson 2002). When models were equally supported, we selected the most parsimonious model (with lowest number of predictors). When necessary, data were $\log_{10}$ or square root-transformed prior to analysis, to meet the assumptions of normality, homoscedasticity, reduce the effect of outliers and to account for possible nonlinear relationships between variables. We calculated the conditional (c) and marginal (m) R^2 for the best model of each process following (Nakagawa & Schielzeth 2013). R^2_c indicates the variance explained by both fixed and random effects, whereas R^2_m indicates the variance explained by fixed effects only. When R^2_m value is close to R^2_c, then most of the variation explained in the biomass components is caused by the predictors (fixed effects), rather than by site differences (random effect). We evaluated the relative importance of each ecological hypothesis (soil fertility, biomass ratio, niche complementarity or green soup) by comparing for each biomass component the standardized regression coefficients (β) of predictors retained in the best multiple regression model. Mixed-effects models were performed using the "lme4" package (Bates et al. 2011) and all subsets regression analyses using the "MuMIn" package (Burnham & Anderson 2002). Bivariate relationships between biomass components and tested predictors can be found in Appendix S4. To evaluate whether predictors were associated, we provided a Kendall's (tau) correlation matrix between all pairs of predictors (standardized for each site) in Appendix S5. We used Kendall's correlation rather than Pearson’s correlation to meet the assumptions of normality and homoscedasticity. All analyses were performed using R 3.1.2 (R Development Core Team 2013).

RESULTS

Average initial biomass across plots was 246.39 $Mg.ha^{-1}$ ± 13.75 (average ± standard error), net biomass change was 0.27 $Mg.ha^{-1}.yr^{-1}$ ± 0.62, biomass growth of surviving trees was 3.88 $Mg.ha^{-1}.yr^{-1}$ ± 0.17, biomass growth of recruiting trees was 0.06 $Mg.ha^{-1}.yr^{-1}$ ± 0.01, and biomass mortality was 3.67 $Mg.ha^{-1}.yr^{-1}$ ± 0.61 (Appendix S2). Multiple regression analysis indicated that net biomass change (Fig. 2, R^2_m = 0.93) was mostly driven by mortality (standardized regression coefficient β = -0.88), followed by biomass growth of surviving trees (β = 0.35). Biomass recruitment did not contribute strongly to net biomass change (β = 0.036) and was not included in the model, probably because of its low absolute values.

Our best model for biomass growth of survivors (AGB_{surv}, R^2_m = 0.42) included the effect of AGB_i (β = 0.59), CWM_{sla} (β = -0.18) and soil calcium (β = -0.13) (Table 1, See Appendix S6 for scatterplots of the bivariate relationships between demographic biomass processes and drivers). This indicates that biomass growth of surviving trees is higher in plots with higher stand biomass, dominated by species with lower specific leaf area, and located on soils with lower calcium concentration. Biomass recruitment (AGB_{recr}, R^2_m=0.10) was best predicted by AGB_i (β = -0.24) and CWM_{dec} (β = 0.21) (Table 1), indicating that communities with lower stand biomass and dominated by deciduous species have higher biomass recruitment. Biomass mortality (AGB_{mort}, R^2_m=0.05) was predicted by AGB_i only (β = 0.22) (Table 1), indicating that communities with higher stand biomass have higher biomass loss from mortality. Initial biomass itself (AGB_i, R^2_m=0.58) was best predicted by CWM_{dmax} (β = 0.59), CWM_{wd} (β = 0.16), F_{div} (β = 0.16) and F_{eve} (β = -0.20) (Table 1), indicating that communities have higher stand biomass when they are dominated by large and dense-wooded species, with lower functional evenness (most of species basal area is concentrated in a constrained area of the multivariate-trait space) and higher functional divergence (most of species basal area is concentrated in the extremes of the multivariate-trait space).

Table 1. Best models obtained from a series of multiple regression analyses for each biomass components (AGB_{surv}, AGB_{recr} AGB_{mort}, AGB_i) and 19 predictors using linear mixed models and including sites as random effect. Standardized multiple regression coefficients (Coef), significance levels (p), conditional (c) and marginal (m) R^2 (R^2_c = both fixed and random effects, and R^2_m = fixed effects only) and Akaike Information Criterion (AIC) are given. AGB_i = stand biomass, AGB_{net} = net biomass change, AGB_{surv} = biomass growth of surviving trees, AGB_{mort} = biomass mortality, AGB_{recr} = biomass recruitment, NI = tree-density (ha^{-1}), CWM = community weighed mean, WD = wood density, D_{max} = maximum stem diameter, SLA = specific leaf area, Dec = deciduousness, S = rarefied species richness, H' = Shannon-Wiener index, J' = Pielou's index, F_{ric} = functional richness, F_{eve} = functional evenness, F_{div} = functional divergence, P = phosphorous, K = potassium, Ca = calcium, Mg = magnesium, Al = aluminum, CEC = cation exchange capacity.

Hypothesis	**Predictor**	**AGB_{surv}**		**AGB_{recr}**		**AGB_{mort}**		**AGB_i**	
		Coef	p	Coef	p	Coef	p	Coef	p
Green soup	AGB_i	0.59	<0.01	-0.24	<0.01	0.22	<0.01	-	-
	NI								
Biomass ratio	CWM_{wd}							0.16	<0.01
	CWM_{sla}	-0.18	<0.01						
	CWM_{dmax}							0.59	<0.01
	CWM_{dec}			0.21	<0.01				
Niche complementarity	F_{ric}								
	F_{eve}							-0.20	<0.01
	F_{div}							0.16	<0.01
	S								
	H'								
	J'								
Soil nutrients	pH								
	P								
	K								
	Al								
	Ca	-0.13	<0.05						
	Mg								
	CEC								
Model	R^2_m	0.42		0.10		0.05		0.58	
	R^2_c	0.43		0.10		0.06		0.58	
	AIC	468.0		556.4		564.5		408.9	

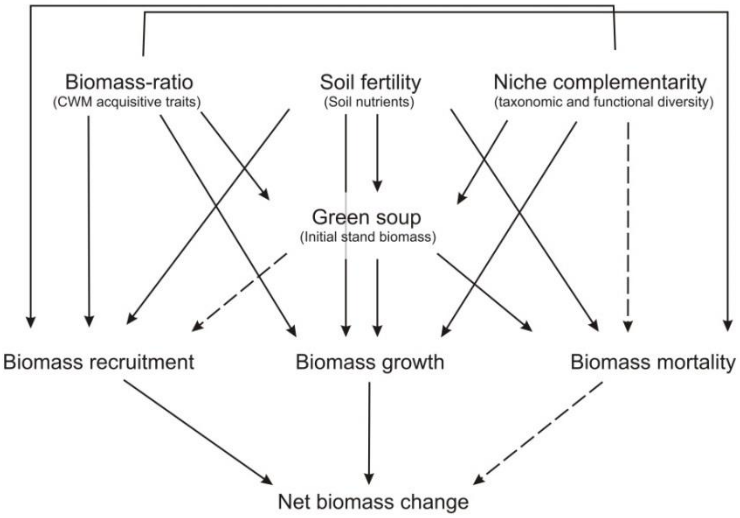

Fig. 1. Conceptual framework showing how changes in net above-ground biomass are determined by underlying dynamical processes (biomass recruitment, growth, and mortality), that are expected to be driven by soil nutrients, trait values of the dominant species (biomass ratio hypothesis), taxonomic and functional diversity (niche complementarity hypothesis) and by the stand biomass-dependent effect (green soup hypothesis). Black arrows refer to positive effects and dash arrows refer to negative effects. See text for further explanation.

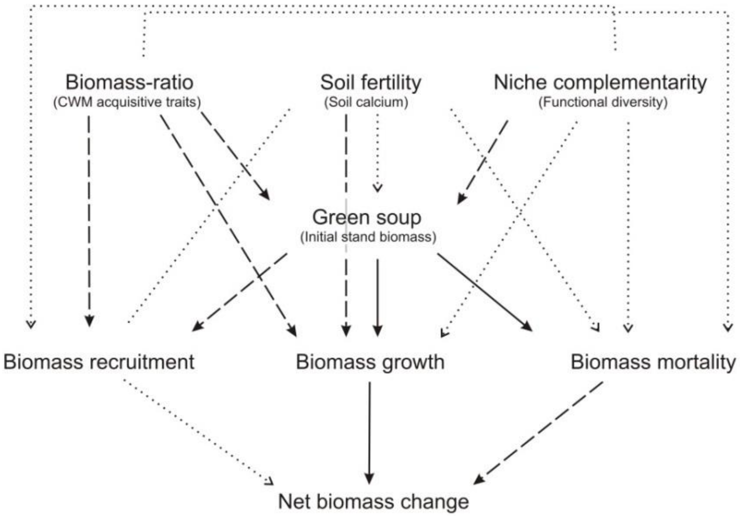

Fig. 2. Combination of the best models obtained from a series of multiple regression analyses for each biomass components (AGB_{surv}, AGB_{recr} AGB_{mort}, AGB_{i}) and the tested hypotheses using linear mixed models and including sites as random effect (see Table 1 for statistics). Black arrows refer to significant positive effects, long dashed arrows refer to significant negative effects and dotted arrows refer to no significant effects.

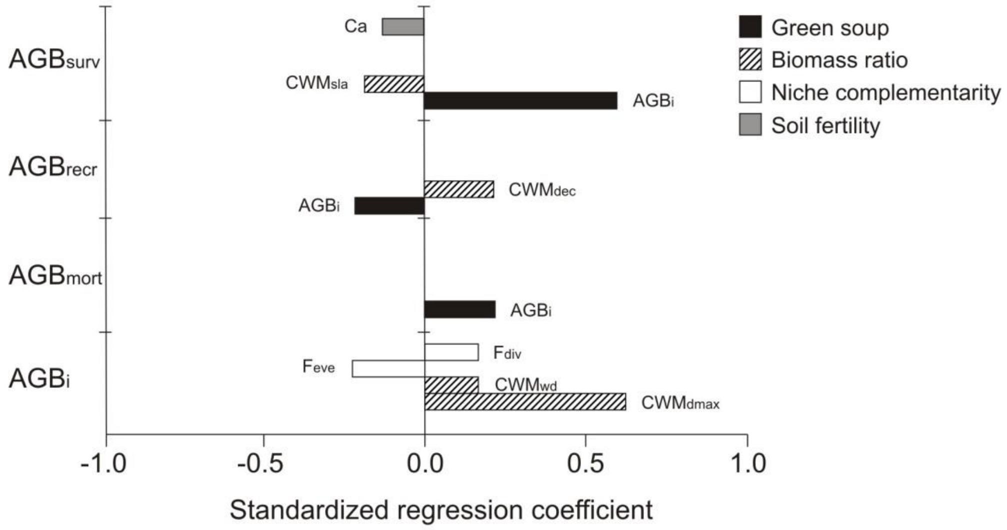

Fig. 3. Comparison among the effect of four ecological hypotheses (soil fertility, biomass ratio, niche complementarity and green soup) on biomass dynamics in tropical dry forests. Standardized regression coefficients can directly be compared among each other; the higher the value, the stronger the relationship observed. Only significant effects are included (see Table 1 for more information). AGB_i = stand biomass, AGB_{net} = net biomass change, AGB_{surv} = biomass growth of surviving trees, AGB_{mort} = biomass mortality, AGB_{recr} = biomass recruitment.

DISCUSSION

We assessed how different ecological hypotheses (soil fertility, biomass ratio, niche complementarity and green soup) shape net biomass change in tropical dry forests. To understand changes in biomass we disentangle its underlying dynamic processes (biomass recruitment, growth, and mortality) (Fig. 1 and 2). We found strong support for the green soup hypothesis for all biomass dynamic processes (Table 1). The biomass ratio hypothesis was also important for growth and recruitment, and contrary to what has been found in moist and wet forests, conservative species rather than acquisitive species were related to higher productivity and biomass storage in dry forests. We found no support for the niche complementarity and soil fertility hypotheses on net biomass change in these dry forests.

Net biomass change is mainly driven by mortality

We evaluated the role of underlying biomass dynamic processes (biomass growth, recruitment and mortality) in the net biomass change of tropical dry forests. We found that biomass mortality (AGB_{mort}) was the major determinant of net biomass change (standardized coefficient -0.88), with a smaller contribution of biomass growth (AGB_{surv} 0.35), whereas biomass recruitment (AGB_{recr} 0.036) was not a strong contributing factor for our net biomass change model (Fig. 2). This is probably due the lower absolute mean values for recruitment (0.06 $Mg.ha^{-1}.year^{-1}$) compared to growth of surviving trees (3.88 $Mg.ha^{-1}.year^{-1}$) and mortality (3.67 $Mg.ha^{-1}.year^{-1}$). Biomass gain from recruitment may be more important in early stages of forest recovery after disturbances (Carreño-Rocabado *et al.* 2012; Rozendaal & Chazdon 2015).

Biomass mortality was only explained by initial stand biomass. It was the process with the lowest R^2_m (variation explained by fixed effects only = 0.05, Table 1). Mortality is less predictable, probably because it is a slow process and a long evaluation period is needed to get accurate mortality estimates (Poorter *et al.* 2008; Brienen *et al.* 2015). The importance of biomass mortality for net biomass change increases with stand age (cf. Malhi 2012) due to reduction in light availability and self-thinning (Rozendaal & Chazdon 2015). However, it is uncertain to what extent light limitation determines tree mortality in dry forests, especially for larger trees that contribute most to biomass mortality. Hence, at community-level, biomass mortality is most important for net biomass change, but it depends itself only on vegetation quantity, and not on other drivers, that are often thought to be important for ecosystem productivity (such as niche complementarity, biomass-ratio or soil nutrient availability).

Biomass recruitment is driven by the abundance and phenology of canopy trees

We predicted that biomass recruitment would decline with initial stand biomass, because the shaded conditions of closed forest provide little opportunity for regeneration in the understory due to light limitations and water competition (Finegan *et al.* 2015). We indeed found that biomass recruitment was higher in stands with a lower initial biomass, and also in stands dominated by deciduous species (i.e., higher CWM_{dec}). This indicates that biomass recruitment in dry forests is determined by the abundance of canopy trees and by leaf phenology of the whole community (Uemura 1994). A deciduous canopy increases light availability in understory, thus enhancing forest regeneration (Komiyama, Kato & Teranishi 2001). In dry-deciduous forests, understory trees flush their leaves up to one month earlier than canopy trees, thus increasing understory growth and recruitment rates (Kato & Komiyama 2002). Recent studies suggest that light is not a major limiting resource in dry forests, due their lower and (seasonally) more open canopy compared to wet forests (Lebrija-Trejos *et al.* 2008; Lohbeck *et al.* 2013). Our results suggest that light availability is still an important driver of biomass recruitment in dry forest. Hence, the abundance and composition of canopy trees provide an ecological filter for dry forest regeneration, either by increasing competition for water or by reducing light availability.

Biomass growth is higher in forests with more biomass

We predicted that biomass growth of surviving trees is higher in forests with higher initial stand biomass, because most trees initially present survive during the census, and the more biomass they initially have, the faster they can grow (cf. Stephenson *et al.* 2014). We indeed found that initial stand biomass had a strong positive effect on biomass growth of survivors (Fig 3). Our results contrast with many studies in moist and wet forest studies that found no or even negative relationships between (biomass) growth rates and initial biomass, probably because of stronger light limitation and resource competition (Hughes, Kauffman & Jaramillo 1999; Peña-Claros *et al.* 2008; Finegan *et al.* 2015). Stands with higher initial biomass show therefore a higher biomass growth of survivors and higher biomass mortality, but lower biomass recruitment. These results highlight that one driver can shape the underlying demographic processes differently, and it is therefore important to disentangle how different drivers affect different processes, and hence net biomass change (Malhi 2012).

Conservative- rather than acquisitive species are associated with high biomass growth

We predicted that forests dominated by fast-growing acquisitive species (with high specific leaf area and low wood density) having high hydraulic conductivity and photosynthetic rates, would have high biomass growth. Surprisingly, we found highest biomass growth in plots dominated by low SLA species. Species with lower SLA have an improved water balance since they transpire less water (Poorter & Bongers 2006; Sterck *et al.* 2011). Species with low SLA also produce leaves with smaller cells and thicker cell walls, thus decreasing cell elasticity and allowing plants to reduce leaf water potential and continue plant functioning during the onset of the dry period (Baltzer *et al.* 2008; Klein 2014). These results suggest that biomass growth of surviving trees in dry forests productivity is limited by water availability rather than by light availability. $\mathrm{CWM}_{\mathrm{wd}}$ was not included in the best model for biomass growth of surviving trees, but it had an indirect effect on biomass growth through its positive effect on initial stand biomass (which, in turn, had a positive effect on biomass growth) (Table 1). Higher wood density can also directly contribute to tree and stand growth, as it enables hydraulic functioning during drought (Markesteijn *et al.* 2011). Our study shows that the acquisitive-conservative trait spectrum has different consequences for wet and dry forests (cf. Lohbeck *et al.* 2013); although conservative trait values lead to lower biomass productivity in wet forests (Malhi *et al.* 2004; Finegan *et al.* 2015), they may increase species performance and productivity in dry forests.

The paradox of low productivity on soils with high nutrient availability

In temperate regions, forest productivity is often limited by nitrogen (Martinelli *et al.* 1999) (which was not measured in our study), whereas in tropical regions like our study site, forest productivity is often limited by phosphorus, because the soils are highly weathered due to a warm and wet climate (i.e. our study sites, Quesada et al 2012). We predicted that soil nutrient availability would increase biomass growth, but we found instead that soil calcium had a negative effect (cf. Wullaert *et al.* 2013; Quintero-Vallejo et al. 2015). In high pH soils, calcium can react with inorganic phosphorus and form mineral insoluble calcium phosphate, which makes phosphorus unavailable for most plants (Tyler 1996). Higher concentration of calcium in plants tissues can also result in nutrient imbalance and calcium toxicity that inhibits growth and causes mortality (Jefferies & Willis 1964; Quintero-Vallejo et al. 2015). Finally, species with conservative trait values (high wood density and low specific leaf area) dominate on nutrient poor soils (Kendall’s correlation between Ca and CEC is 0.8, $p<0.01$, N=200) because these traits enhance nutrient residence time in the plants (Reich *et al.* 2003; Baraloto *et al.* 2011; Unger, Homeier & Leuschner 2012). In our dry forest, the same conservative trait values are important to deal with drought, and may enhance productivity. Therefore, our results suggest that in dry forests, soil water availability may be a stronger driver of biomass productivity than soil fertility.

High stand biomass in forests with low trait diversity and dominated by conservative species

Forests dominated by species with large potential adult stature (high maximum stem diameter) and conservative trait values (higher wood density) had higher stand biomass. Large species have a large stem volume, and species with dense wood have a higher biomass per unit stem volume (Chave *et al.* 2009), thus leading to higher stand biomass (cf. Slik *et al.* 2010). Moreover, life-history theory predicts that large species have lower inherent mortality and turnover (Pianka 1970; Poorter *et al.* 2008), and dense wood enhances resistance to stem breakage (van Gelder, Poorter & Sterck 2006; Chave *et al.* 2009) and hydraulic failure especially in dry environments (Poorter & Markesteijn 2008). In combination these adaptations may lead to less biomass turnover, and hence, a larger standing biomass over time (Malhi *et al.* 2006; Malhi 2012; Conti & Díaz 2013).

Stand biomass was positively affected by functional divergence and negatively affected by functional evenness (Table 1). High functional divergence indicates that basal area is concentrated in the extremes of multivariate-trait space while low functional evenness indicates that basal area is concentrated in a restricted part of this same multivariate-trait space (Villéger, Mason & Mouillot 2008). In combination, low trait diversity (high functional divergence and low functional evenness) and high CWM for wood density and D_{max} suggest that in high biomass stands, plot basal area is concentrated in species with high D_{max} and WD.

Stands dominated by mostly tall and dense wooded species with a narrow range of trait values have, therefore, higher standing biomass (cf. Conti & Díaz 2013). This is in agreement with other studies that show that biomass storage is better explained by the biomass ratio hypothesis than by the niche complementarity hypothesis (Conti & Díaz 2013; Finegan *et al.* 2015; Lohbeck *et al.* 2015).

Green soup and biomass ratio hypotheses better explain demographic drivers of biomass change than do the niche complementarity and soil fertility hypotheses

We assessed how different ecological hypotheses (soil fertility, biomass ratio, niche complementarity and green soup) shape net biomass change in tropical dry forests. We predicted that there would be higher biomass growth, recruitment and mortality on fertile soils and for communities that are dominated by fast-growing acquisitive species, that niche complementarity increases recruitment and growth and reduces mortality, and that higher stand biomass reduces recruitment and increases growth and mortality (Fig. 1). Initial stand biomass was the best predictor of all three demographic biomass processes (Table 1, Fig. 3), providing strong support for the green soup hypothesis that vegetation biomass shapes ecosystem processes (Lohbeck *et al.* 2015). The biomass ratio hypothesis was supported for biomass growth (CWM_{sla}) for biomass recruitment (CWM_{dec}) and for initial biomass (CWM_{dmax} and CWM_{wd}). The soil fertility hypothesis (Ca for biomass growth) and the niche complementarity hypothesis (F_{eve} and F_{div} for initial biomass) had a limited effect on forest biomass processes (Table 1, Fig. 3). We found no support for the niche complementarity hypothesis (Conti & Díaz 2013; Finegan *et al.* 2015; Lohbeck *et al.* 2015) on biomass dynamics. Since these forests are already diverse, an increase in species richness may lead to niche overlap (species redundancy), instead of to niche differentiation, causing negative interspecific interactions through competition (Walker 1992). Besides, recent studies show that interspecific trait-mediated and trait-hierarchy plays a major role in species performance (Uriarte *et al.* 2010; Lasky *et al.* 2014) instead of trait dissimilarity (niche complementarity). In this way, an increase in dominance of certain trait species (in our study conservative traits) may enhance stand productivity since they are better able to face environmental filtering (Lasky *et al.* 2014). We also found no or even negative effect of soil nutrients on biomass processes. Since dry forest species may be strongly constrained by water availability, soil nutrient availability may be less important, as plants cannot show their full potential response to increases in soil fertility. The productivity of dry forests is therefore shaped by species with conservative trait values that are better competitors under dry and infertile conditions.

We acknowledge that our study has some limitations; first is that we did not have quantitative data on past anthropogenic disturbances in the plots, although we feel that they had a minor impact on the study. Second, we did not measure the traits of each individual tree in each, thus ignoring the effect of trait plasticity (although other studies have shown that intraspecific differences are small compared to interspecific differences, Rozendaal, Hurtado & Poorter (2006)). Third, the plot size (20 x 20 m) was relatively small to accurately quantify biomass dynamics, although it might be the most relevant scale to link it to small-scale spatial heterogeneity in soil fertility and species composition. Future studies could benefit from measuring disturbances, traits, and actual nutrient availability (i.e., mineralization rates) in more detail. Nevertheless, our results show clear trends that can be discussed in the light of current theory.

CONCLUDING REMARKS

Our study can be summarized in three main results. First, biomass dynamic processes were mostly driven by the vegetation quantity and biomass ratio hypotheses, while we found no or even negative effects of soil fertility and niche complementarity. Second, different drivers affect different biomass dynamic processes. To understand changes in forests productivity, it is therefore important to disentangle the processes underlying net biomass change. Third, from a functional point of view, dry forests show different trait-productivity relationships than what has been shown for wet forests. In dry forests, the dominance of conservative species, rather than of acquisitive species, is associated with high biomass growth and storage, probably because these conservative species perform better in drought-stressed systems. Our results suggest that the lack of globally consistent effects of functional traits on forest productivity (cf. Paine *et al.* 2015) is caused by different traits becoming important in different environments (Lohbeck *et al.* 2013). This study advances understanding of dry forest biomass productivity, and can help predicting how tropical forests will respond to future increases in drought stress (Brienen *et al.* 2015), changing the overall trait-productivity relationships in worldwide traits economic spectrum.

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Appendix S1. Environmental and forest characteristics of the sites included in this study.

Parameters	**Sites**							
	A1	A2	A3	A4	A5	A6	A7	A8
Latitude	-18.498	-18.952	-19.146	-18.748	-19.169	-18.930	-18.860	-19.676
Longitude	-48.385	-48.205	-48.146	-47.513	-48.394	-48.065	-48.230	-48.034
Mean annual precipitation (mm)	1375	1491	1465	1124	1450	1469	1445	1547
Months < 100 mm	6	6	6	8	6	6	6	6
Months < 100 mm	5	5	5	5	5	5	5	5
Altitude	680	911	926	904	794	884	898	735
Mean temperature	21.2	21.5	21.5	21.2	21.5	21.5	21.5	22.3
Number of species	80	89	74	99	98	103	88	89
Number of trees (ha^{-1})	840	976	943	798	1298	1144	1064	805
Basal area (m^2.ha^{-1})	26.4	26.3	27.1	26.3	21.8	27.5	34.6	45.1
Number of trees DBH > 30 cm	90	98	95	111	64	78	128	96
Number of trees DBH > 50 cm	28	20	23	19	6	28	30	56

Appendix S2. Descriptive statistics of biomass processes, structural-taxonomic diversity, functional diversity, community weighted mean traits and soil nutrients availability for 8 tropical dry forests in Brazil (A1-A8). In each forest, 25 contiguous permanent sample plots (20 × 20 m) were established totalling one-ha per site. AGB$_i$ = stand biomass, AGB$_{net}$ = net biomass change, AGB$_{surv}$ = biomass growth of surviving trees, AGB$_{mort}$ = biomass mortality, AGB$_{recr}$ = biomass recruitment, NI = tree-density (ha^{-1}), S = rarefied species richness, H' = Shannon-Wiener index, J' = Pielou's index, CWM = community weighed mean, WD = wood density, D$_{max}$ = maximum stem diameter, SLA = specific leaf area, Dec = deciduousness, F$_{ric}$ = functional richness, F$_{eve}$ = functional evenness, F$_{div}$ = functional divergence, P = phosphorous, K = potassium, Ca = calcium, Mg = magnesium, Al = aluminum, CEC = cation exchange capacity.

Predictors	**A1**		**A2**		**A3**		**A4**		**A5**		**A6**		**A7**		**A8**		**TOTAL**	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
AGB$_i$	203.36	28.72	217.37	18.12	187.32	19.41	209.60	21.46	148.58	10.96	232.82	15.42	268.00	25.95	504.12	77.51	246.39	13.75
AGB$_{net}$	-1.47	1.38	2.48	0.56	2.39	0.40	1.73	0.86	1.79	0.63	-3.42	2.71	-0.23	2.19	-1.07	2.93	0.27	0.62
AGB$_{surv}$	2.44	0.36	4.18	0.36	3.46	0.25	3.79	0.41	3.55	0.37	3.62	0.26	4.80	0.34	5.21	0.92	3.88	0.17
AGB$_{mort}$	3.96	1.26	1.76	0.47	1.10	0.30	2.11	0.64	1.88	0.41	7.11	2.62	5.08	2.26	6.32	2.99	3.67	0.61
AGB$_{recr}$	0.06	0.01	0.06	0.02	0.03	0.01	0.05	0.01	0.11	0.02	0.07	0.01	0.05	0.01	0.04	0.01	0.06	0.01
NI	840.00	44.86	976.00	39.83	943.00	47.12	798.00	37.47	1298.00	56.12	1144.00	39.03	1064.00	44.28	805.00	38.13	983.50	19.20
S	15.48	0.61	18.06	0.45	16.62	0.41	18.24	0.76	17.74	0.44	19.14	0.37	15.69	0.54	14.15	0.65	16.89	0.22
H'	2.51	0.06	2.82	0.04	2.69	0.04	2.79	0.07	2.88	0.04	2.98	0.04	2.63	0.05	2.37	0.07	2.71	0.02
J'	0.89	0.01	0.93	0.01	0.91	0.01	0.94	0.01	0.90	0.01	0.93	0.01	0.90	0.01	0.88	0.01	0.91	0.00
CWM$_{wd}$	0.62	0.02	0.65	0.01	0.63	0.01	0.72	0.01	0.72	0.01	0.66	0.01	0.69	0.01	0.69	0.01	0.67	0.00
CWM$_{sla}$	15.18	0.50	12.47	0.23	11.81	0.14	11.90	0.15	12.23	0.22	12.03	0.16	11.53	0.10	16.50	0.51	12.96	0.16
CWM$_{dmax}$	49.72	3.96	49.01	3.35	43.35	1.72	46.03	2.02	41.16	2.49	55.27	2.75	56.03	3.00	85.91	5.47	53.31	1.48
CWM$_{dec}$	0.36	0.04	0.33	0.03	0.19	0.02	0.34	0.03	0.61	0.03	0.31	0.03	0.35	0.03	0.24	0.05	0.34	0.01
F$_{ric}$	0.45	0.03	0.40	0.02	0.34	0.01	0.43	0.02	0.49	0.02	0.48	0.02	0.42	0.02	0.37	0.02	0.42	0.01
F$_{eve}$	0.56	0.02	0.62	0.01	0.58	0.02	0.53	0.02	0.62	0.01	0.59	0.01	0.55	0.02	0.61	0.02	0.58	0.01
F$_{div}$	0.80	0.02	0.79	0.02	0.81	0.02	0.74	0.02	0.75	0.02	0.83	0.02	0.73	0.02	0.88	0.02	0.79	0.01
pH	6.35	0.05	4.90	0.06	4.74	0.02	5.48	0.09	5.88	0.04	4.65	0.03	4.64	0.09	5.71	0.10	5.29	0.05
P	4.67	0.32	2.30	0.16	1.87	0.11	1.26	0.10	2.08	0.24	1.10	0.04	2.78	0.23	1.51	0.10	2.20	0.10
K	164.80	6.40	64.13	3.08	35.20	0.86	59.48	3.27	113.64	3.07	30.04	1.12	47.52	2.96	86.44	3.73	75.16	3.22
Al	0.00	0.00	1.20	0.04	1.70	0.06	0.09	0.03	0.00	0.00	1.00	0.03	1.12	0.12	0.09	0.03	0.65	0.05
Ca	7.00	0.17	3.18	0.18	0.12	0.01	3.42	0.34	4.06	0.12	0.26	0.05	0.76	0.22	3.44	0.33	2.78	0.17
Mg	1.86	0.09	0.73	0.06	0.09	0.01	0.80	0.09	1.49	0.04	0.14	0.02	0.34	0.09	0.94	0.07	0.80	0.05
CEC	9.28	0.20	7.17	0.19	1.99	0.06	4.36	0.33	5.83	0.15	1.48	0.05	2.35	0.21	4.69	0.36	4.64	0.19

Appendix S3. Overview of the 171 dry forest tree species included in the study. Scientific name, family, maximum stem diameter (Dmax, cm), wood density (WD, g.cm^{-3}), specific leaf area (SLA; mm^2.mg^{-1}), and deciduousness (Dec, deciduous D, or evergreen E) are given.

Species	Family	Dmax	WD	SLA	Dec
Acalypha gracilis	Euphorbiaceae	7.6	0.56	24.9	E
Acrocomia aculeata	Arecaceae	27.9	0.46	NA	E
Aegiphila integrifolia	Lamiaceae	22.7	0.86	NA	D
Agonandra brasiliensis	Opiliaceae	43.0	0.82	NA	D
Albizia niopoides	Fabaceae	12.5	0.55	NA	D
Albizia polycephala	Fabaceae	33.6	0.55	NA	D
Alchornea glandulosa	Euphorbiaceae	46.8	0.38	18.1	E
Allophylus sericeus	Sapindaceae	9.8	0.48	19.0	E
Amaioua guianensis	Rubiaceae	15.3	0.63	12.0	E
Anadenanthera colubrina	Fabaceae	46.4	0.87	7.4	D
Andira fraxinifolia	Fabaceae	13.3	0.92	NA	D
Annona cacans	Annonaceae	64.1	0.44	9.8	D
Apeiba tibourbou	Malvaceae	35.5	0.20	NA	E
Apuleia leiocarpa	Fabaceae	60.2	0.80	17.9	D
Aralia warmingiana	Araliaceae	62.9	0.42	NA	D
Ardisia ambigua	Myrsinaceae	12.3	0.62	13.9	E
Aspidosperma cuspa	Apocynaceae	18.2	0.83	16.9	E
Aspidosperma cylindrocarpon	Apocynaceae	33.4	0.73	13.5	D
Aspidosperma discolor	Apocynaceae	39.3	0.76	10.4	D
Aspidosperma parvifolium	Apocynaceae	50.6	0.78	15.5	D
Aspidosperma polyneuron	Apocynaceae	22.6	0.77	NA	E
Aspidosperma subincanum	Apocynaceae	19.5	0.82	20.8	D
Astronium fraxinifolium	Anacardiaceae	21.6	0.87	11.3	D
Astronium nelson-rosae	Anacardiaceae	25.6	0.87	11.3	D
Bauhinia ungulata	Fabaceae	9.7	0.64	35.7	E
Byrsonima laxiflora	Malpiguiaceae	21.5	0.63	15.9	E
Cabralea canjerana	Meliaceae	17.2	0.55	NA	D
Calyptranthes clusiifolia	Myrtaceae	14.2	0.78	NA	E
Calliandra foliolosa	Fabaceae	16.6	0.84	NA	E
Callisthene major	Vochysiacaeae	65.2	0.75	10.0	D
Calyptranthes widgreniana	Myrtaceae	6.2	0.78	14.0	E
Campomanesia vellutina	Myrtaceae	15.4	0.82	22.6	D
Cariniana estrellensis	Lecytidaceae	165.6	0.64	9.2	D
Cassia ferruginea	Fabaceae	54.4	0.50	NA	D
Casearia gossypiosperma	Salicaceae	30.5	0.67	18.4	D
Casearia grandiflora	Salicaceae	14.6	0.77	12.8	D
Casearia rupestris	Salicaceae	9.9	0.67	NA	D
Casearia sylvestris	Salicaceae	14.3	0.72	20.0	E
Cedrela fissilis	Meliaceae	55.9	0.47	12.0	D
Ceiba speciosa	Malvaceae	63.3	0.26	21.1	D
Celtis iguanae	Cannabaceae	13.7	0.64	NA	D

Cheiloclinium cognatum	Celastraceae	20.9	0.77	12.8	E
Chomelia pohliana	Rubiaceae	6.9	0.58	34.1	E
Chrysophyllum gonocarpum	Sapotaceae	18.0	0.67	13.9	E
Chrysophyllum marginatum	Sapotaceae	20.3	0.70	16.3	E
Citronella paniculata	Cardiopteridaceae	18.6	0.49	NA	E
Coccoloba mollis	Polygonaceae	10.2	0.83	NA	D
Copaifera langsdorffii	Fabaceae	88.9	0.65	11.1	E
Cordia sellowiana	Boraginaceae	28.8	0.52	12.3	E
Cordiera sessilis	Rubiaceae	9.5	0.88	12.0	E
Cordia superba	Boraginaceae	49.3	0.52	12.3	E
Cordia trichotoma	Boraginaceae	15.8	0.56	NA	D
Coutarea hexandra	Rubiaceae	20.4	0.60	NA	E
Coussarea hydrangeaefolia	Rubiaceae	12.8	0.65	19.8	E
Cryptocarya aschersoniana	Lauraceae	60.5	0.57	11.8	E
Cupania vernalis	Sapindaceae	20.5	0.66	10.5	E
Dendropanax cuneatus	Araliaceae	19.9	0.42	NA	E
Dilodendron bipinnatum	Sapindaceae	15.4	0.71	15.6	D
Diospyros hispida	Ebenaceae	29.0	0.62	12.5	D
Duguetia lanceolata	Annonaceae	24.2	0.87	12.6	E
Erioteca condolleana	Malvaceae	39.3	0.43	NA	E
Eugenia florida	Myrtaceae	21.3	0.68	16.2	E
Eugenia involucrata	Myrtaceae	24.2	0.76	16.6	E
Eugenia ligustrina	Myrtaceae	11.0	0.76	14.8	E
Eugenia subterminalis	Myrtaceae	10.3	0.75	12.9	E
Faramea hyacinthina	Rubiaceae	19.9	0.58	12.8	E
Ficus guaranitica	Moraceae	12.8	0.41	NA	E
Galipea jasminifolia	Rutaceae	12.5	0.75	22.8	E
Garcinia gardneriana	Clusiaceae	20.9	0.72	10.7	E
Guatteria australis	Annonaceae	19.7	0.54	14.7	E
Guarea guidonia	Meliaceae	44.7	0.57	9.1	E
Guarea kunthiana	Meliaceae	24.3	0.62	NA	E
Guapira opposita	Nyctaginaceae	19.4	0.83	22.0	E
Guazuma ulmifolia	Malvaceae	23.6	0.51	13.8	E
Guapira venosa	Nyctaginaceae	20.2	0.58	NA	E
Guettarda viburnoides	Rubiaceae	29.4	0.66	16.6	E
Handroanthus serratifolius	Bignoniaceae	56.4	0.92	NA	D
Heisteria ovata	Olacaceae	30.9	0.70	9.7	E
Hirtella glandulosa	Chrysobalanaceae	41.0	0.92	10.7	E
Hirtella gracilipes	Chrysobalanaceae	25.4	0.80	15.1	E
Hymenaea courbaril	Fabaceae	116.3	0.81	10.5	D
Inga laurina	Fabaceae	18.5	0.62	NA	E
Inga marginata	Fabaceae	7.5	0.72	19.0	E
Inga sessilis	Fabaceae	17.3	0.43	NA	E
Inga vera	Fabaceae	24.1	0.58	14.1	E
Ixora brevifolia	Rubiaceae	22.8	0.88	12.2	E
Jacaranda macrantha	Bignoniaceae	27.3	0.42	NA	D

Jacaratia spinosa	Caricaceae	76.7	0.27	29.7	E
Lamanonia ternata	Cunoniaceae	49.2	0.51	12.1	E
Lithrea molleoides	Anacardiaceae	23.6	0.47	NA	E
Lonchocarpus cultratus	Fabaceae	52.7	0.73	NA	D
Luehea divaricata	Malvaceae	23.4	0.64	NA	D
Luehea grandiflora	Malvaceae	24.0	0.54	19.3	D
Machaerium acutifolium	Fabaceae	23.0	1.12	NA	D
Machaerium brasiliense	Fabaceae	24.1	0.66	15.0	D
Machaerium hirtum	Fabaceae	36.7	0.66	11.8	D
Machaerium oblongifolium	Fabaceae	13.1	0.81	NA	D
Machaerium stipitatum	Fabaceae	33.4	0.81	NA	D
Machaerium villosum	Fabaceae	35.2	0.78	18.9	E
Maprounea guianensis	Euphorbiaceae	38.8	0.59	NA	E
Margaritaria nobilis	Phyllanthaceae	26.7	0.48	NA	D
Matayba elaeagnoides	Sapindaceae	18.8	0.75	12.0	E
Matayba guianensis	Sapindaceae	18.2	0.82	11.9	E
Maytenus floribunda	Celastraceae	20.0	0.72	10.6	E
Maytenus robusta	Celastraceae	8.5	0.77	NA	E
Metrodorea stipularis	Rutaceae	6.4	1.05	NA	E
Micrandra elata	Euphorbiaceae	109.6	0.72	19.8	E
Miconia latecrenata	Melastomataceae	22.0	0.62	NA	E
Miconia minutiflora	Melastomataceae	26.7	0.62	NA	E
Micropholis velunosa	Sapotaceae	75.6	0.67	14.3	E
Mollinedia widigrenii	Monimiaceae	6.8	0.67	NA	E
Myrciaria glanduliflora	Myrtaceae	7.0	0.70	NA	E
Myrsine umbellata	Myrsinaceae	29.0	0.59	11.3	E
Myracrodruon urundeuva	Anacardiaceae	54.2	1.00	10.6	D
Nectandra cissiflora	Lauraceae	24.5	0.59	9.5	E
Nectandra megapotamica	Lauraceae	29.5	0.59	10.4	E
Nectandra membranacea	Lauraceae	31.3	0.59	12.8	E
Neea hermaphrodita	Nyctaginaceae	17.1	0.68	NA	E
Ocotea corymbosa	Lauraceae	56.6	0.53	10.2	E
Ocotea minarum	Lauraceae	9.7	0.76	NA	E
Ocotea pulchella	Lauraceae	19.6	0.65	NA	E
Ocotea spixiana	Lauraceae	36.0	0.66	8.9	E
Ormosia arborea	Fabaceae	42.3	0.70	NA	E
Ouratea castaneifolia	Ochnaceae	25.0	0.57	NA	E
Pera glabrata	Euphorbiaceae	46.8	0.65	NA	E
Piptadenia gonoacantha	Fabaceae	26.1	0.68	NA	D
Piptocarpha macropoda	Asteraceae	23.4	0.65	NA	E
Platypodium elegans	Fabaceae	44.6	0.81	12.3	D
Platycyamus regnellii	Fabaceae	43.1	0.81	16.4	D
Pouteria gardneri	Sapotaceae	26.2	0.78	12.8	E
Pouteria torta	Sapotaceae	38.1	0.77	12.8	E
Prockia crucis	Salicaceae	7.1	0.58	NA	D
Protium heptaphyllum	Burseraceae	32.8	0.63	11.5	E

Pseudolmedia laevigata	Moraceae	7.9	0.64	NA	E
Psidium rufum	Myrtaceae	12.3	0.88	NA	E
Psidium sartorianum	Myrtaceae	68.6	0.79	15.3	E
Qualea dichotoma	Vochysiacaeae	60.0	0.65	NA	D
Qualea multiflora	Vochysiacaeae	77.3	0.71	12.9	E
Quararibea turbinata	Malvaceae	18.3	0.50	22.2	E
Rhamnidium elaeocarpum	Rhaminaceae	16.1	0.83	22.9	D
Roupala montana	Proteaceae	31.9	0.73	9.6	D
Rudgea viburnoides	Rubiaceae	7.3	0.57	NA	E
Schefflera morototoni	Araliaceae	74.8	0.45	NA	E
Senegalia polyphylla	Fabaceae	58.2	0.63	4.4	D
Simira sampaioana	Rubiaceae	29.8	0.66	12.3	D
Siphoneugena densiflora	Myrtaceae	19.5	0.91	9.3	E
Siparuna guianensis	Siparunaceae	9.2	0.65	18.3	E
Sloanea hirsuta	Elaeocarpaceae	27.1	0.81	NA	E
Sorocea bomplandii	Moraceae	11.3	0.62	NA	E
Styrax camporum	Styracaceae	19.9	0.38	12.5	E
Sweetia fruticosa	Fabaceae	55.3	0.78	12.5	D
Symplocos pubescens	Symplocaceae	6.3	0.49	NA	E
Tabebuia roseoalba	Bignoniaceae	21.8	0.78	NA	D
Tapirira guianensis	Anacardiaceae	28.7	0.46	9.8	E
Tapirira obtusa	Anacardiaceae	55.4	0.46	11.9	E
Terminalia glabrescens	Combretaceae	38.4	0.77	11.4	D
Terminalia phaeocarpa	Combretaceae	81.4	0.70	12.9	D
Trichilia catigua	Meliaceae	19.8	0.69	14.1	E
Trichilia clausseni	Meliaceae	19.2	0.66	15.1	E
Trichilia elegans	Meliaceae	19.8	0.66	16.9	E
Trichilia pallida	Meliaceae	13.5	0.70	21.4	E
Unonopsis guatterioides	Annonaceae	20.8	0.52	16.0	E
Urera baccifera	Urticaceae	18.5	0.17	NA	E
Virola sebifera	Myristicaceae	22.3	0.45	9.5	E
Vitex polygama	Lamiaceae	15.5	0.59	NA	E
Vochysia magnifica	Vochysiacaeae	74.7	0.78	10.0	E
Vochysia tucanorum	Vochysiacaeae	10.1	0.48	NA	E
Xylopia aromatica	Annonaceae	15.0	0.56	9.3	E
Xylopia brasiliensis	Annonaceae	17.6	0.70	9.3	E
Zanthoxylum riedelianum	Rutaceae	23.5	0.61	NA	D
Zollernia ilicifolia	Fabaceae	44.5	1.05	NA	D

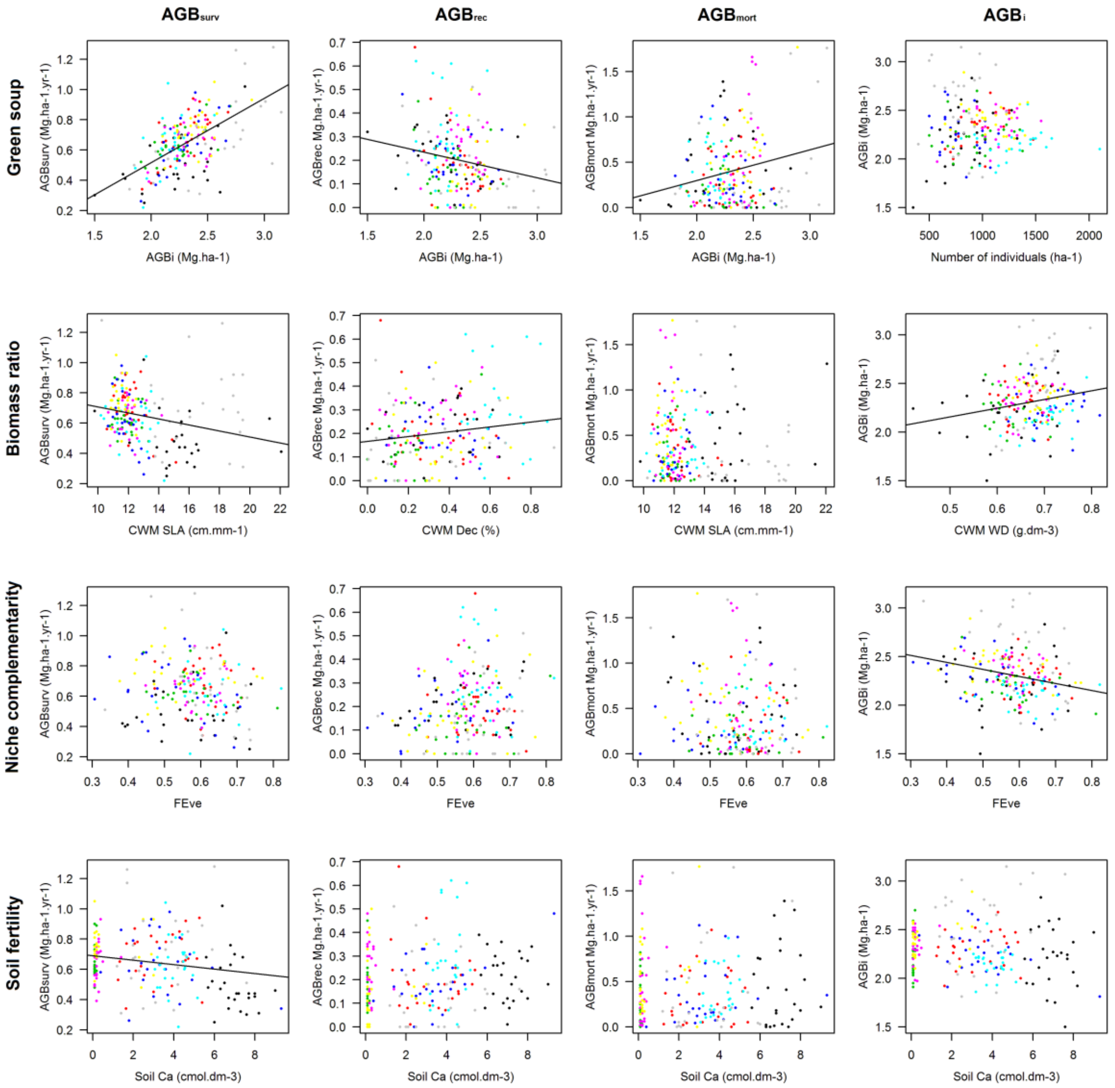
Appendix S4. Bivariate regressions between biomass components (AGB_{surv}, AGB_{recr} AGB_{mort}, AGB_i) and each (a)biotic predictors performed using linear mixed models including sites as random effect. Regression coefficients and significance levels are shown. AGB_i = stand biomass, AGB_{net} = net biomass change, AGB_{surv} = biomass growth of surviving trees, AGB_{mort} = biomass mortality, AGB_{recr} = biomass recruitment, NI = tree-density (ha^{-1}), CWM = community weighted mean, WD = wood density, D_{max} = maximum stem diameter, SLA = specific leaf area, Dec = deciduousness, S = rarefied species richness, H' = Shannon-Wiener index, J' = Pielou's index, F_{ric} = functional richness, F_{eve} = functional evenness, F_{div} = functional divergence, P = phosphorous, K = potassium, Ca = calcium, Mg = magnesium, Al = aluminum, CEC = cation exchange capacity. Bold numbers indicate significant regressions ($p < 0.05$).

Hypothesis	**Predictor**	**AGB_{surv}**		**AGB_{recr}**		**AGB_{mort}**		**AGB_i**	
		Coef	p	Coef	p	Coef	p	Coef	p
Green soup	AGB_i	**0.11**	**0.00**	**-0.03**	**0.00**	**0.09**	**0.00**	-	-
	NI	**0.03**	**0.02**	0.01	0.37	0.04	0.19	0.03	0.19
Biomass ratio	CWM_{wd}	0.02	0.15	0.00	0.83	0.00	0.89	**0.05**	**0.01**
	CWM_{sla}	**-0.04**	**0.01**	-0.01	0.46	0.01	0.86	-0.04	0.12
	CWM_{dmax}	**0.07**	**0.00**	-0.02	0.14	0.03	0.34	**0.18**	**0.00**
	CWM_{dec}	**0.03**	**0.03**	**0.02**	**0.04**	-0.01	0.75	**0.06**	**0.00**
Niche complementarity	F_{ric}	0.02	0.07	0.02	0.09	0.02	0.54	0.03	0.12
	F_{eve}	-0.02	0.19	0.02	0.12	-0.05	0.08	**-0.07**	**0.00**
	F_{div}	**0.03**	**0.01**	**-0.02**	**0.03**	0.03	0.27	**0.11**	**0.00**
	S	0.02	0.20	0.01	0.40	0.02	0.50	0.00	0.95
	H'	0.03	0.06	0.01	0.40	0.02	0.53	0.00	0.91
	J'	0.01	0.60	0.00	0.94	-0.01	0.63	-0.01	0.44
Soil fertility	pH	-0.03	0.13	0.02	0.22	0.02	0.57	0.03	0.29
	P	-0.01	0.42	-0.01	0.49	0.04	0.16	0.03	0.16
	K	-0.03	0.12	0.02	0.15	0.06	0.12	**0.09**	**0.01**
	Al	0.02	0.35	-0.02	0.11	-0.03	0.37	-0.03	0.35
	Ca	**-0.04**	**0.01**	0.02	0.20	0.03	0.39	0.00	0.95
	Mg	**-0.04**	**0.04**	0.02	0.12	0.02	0.50	0.00	0.95
	CEC	**-0.04**	**0.04**	0.01	0.35	0.02	0.54	0.00	0.91

Appendix S5. Kendall's correlation coefficient (tau) between 18 drivers of biomass demographic processes among 200 sample plots in tropical dry forests in Brazil. Plot-level variables values were standardized for each site to reduce the effect of nestedness within one site. NI = tree-density (ha^{-1}), CWM = community weighted mean, WD = wood density, D_{max} = maximum stem diameter, SLA = specific leaf area, Dec = deciduousness, S = rarefied species richness, H' = Shannon-Wiener index, J' = Pielou's index, F_{ric} = functional richness, F_{eve} = functional evenness, F_{div} = functional divergence, P = phosphorous, K = potassium, Ca = calcium, Mg = magnesium, Al = aluminum, CEC = cation exchange capacity. Bold numbers indicate significant correlations ($p < 0.05$).

	NI	**S**	**H'**	**J'**	**F_{ric}**	**F_{eve}**	**F_{div}**	**CWM_{wd}**	**CWM_{sla}**	**CWM_{dmax}**	**CWM_{dec}**	**pH**	**P**	**K**	**Al**	**Ca**	**Mg**	**CEC**
NI	-																	
S	**0.12**	-																
H'	**0.20**	**0.32**	-															
J'	-0.22	0.06	**0.5**	-														
F_{ric}	**0.12**	**0.23**	**0.30**	**0.16**	-													
F_{eve}	0.04	0.03	**0.12**	0.05	0.00	-												
F_{div}	-0.02	0.01	0.02	0.03	0.03	0.01	-											
CWM_{wd}	0.05	-0.03	-0.11	-0.13	-0.06	0.05	0.04	-										
CWM_{sla}	0.04	0.08	0.02	-0.03	-0.02	0.01	-0.08	0.02	-									
CWM_{dmax}	-0.05	0.01	0.06	**0.11**	**0.11**	-0.09	**0.39**	-0.02	**-0.17**	-								
CWM_{dec}	0.01	0.01	-0.01	0.01	**0.12**	-0.08	0.04	**0.18**	**-0.13**	**0.17**	-							
pH	-0.06	**0.13**	0.07	0.05	**0.11**	-0.03	0.05	-0.04	-0.03	0.06	**0.11**	-						
P	0.00	0.07	0.09	0.07	**0.14**	-0.03	**0.10**	-0.02	0.03	0.09	0.01	**0.24**	-					
K	0.01	0.05	-0.04	-0.09	0.08	-0.01	0.01	0.06	-0.06	0.08	**0.10**	**0.29**	**0.24**	-				
Al	**0.15**	-0.06	-0.01	-0.08	-0.05	0.02	-0.01	0.05	0.05	-0.07	**-0.11**	-0.46	-0.08	-0.17	-			
Ca	-0.03	0.08	0.05	0.05	0.09	-0.02	0.00	-0.06	0.05	0.00	0.05	**0.60**	**0.37**	**0.29**	**-0.4**	-		
Mg	-0.05	0.06	0.02	0.02	**0.10**	0.06	0.03	0.02	-0.06	0.05	**0.14**	**0.48**	**0.34**	**0.32**	**-0.38**	**0.49**	-	
CEC	0.00	0.06	0.01	-0.01	**0.11**	0.01	-0.01	-0.01	0.03	0.00	0.07	**0.52**	**0.45**	**0.35**	**-0.27**	**0.80**	**0.59**	-

Appendix S6. Scatterplots of the bivariate relationships between processes of biomass dynamics and one predictor of each tested hypotheses. See table 1 for abbreviations.



CAPÍTULO 2

INTERSPECIFIC FUNCTIONAL TRAITS SHAPE SIZE-DEPENDENT GROWTH AND MORTALITY RATES OF DRY FOREST TREE SPECIES

Interspecific functional traits shape size-dependent growth and mortality rates of dry forest tree species[2]

ABSTRACT

There is a general consensus that functional traits drive plant performance. However, the environmental conditions and ecological pressures that plants face change with their size, and the relationship between traits and plant performance should therefore be size-dependent, which has rarely been tested. Here we evaluated over a broad range of tree sizes the interspecific relationship between tree growth and mortality and eight functional stem, leaf and seed traits. We did so across 59 tree species in Brazilian dry forests and evaluated whether the relationships found for other forests types in the literature also hold for dry forests, where water rather than light might limit tree performance. We indeed found a strongly size-dependent relationship between demographic rates and functional traits. At small sizes, when trees are in the shaded understory, species with functional traits that enhance light capture or shade tolerance (i.e., higher maximum adult stature, taller heights, wider crowns, higher seed mass) have higher growth and/or lower mortality rates. This relationship disappears at larger sizes when trees attain better light conditions. Drought adaptations play only a role at larger tree sizes; once trees are in the dry and exposed canopy do species with higher wood density (an indicator of cavitation resistance) have lower mortality rates. Our study shows that both drought and shade adaptations are important in this dry forest, and that the relationships between functional traits and plant performance changes with plant size. Plant size should therefore explicitly be included as an axis of variation in functional analyses, to better understand the relationship between functional traits and demographic rates.

Keywords: demographic rates, interspecific variation, leaf traits, seed mass, tree architecture, wood density.

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INTRODUCTION

The influence of plant functional traits on interspecific demographic rates (growth and mortality) has received an increasing attention because it allows to understand the underlying determinants of species' success (Grime 2001; Westoby and Wright 2006). Trait-driven variation in species growth and survival promotes species coexistence through different exploitation of resources (Wright 2002), and affects ecosystem functioning by increasing productivity and resilience to disturbances (Lebrija-Trejos et al. 2008).

Among the several functional traits studied, there is a general consensus that adult stature, plant architecture, wood density, leaf traits and seed mass are good predictors of the growth and survival trade-offs (Westoby 1998; Reich et al. 2003; Ackerly 2004; Martínez-Vilalta et al. 2010; Rüger et al. 2012; Iida et al. 2014a,b). Relationships between functional traits and demographic rates can have multiple reasons; they can have a mechanistic basis, can be the result of fixed programs of plant development or the result of covariation with another trait that affects the demographic rate. Our current knowledge for trees indicates that (I) higher adult stature species grow faster to reach the highest strata at which they are reproductive (Thomas 2011) and have lower mortality due to their lower population turnover (Kohyama et al. 2003; Chazdon et al. 2005); (II) species with taller and wider crowns have higher growth as they intercept a higher amount of light and overtop competing neighbors (Poorter et al. 2006,2008), while they have a higher mortality because they are more sensitive to dynamic loading due to wind or falling debris (Sterck and Bongers 1998; Iida et al. 2014a); (III) species with dense wood have lower growth because of higher construction costs per wood volume, and lower mortality because of enhanced resistance to stem breakage and to fungal and pathogen attack (King et al. 2006; Poorter et al. 2006; Chave et al. 2009); (IV) species with higher leaf area and specific leaf area have higher growth because of a higher interception of light, photosynthesis and carbon net gain, whereas they have a higher mortality because of higher respiratory rates, herbivory, pathogen attack and leaf turnover (Baltzer and Thomas 2007; Kitajima and Poorter 2010; Iida et al. 2014b); and (V) species with higher seed mass have slower growth because they have a higher biomass investment in long-lived leaves than in stem or roots as their higher seed resources enable them to become autotrophic later (Paz et al. 2005), while they have lower mortality because the large seed reserves allow them to make large, robust seedlings that can escape size-dependent mortality caused by defoliation, drought, and shading by neighbors, and recover after damage (Harms and Dalling 1997; Leishman et al. 2000). We expect that seed mass is also related to the growth and mortality rates of large trees, because seed mass is an important life history trait and correlated to a suite of morphological and physiological traits of small-seeded fast-growing pioneer species and large-seeded slow growing shade-tolerant species; Leishman et al. 2000; Poorter and Rose 2005).

Most of our knowledge on the relationship between functional traits and plant performance comes from comparative studies on seedlings growing under controlled conditions (Poorter and Remkes 1990; Kitajima 1994). A central but yet understudied question in functional ecology is whether in natural communities functional traits really affect demographic rates and hence, what traits are ecologically relevant. Moreover, the environmental conditions and ecological pressures that plants face change with their size, and the relationship between traits and plant performance should therefore be size-dependent, especially for plants that can attain large sizes, such as trees. Very few studies showed how these trait-rate relationships change over the whole size trajectory in from saplings to large trees (Iida et al. 2014a,b), and such a whole life cycle approach is needed, if we better want to understand species- and community dynamics (Wright et al. 2010, Ibáñez et al. 2014). The effects of these functional traits on demographic rates should especially be strongly size-dependent in forests communities, as in forests species are exposed to a strong vertical gradient in abiotic conditions (Iida et al. 2014a). From the understory to the canopy, there is an increase in irradiance, temperature, wind exposure and atmospheric water stress (Yoda 1974). Thus, functional traits that enhance light capture, photosynthetic carbon gain and shade tolerance (e.g. tree architecture and leaf traits) should influence demographic rates mainly at small sizes when trees are in the shaded understory (Sterck et al. 2003; Iida et al. 2014a,b), whereas functional traits that enhance species' resistance to water stress and wind exposure (e.g. wood density) should influence demographic rates mainly at larger sizes when trees are in the exposed canopy (Koch et al. 2004).

Most community-level studies that indicate how functional traits affect growth and mortality rates were conducted in tropical wet forests, where light is a strongly limiting resource in the forest understory (Poorter et al. 2008; Wright et al. 2010; Herault et al. 2011; Iida et al. 2014a,b). However, trait-rate relationships may be fundamentally different in other forest types where other resources limit plant performance. For example, in Mediterranean forests are strongly limited by water availability and seasonality in temperature, demographic rates were closely associated to changes in temperature and rainfall (Ibáñez et al. 2014). Other studies in temperate and Mediterranean forests also find that the classical trade-off between growth and mortality based on high-light demanding species and shade tolerant species is weaker or compared to them in wet forests (Kunstler et al. 2009; Martínez-Vilalta et al. 2010). Few comparative studies have been carried out in tropical dry forests. In dry forests, light should not be a major limiting resource, due their lower and open canopy (Lebrija-Trejos et al. 2008; Lohbeck et al. 2013), and traits that enhance light capture may therefore be weakly correlated with demographic rates. Instead water availability may become limiting in dry forests, because they are exposed to strong seasonal variation in rainfall. Dry forests species possess a suite of traits such as a deciduousness, leaf habit, higher wood density and specific leaf area (Borchert 1994; Reich et al. 2003) that enhance drought avoidance and/or resistance

(Barajas-Morales 1987; Pennington et al. 2009). These traits could therefore also be more closely related to species variation in demographic rates.

The aim of this study is to evaluate 1) to what extent demographic rates (growth and mortality) of dry forests tree species are shaped by functional traits, and 2) how this changes with tree size. Based on the literature discussed above we expect that (1) growth and mortality rates will be higher for species with higher maximum diameter, taller heights, wider crowns, larger (specific) leaf area and lower wood density and seed mass; (2a) the relationships between demographic rates and functional traits that enhance species light capture and shade tolerance (e.g. tree architecture, leaf traits and seed mass) will be strong at small sizes when light is strong limiting resource, and will be weaker at larger sizes when trees attain the canopy; 2b) the relationships between demographic rates and functional traits that enhance species' resistance to water stress and wind exposure (e.g. wood density) should influence demographic rates mainly at larger sizes when trees are in the dry and exposed canopy. These hypotheses were tested by evaluating the relationship between size-dependent growth and mortality and eight functional stem-leaf-and seed traits of 59 common tree species (~6,000 trees) in Brazilian dry forests.

METHODS

Research sites and species

This study was conducted in eight seasonal dry forests (18º29' to 19º40' S and 47º30' to 48º24' W), at extreme west of Minas Gerais state, Southeastern Brazil. The region experiences a tropical savanna climate (Aw Megathermic of Köppen), characterized by rainy summers (October to March) and dry winters (April to September. Annual rainfall ranges from 1160 to 1460 mm, the dry season length from four to six months of drought (< 100 mm in the whole dry season) and mean annual temperature from 23 to 25º (Lopes et al. 2012). The study areas are secondary forests located in conservation units or legal reserves that in the past had different disturbance (e.g selective logging and cattle grazing) and are surrounded by an agricultural or urban matrix (Lopes et al. 2012). Soil type in studied areas is primarily red latosols that vary from moderately to strongly acidic (Embrapa 1982).

In each forest a one-ha permanent sample plot was established. In the first census (2006-2009), all trees with stem diameter at breast height (DBH, 1.30 m) ≥ 5 cm were tagged, their diameter was measured, height estimated, and identified to species. In the second census, after five years (2011–2014), all trees were re-measured and growth and mortality rates were evaluated. A total of 7868 individuals were measured, belonging to 237 species, 161 genera and 58 families. For this study, we used the 59 species most abundant species (comprising 76% of all individuals) that had at least 25 individuals and sufficient information about their functional traits (Online Resource 1).

Functional traits

Adult stature – To quantify species-specific adult stature, we used potential maximum stem diameter rather than tree height because stem diameter was measured more precisely, and height estimations are especially difficult in tropical forests, where there is a large error for large trees. Since maximum tree height scales closely with maximum stem diameter of the species (e.g. King et al. 2006), maximum stem stem diameter (D_{max}) is a proper indicator of the potential maximum size of the species (Iida et al. 2014b). D_{max} was calculated for each species as the upper 95-percentile stem diameter for those trees whose diameter was equal to or greater than 10% of the observed maximum diameter of a population (King et al. 2006). This method minimizes the effect of the shape of the population structure on the maximum stem diameter estimate and reduces the probability of underestimating the potential maximum size for a specific population with a large proportion of small individuals (King et al. 2006). We used the DBH dataset of the first census to determine species D_{max}. Maximum diameter across the selected species ranged from 8.9 to 169.7 cm, with an average of 33.7 cm (Online Resource 1).

Tree architecture – Tree architectural variables as diameter at breast height (DBH), tree height (H), first branch height (FBH), and the average of two perpendicular projected crown widths (CW) were collected from 5-10 (average 7.8) adult trees (with DBH near to D_{max}) for each species, totaling 464 trees. DBH and CW were measured with a tape-measure, and H and FBH with a clinometer (Haglof HEC, Langsele, Sweden). As the aim of this study was to link demographic rates to absolute values of tree architecture at different reference diameters, and FBH and CW vary with tree height we used a three-step approach. First, we calculated for each species a relative measure of tree architecture by calculating the median crown length ratio (FBH/H) and crown width ratio (CW/H) for each species. The average coefficient of variation among species for FBH/H was 23% and for CW/H was 25% (Online Resource 1). Secondly, we used this relative measure to calculate the absolute FBH and CW for the 5988 individuals for which DBH and H values were available from the census. By doing so we assumed that the relative architecture does not change with size. Third, we used the absolute data of these 5988 individuals to make species-specific allometric regressions relating absolute H, FBH, and CW to DBH. The explained variation of these species-specific regressions was on average 52% for H–DBH, FBH–DBH and CW–DBH. We used the species-specific regression to predict H, FBH and CW at each reference stem diameter at 1 cm interval from 5 cm to 40 cm (see below; Online Resource 1).

Wood density – Species-specific wood density data were obtained from a global wood density database (Zanne et al. 2009; Global Wood Density Database, *available online*). Wood density (WD) data were selected from the South America tropical region in the database to reduce region-specific differences as much as possible. When species-level wood density values were not available, then genus-level wood density values were used, since wood density is a trait that is phylogenetically conserved (Chave et al. 2006). Wood density across the selected species ranged from 0.46 to 0.93 g.cm^{-3}, with an average of 0.70 g.cm^{-3} (Online Resource 1).

Leaf traits – A mixture of fully expanded sun and shade leaves with no obvious symptoms of pathogen or herbivore damage were collected from the same adult trees for which tree architecture was measured (DBH near to D_{max}, between 7-18 m). Ten leaves were collected from 5-10 individuals for each species (average 7.8 individuals). Leaves were sealed in plastic bags to remain turgid until leaf traits were measured in the laboratory. Leaves including the petiole were scanned with a metric reference scale and the leaf area (LA in cm^2) was calculated using the program ImageJ (version 1.34, National Institutes of Health, http://imagej.nih.gov/ij/). Leaves were placed in an oven at 60°C for 72 h before measurement of leaf dry mass (LDM in mg). Specific leaf area (SLA in mm^2 mg^{-1}) was calculated as leaf area divided by leaf mass. For species with compound leaves, leaf traits were calculated for the whole leaf, including the rachis. Leaf area across species ranged from 9.4 to 460.6 cm^2, with an average of 89.4 cm^2; and specific leaf area ranged from 7.4 to 22.8 mm^2 mg^{-1}, with an average of 13.5 $mm^2 mg^{-1}$ and across species, the average coefficient of variation for LA was 32% and for SLA was 18% (Online Resource 1).

Seed mass – Species-specific fresh seed mass data were obtained from literature (Lorenzi 1992,1998) for 49 of the 59 studied species. Seed mass (SM) across the selected species ranged from 3.4 to 3225.8 mg, with an average of 474.6 mg (Online Resource 1).

Size-dependent growth and mortality rate

We estimated the size-dependent relative diameter growth rate (RGR) and mortality rate (MR) following Iida et al. (2014a). First, we calculated the RGR of each tree that survived during the census interval as $\mathrm{RGR} = \left(\ln \mathrm{DBH}_2 - \ln \mathrm{DBH}_1\right).(t_2 - t_1)^{-1}$. Thus, we estimated the RGR of *i*th individual tree, RGR_i, as a linear function of the natural logarithm of the initial stem diameter DBH_{1i} of individual tree *i* of the species *j*:

$$\mathrm{RGR}_{ij} = r_{1j} + r_{2j} \ln(\mathrm{DBH}_{1i}) \quad \text{(Eq. 1)}$$

The parameter r_{1j} shows the initial relative growth rate and r_{2j} show the effect of increased DBH on growth. We calculated growth rates for 5282 individual trees belonging to 59 species (average number of trees per species is 89.5, range 26 - 302 trees; Online Resource 2).

Our mortality model is based on the observation of a tree individual *i* and whether it survived through the census period ($S_i = 1$) or not ($S_i = 0$). Mortality probability (p_i) of the *i*th individual tree was predicted as a binary logistic function of the stem diameter of individual *i* at the first census, DBH_{1i}:

$$\mathrm{MR}_{ij} = \frac{1}{1+\exp(-(m_{1j} + m_{2j}\,\mathrm{DBH}_{1i})} \quad \text{(Eq. 2)}$$

Parameter m_{1j} shows the initial mortality rate, and m_{2j} show the effect of increased DBH on mortality. After that, the mortality rate was adjusted for the time period between the first census (t_{1i}) and the second census (t_{2i}) as $p_i = \exp[\mathrm{MR}_i(t_{2i} - t_{1i})]$. We calculated mortality rates for 5988 individual trees belonging to 59 species (average number of trees per species is 101.5, range 28 – 388 trees; Online Resource 2).

Interspecific relationships between demographic rates and functional traits

We related demographic rates to the average functional traits of the species. We acknowledge that many species do show plastic trait responses to environmental conditions (e.g., Poorter et al 2012; Sendall and Reich 2013), and that traits vary during ontogeny. Yet, the variation explained by intraspecific trait differences is in general small (R^2=0.08) compared to interspecific differences (R^2=0.78, Rozendaal et al. 2006), and across species, seedling traits and adult traits are strongly correlated (Poorter 2008), indicating that plastic trait changes will confound our results only to a limited extend.

Using the species-specific regression equations, we calculated for each species its demographic rate (RGR and MR) using Eq. 1, Eq. 2, and tree architecture (H, FBH and CW) at several standardized reference stem diameters from 5 cm to 40 cm, using 1-cm intervals. Thereafter, we calculated for each reference stem diameter Kendall's rank correlation coefficient (tau) between species demographic rates and functional traits. Kendall's tau is used to measure the association between two non-parametric variables (i.e. species demographic rates and functional traits of this study), as well as Spearman's correlation coefficient (rho). Although Kendall's tau is less popular than Spearman's rho (possibly due to its infrequent use), it is a better estimator of non-parametric correlations because it provides much tighter confidence intervals and less biased estimation of the true correlation than Spearman' rho and allow for more accurate generalizations (Howell 1997).

D_{max} and WD are the main predictors of growth and mortality (e.g. King et al. 2006; Poorter et al. 2008; Martínez-Vilalta et al. 2010; Wright et al. 2010; Herault et al. 2011; Iida et al. 2014a,b), but they can also be correlated with our other functional predictor traits. We therefore first examined the correlations between D_{max} and WD versus the other functional traits (H, FBH, CW, LA, SLA and SM) (Online Resource 3). As tree architecture varies with stem diameter, we examined these correlations at different reference diameters (5, 10, 15, 20 and 25 cm), where most of species were included. D_{max} was positively correlated with tree architecture (H, FBH, CW) for most of reference diameters, negatively with SLA and not significantly correlated with LA or SM. WD was not related to any other functional traits (Online Resource 3). Thus, to evaluate the interspecific relationships between growth and mortality rates and H, FBH, CW and SLA, we used Kendall's partial rank correlation, thus eliminating the confounding effect of D_{max} on these relationships (Siegel and Castellan 1988). To relate demographic rates to leaf area (LA) and seed mass (SM) we used the normal Kendall's tau correlation, because these two predictor traits were not related to D_{max} or WD. Kendall's correlation was considered to be significant if probability value was smaller than 5% ($p < 0.05$). Species were included in the correlation analysis when their D_{max} was larger than each reference stem diameter. The number of species used in the correlation analysis decreased with reference stem diameter due to the dropout of small-statured species from 59 species at the smallest reference diameter (5 cm) to 15 species at the largest reference diameter (40 cm). To evaluate whether the observed size-dependent patterns of correlations were due to decreasing sample size, dropout of species with smaller D_{max} or size-dependent changes in demographic rates, we repeated the analysis for the largest 25 species. All statistical analyses were conducted using the statistical program R 3.1.2 (R Developing Core Team 2014).

RESULTS

Interspecific relationships between RGR and functional traits

Relative growth rate (RGR) declined with increasing stem diameter for most species (Fig.1a). Across species, RGR was positively correlated with maximum diameter (D_{max}) for small trees (reference stem diameters up to 25 cm) (Fig. 2a) indicating that, at small sizes, larger species tend to grow faster in stem diameter than small species. RGR was not related to wood density (WD) for any of the reference stem diameters (Fig 2c).

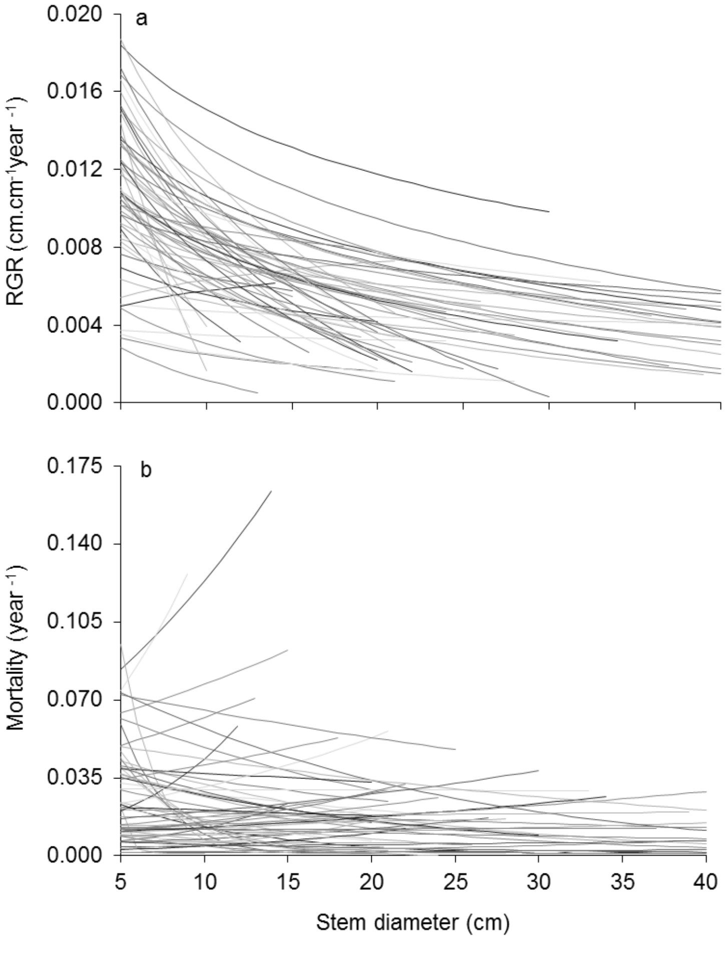

Fig. 1. Size-dependent changes in relative stem diameter growth rate (RGR) and mortality rate (MR) across 59 dry-forest tree species. Lines show changes in RGR (a) and Mortality (b) with increasing stem diameter (cm) by applying medians of probability distributions of RGR and MR for 59 tree species.

At small sizes, RGR was positively correlated with H and FBH (most of reference diameters up to 22-25 cm) (Fig. 2a,c) and with CW and LA (up to 8-13 cm) (Fig. 2e,g). RGR was negatively correlated with SLA from 16 to 18 cm stem diameter (Fig. 2i) and not correlated with SM (Fig. 2k). These results indicate that, at small sizes, species with taller heights, higher first branch height, wider crowns, larger leaf area and lower specific leaf area tend to grow faster in stem diameter, independently of their maximum diameter.

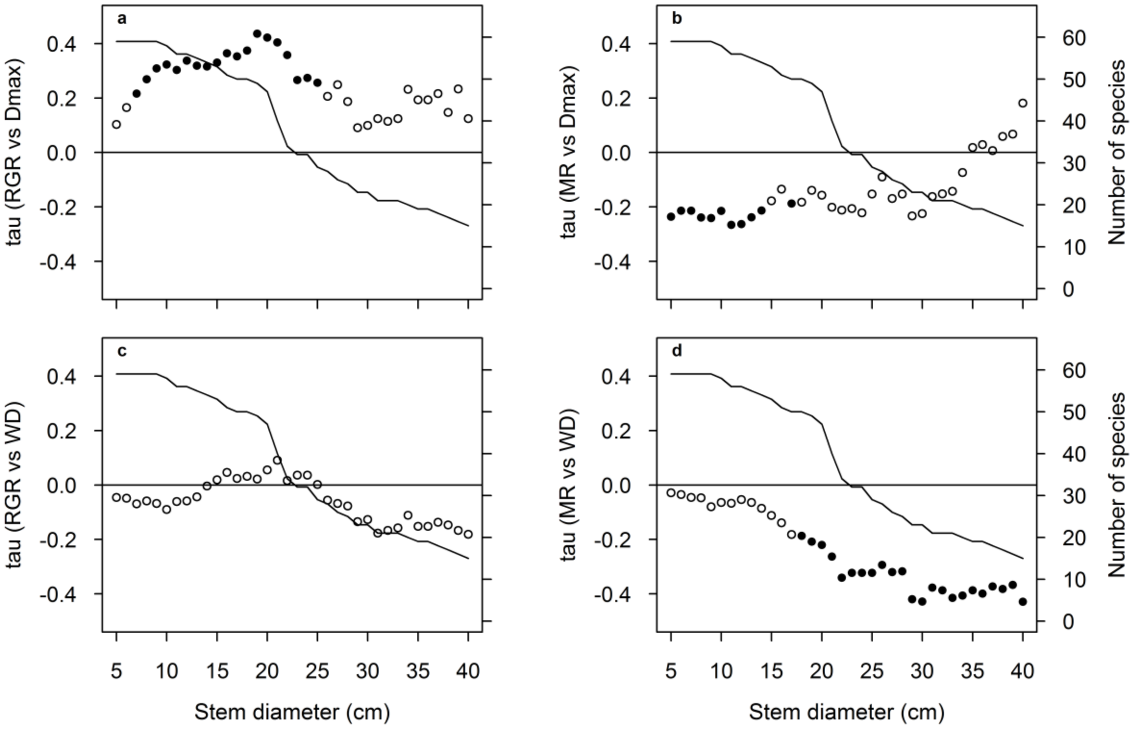

Fig. 2. Size-dependent changes in correlation coefficients (Kendall's tau) between demographic rates (RGR and MR) and maximum diameter (a,b) and wood density (c,d) across dry forest tree species. Correlations are shown between relative stem diameter growth rate (RGR) and mortality rate (MR) vs. maximum diameter (D_{max}) and wood density (WD) at different reference stem diameters, from 5 to 40 cm. Solid symbols indicate significant correlations (p < 0,05), and open symbols indicate nonsignificant correlations (p > 0,05). Solid gray lines show a decline in the number of species with increasing stem diameter from 59 species at the smallest reference diameter (5 cm) to 15 species at the largest reference diameter (40 cm).

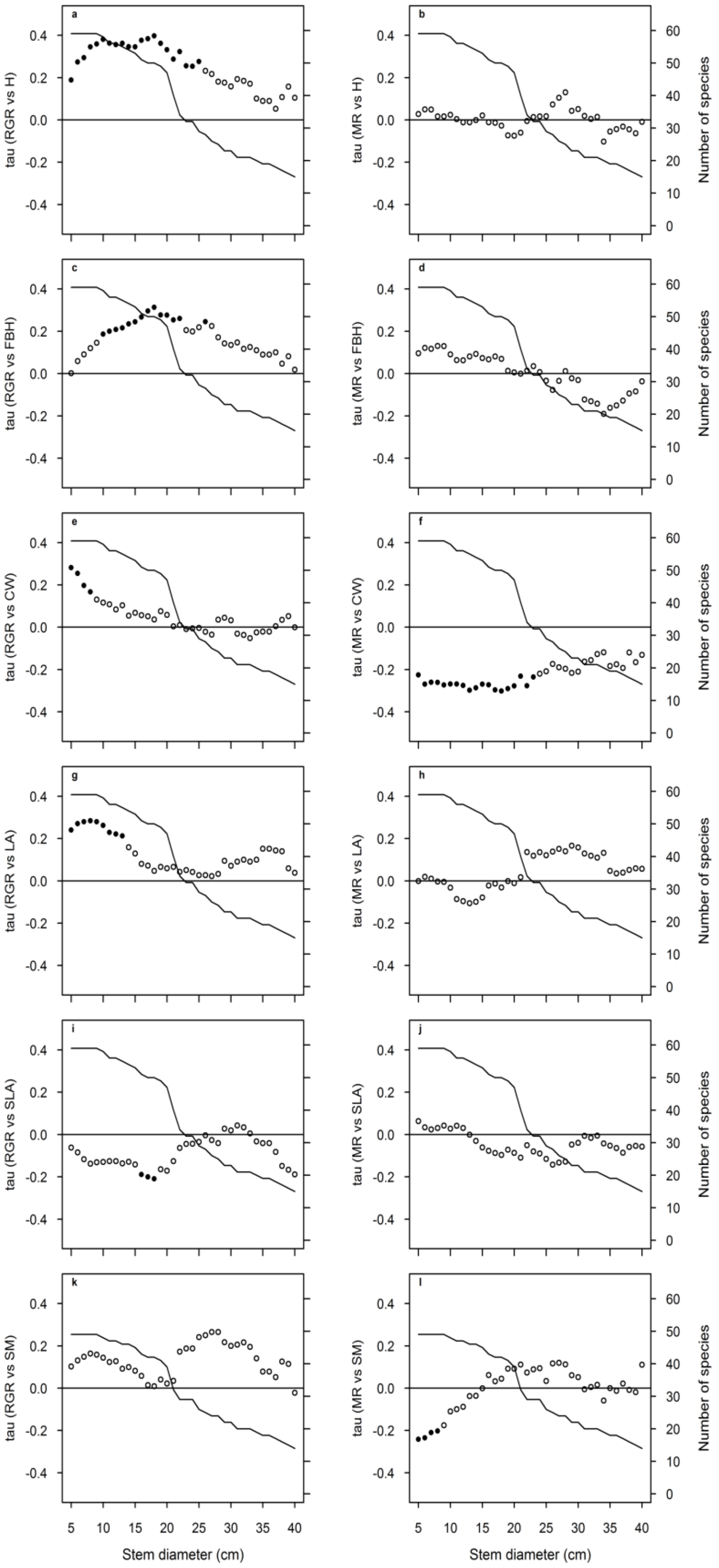

Fig. 3. Size-dependent changes in partial correlation coefficients (Kendall's tau) between demographic rates (RGR and MR) and tree architectural variables (height [H], first branch height [FBH] and crown wide [CW]), leaf traits (leaf area [LA] and specific leaf area [SLA]) and seed mass (SM), controlling the effect of maximum diameter (D_{max}) for H, FBH, CW and SLA. Symbols show medians of distributions of Kendall's partial correlation coefficients between probability distributions of RGR (left panels) and mortality rate (right panels) vs. tree architectural variables and leaf traits at different reference stem diameters, from 5 to 40 cm. Solid symbols indicate significant correlations (p < 0,05), and open symbols indicate non-significant correlations (p > 0,05). Solid gray lines show a decline in the number of species with increasing stem diameter from 59 species at the smallest reference diameter (5 cm) to 15 species at the largest reference diameter (40 cm).

To determine whether size-dependent growth rate changes were due to the dropout of species with small maximum diameter from interspecific comparisons, we repeated the same analyses for the 25 largest species. Similar relationships between RGR-H and RGR-FBH were found as in the analysis in which all species were included (Online Resource 4) whereas the relationships between RGR and the other traits (CW, LA, and SLA) became non-significant. These results reaffirm that relationships between RGR-H and RGR-FBH across species are size-dependent, are stronger and significant at small sizes and become weaker at larger sizes, and that they were not due to a decrease in species number or the dropout of small species from the comparison.

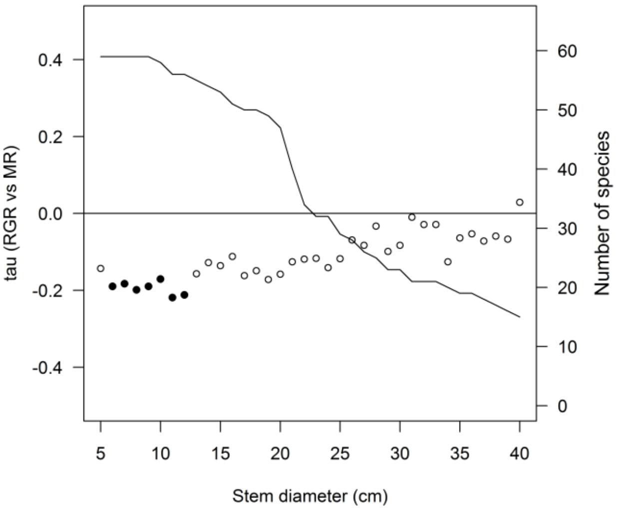

Fig. 4. Size-dependent changes in correlation coefficients between relative growth rate (RGR) and mortality rate (MR) across 59 species. Symbols show medians of distributions of Kendall’s correlation coefficients between probability distributions of RGR vs MR at different reference stem diameters, from 5 to 40 cm. Solid symbols indicate significant correlations ($p < 0,05$) and open symbols indicate non-significant correlations ($p > 0,05$). Solid gray line shows a decline in the number of species with increasing stem diameter, from 59 species at the smallest reference diameter (5 cm) to 15 species at the largest reference diameter (40 cm).

Interspecific relationships between MR and functional traits

Species differed largely in their size-dependent changes in mortality rate (MR); some species decreased mortality with increasing stem diameter and others increased their mortality with stem diameter (Fig. 1b). MR was negatively correlated with maximum diameter (D_{max}) across species for most of reference diameters up to 17 cm (Fig. 2b), and with wood density (WD) for the reference stem diameters larger than 18 cm (Fig. 2d). These results indicate that, at small sizes, larger species have lower mortality rates, whereas at large sizes, species with higher wood density have lower mortality rates.

Kendall's partial rank correlation across species was negative between MR-CW and MR-SM for small trees (reference stem diameters up to 8-23 cm) (Fig. 2f,l). MR was not related with the other tree architecture variables (H and FBH) or leaf traits (LA and SLA) (Fig. 2b,d,h,j). These results indicate that, at small sizes, species with wider crowns and higher seed mass tend to have lower mortality rates. For the 25 largest species, similar relationships were found between MR-CW, but not for MR-SM (Online Resource 4).

Relative growth rate (RGR) and mortality rate (MR) showed a significant negative correlation for small trees (reference diameters up to 15 cm), indicating that, at small sizes, species with higher growth rates have lower mortality rates. However, this relationship disappeared when we used a Kendall's partial rank correlation (controlled by D_{max}) or when this analysis was applied to the 25 largest species only (Online Resource 5).

DISCUSSION

The aim of this study was to evaluate to what extent demographic rates (growth and mortality) are shaped by functional traits and how this changes with tree size. We indeed found that the effect of functional traits on growth and mortality is strongly size-dependent. At small sizes, species with functional traits that enhance light capture (i.e., maximum adult stature and crown width) have higher growth and lower mortality rates, whereas only at larger sizes, species with functional traits that enhance drought tolerance (i.e., higher wood density) have lower mortality rates.

Species growth and mortality are size-dependent

We predicted that most species would show a decrease in relative growth rate (RGR) with an increase in stem diameter because they 1) change their morphology (larger trees suffer more from self-shading, they have a relative lower light capturing leaf area per unit living biomass, and more stem respiration costs; King 1998; Reich et al. 2003), 2) face more water stress because taller trees have longer hydraulic pathways (Koch et al. 2004), 3) shift allocation from growth towards reproduction (Thomas 2011), or 4) become senescent (Thomas 2011). The results confirmed our hypothesis and are supported by many other wet, temperate and Mediterranean forests studies (King et al. 2006; Poorter et al. 2008; Martínez-Vilalta et al. 2010, Iida et al. 2014a,b).

Species mortality rates (MR) decreased or increased with increasing stem diameter, which can reflect differences in species life histories based and their capacity to either survive well in the understory or to survive well in the exposed conditions of the forest canopy. Small trees may have a higher MR because of the low carbon gain in the shaded understory (Poorter and Bongers 2006), or because they face higher risks of mechanical damage by falling debris (Sterck and Bongers 1998). Alternatively, larger trees may have higher MRs due to increased water limitation with height in combination with sudden droughts (Carnicer et al. 2011), physical damages by strong winds (Sterck et al. 2003) or because of senescence (Mencuccini et al. 2005; King et al. 2006; Thomas 2011; Iida et al. 2014a).

Species with larger adult stature have higher RGR and lower MR

Species differences in growth and mortality rates are likely driven by interspecific differences in functional traits. We predicted that, in the sapling stage, larger species would grow faster than small species to rapidly attain their large reproductive size and to attain the higher light conditions in the canopy at which can become reproductive (Thomas 2011). Conversely, small species may grow slowly because they allocate resources to early reproduction rather than growth (Mencuccini et al. 2005; Thomas 2011). We indeed found that larger species grew faster, especially at small stem diameters (7-25 cm dbh), which has also been found in many others comparative studies (King et al. 2006; Poorter et al. 2008; Martínez-Vilalta et al. 2010; Wright et al. 2010; Herault et al. 2011; Iida et al. 2014a,b, Shen et al. 2014).

Based on life-history theory, larger trees are relatively K-selected and should have large offspring, high survival and long life span (Pianka 1970). Thus, we predicted that larger, and hence, longer-lived species should have lower inherent mortality rates than small species (Pianka 1970; Poorter et al. 2008). Small species might have inherent higher mortality rates because, for the minimum diameter range considered in this study (5 cm), they are closer to their maximal size (near to senescence) (Kohyama et al. 2003; King et al. 2006; Poorter et al. 2008). Our results confirmed our hypothesis for small reference diameters, but at larger stem diameters, mortality rate was not related to maximum diameter. Previous studies also found negative relationships between mortality and adult stature (e.g. Poorter et al. 2008; Iida et al. 2014a) whereas others found non-significant relationships (Martínez-Vilalta et al. 2010;

Wright et al. 2010) between mortality and adult stature, probably because they used average demographic rates over a large diameter range. Our results show that the negative relationship between MR and D_{max} is especially found for small trees and disappears at a dbh of 15 cm. When this analysis was repeated by including only the largest species then the MR and D_{max} relationship became non-significant (Online Resource 4), suggesting that by 15 cm stem diameter all really small-statured species that drive the pattern have dropped out of the comparison, and which shows strong differences in life histories between canopy and understory species.

Dense wood enhances drought survival of larger trees

We predicted that wood density (WD) would have a negative effect on stem diameter growth rates because of the higher construction costs per unit stem wood volume. Surprisingly, our results showed that WD was not related with RGR for any of the reference stem diameters, in contrast with the findings of wet, temperate, Mediterranean and subtropical forests studies (Poorter et al. 2008; Chave et al. 2009; Martínez-Vilalta et al. 2010; Wright et al. 2010, Shen et al. 2014). A possible explanation for the absence of a WD effect on growth is that although higher WD implies in higher wood cost production, dense wood species can grow faster per unit time in dry forests because they are less sensitive to water availability (Mendivelso et al. 2013). Thus, the relationship between RGR and WD for dry forest species is weak compared to that of others forests types species because it is more related to enhance species' drought avoidance and/or resistance.

We predicted that species with high WD would have lower MR because they are more resistant to hydraulic failures. In wet forest, there is especially a close negative relationship between WD and MR at small reference sizes and a weaker relationship at larger sizes (Poorter et al. 2008; Chave et al. 2009; Wright et al. 2010) whereas for our dry forest trees we only found a strong and negative relationship at larger sizes. Dry forests are exposed to long periods of drought (i.e. 6 months with < 100mm) with low soil water potentials, leading to reduced hydraulic conductivity and potentially to cavitation, hydraulic failure, and tree death (Wheeler et al. 2005). This water stress become stronger with increasing tree height because of longer hydraulic pathways (Koch et al. 2004) and more exposed tree crowns that experience larger vapor pressure deficits. Higher WD enhances the cavitation resistance of dry forest and Mediterranean tree species (Martínez-Vilalta et al. 2010; Pineda-García et al. 2013) and reduces their sensitivity to dry-season water stress (Mendivelso et al. 2013). High WD is therefore of adaptive benefit in dry environments, and it is for this reason that dry forests species have, on average, higher wood density than wet forest species (Barajas-Morales 1987; Borchert 1994). Our results suggest that WD plays a fundamentally different role in wet and dry forests. Where in wet forest WD is closely associated with shade tolerance (van Gelder et al. 2006) and the protection of small trees against the abundant pathogens and physical damage, in dry forest it is closely associated with drought tolerance (Markesteijn et al. 2009) and the protection of large, exposed, trees to drought-induced hydraulic failure.

Tree architecture enhances light capture and performance of small trees

We predicted that species with taller heights and shallow crowns (i.e. higher first branch height) at a given stem diameter, should have higher growth rates. Light increases exponentially with height in forest and thus, taller species may intercept a higher amount of light compared to smaller species (Poorter et al. 2006). Furthermore, by postponing the first branch height, or by investing in cheap, throw-away branches (resulting in a shallower crown) species may invest more biomass in height expansion, thus rapidly getting access to better light conditions higher up in the canopy, and beyond shallow crowns are less self-shading (King 1998; Poorter et al. 2006). We indeed found that RGR was positively related to H and

FBH at small sizes (<25 cm dbh) when trees are still not in the canopy and light is a strong limiting resource (Sterck et al. 2003; Iida et al. 2014a). We also predicted that species with a wider crown at a given stem diameter should have higher growth rates, because although their investment in horizontal crown expansion implies in less available carbon for horizontal stem expansion (Sterck et al. 2003; Iida et al. 2014a), wider crowns enhance a higher area for foraging light capture, and unlike deep crowns, does not implies in increase of species self-shading. The relationship between RGR and CW was positive at small sizes, which means that in the shaded understory the benefits of a larger foraging capacity for light through wider crowns exceeds their construction costs.

We predicted that species with taller heights, deeper (lower first branch height) and wider crowns (higher crown width) would have higher mortality rates because they are more sensitive to dynamic loading due to wind or falling debris (Sterck and Bongers 1998, Iida et al. 2014a). However, mortality was not related to height or first branch height, whereas at small sizes, species with wider crowns had actually lower mortality rates (Sterck et al. 2003; Poorter et al. 2006) probably because wider crowns enhance light capture, and hence, carbon gain and tree persistence in the shaded understory (Poorter et al. 2006). Although it is often suggested that light is not a major limiting resource for dry forests understories, due their lower and (seasonally) more open canopy (Lebrija-Trejos et al. 2008; Lohbeck et al. 2013), our results show that light is an important resource for growth and survival in dry forest species, and that species tree architecture seems to be more important to enhance current or future light capture of trees when they are young, then to reduce or avoid physical damage.

Leaf traits

We predicted that species with higher leaf area (LA) and specific leaf area (SLA) have higher growth rate because they intercept a higher amount of light (per unit leaf mass invested) (Falster and Westoby 2003; Reich et al. 2003). We indeed found a positive correlation between RGR and LA at small sizes (when all species were included). At larger sizes this relationship became weaker, possibly because larger leaves suffer more from overheating, especially when they are in the canopy, which can reduce the photosynthetic net gain of large-leaved species (King 1998). Rather than a positive relation between RGR and SLA, we found no relationship, or at some reference diameters even a significant negative relationship between RGR and SLA (when all species were included). An explanation for absence (or also a weak negative correlation in small sizes) is that shade-tolerant species may persist under shade by producing leaves with large SLA and consequently higher light harvesting efficiency per unit leaf mass invested. In contrast light-demanding species may be exposed to high radiation in gaps with adaptive leaf habits of small SLA and must grow faster at small sizes (Iida et al. 2014b).

For the mortality rates, no correlations were found for the leaf traits. Positive relationships between demographic rates and LA and SLA have often been found for small seedlings (Kitajima 1994; Poorter and Bongers 2006), but this relationship is weak or absent for large trees growing in the field (Poorter et al. 2008; Martínez-Vilalta et al. 2010; Wright et al. 2010; Herault et al. 2011; Shen et al. 2014), consistent with our results. For larger trees other leaf-related functional traits could become important; the amount of biomass allocated to leaves (leaf mass fraction, LMF) and biomass growth per unit leaf area (net assimilation rate, NAR) should be stronger correlated to RGR and mortality (Reich et al. 2003; Tomlinson et al. 2014).

Species with higher seed mass have lower MR

We predicted that species with lower seed mass (SM) have higher growth rates because small seed sizes are typical of fast-growing pioneer species. However, our results showed that RGR was not related with SM for any of the reference stem diameters, which is in agreement with other studies showing that correlations between RGR and seed mass are especially high for seedlings, just after germination (Poorter and Rose 2005; Martínez-Vilalta et al. 2010; Wright et al. 2010). We predicted that species with lower seed mass (SM) should have higher mortality rates (when all species were included), because they produce less robust seedlings that suffer more from stress and disturbance (Harms and Dalling 1997; Leishman et al. 2000) and because low SM is typical for pioneer species that have high inherent mortality rates. We indeed found that MR was higher for small-seeded species at small sizes. This relationship may disappear at larger sizes because then most species have very low mortality rates, and mortality becomes more stochastically (Poorter et al. 2008).

Growth vs. survival trade-off and the relative importance of functional traits

We predicted that species with faster growth have higher mortality, especially at small sizes. The growth and survival trade-off is mainly driven by the contrasts between slow-growing shade-tolerant species that survival very well in the shade versus light-demanding pioneer species that grow very fast in high light but die very fast as well (Poorter and Bongers 2006; Poorter et al. 2008; Wright et al. 2010). This relationship tends to become weaker with increasing stem diameter when trees escape shade suppression and both shade-tolerant and pioneer species gradually attain more similar exposed conditions in the canopy (Wright et al. 2010; Iida et al. 2014a,b). Surprisingly, we found that growth and mortality were *negatively* correlated at small sizes (when all species were included). This absence of a trade-off between growth and mortality was also reported in temperate and Mediterranean forests (Kunstler et al. 2009, Martínez-Vilalta et al. 2010). At small sizes, species with higher growth should have higher light availability and they escape gradually from elevated risk of desiccation (Tomlinson et al. 2014), while they develop longer and deeper roots to reach deeper soil layers for water as well as larger water and starch and sugars reserves, thus surviving better. When this analysis was repeated by including only the largest species or by controlling for the effect of D_{max}, then the growth-mortality relationship became non-significant. These results indicate that this negative relation between RGR and MR was driven mainly by the higher growth and lower mortality of large species compared to small species, as well as some traits increased the growth (higher leaf area and lower specific leaf area) or reduced the mortality (higher seed mass) at small sizes only when all species were analyzed together (large and small statured species), which shows strong differences in life histories between canopy and understory species.

The (size-dependent) trade-off between growth and survival is thought to contribute to species coexistence and, therefore, to the maintenance of forest diversity in wet forests (Poorter et al. 2008; Wright et al. 2010). We found for our dry forest as well as other dry forest systems that there is no growth-survival trade-off (Kunstler et al. 2009, Martínez-Vilalta et al. 2010),. If any, there is a positive relationship between growth and survival, indicating that, from a demographic point of view, there are superperformers species that combine high growth with high survival (e.g. large statured and wider crown species), thus outcompeting other species, and potentially leading to reduced species diversity (which is also observed to be lower in dry compared to wet forests).

CONCLUDING REMARKS

We reported size-dependent correlations between functional traits and demographic rates. Correlation does not necessary mean causation, but our results shows that these traits are related to species performance, we have good mechanistic reasons to assume why and how these traits are important, and this is also supported by controlled experiments (Kitajima 1994, Tomlinson et al. 2014) and models (Herault et al. 2011, Sterck et al. 2014). Our study can be summarized in four main results. First, the effect of functional traits on growth and mortality is strongly size-dependent; at small sizes, functional traits that enhance light capture lead to higher growth and lower mortality rates, whereas at larger sizes functional traits that enhance drought tolerance lead to lower mortality rates. Second, we found that, despite the high light levels in dry forest understories, light can still be an important factor for plant adaptations and performance in dry forest. Third, from a functional point of view, dry forests show different trait-rate relationships than wet forests; where in wet forest wood density and specific leaf area are tightly linked to shade tolerance, growth and survival, is in dry forest wood density related to drought tolerance and survival, and one of the most frequently measured traits, specific leaf area, was not related to plant performance at all. Finally, we observed for some tree sizes a positive relationship between growth and survival, rather than a trade-off, which could potentially lead to species dominance and a reduced diversity. Dry forests are among the most fragmented and threatened ecosystems in the world (Miles et al. 2006). Insight in their functioning, and how functional traits affects species dynamics can help to improve their management and conservation. Environmental conditions and ecological pressures that plants face change with their size, and our study shows that the relationships between functional traits and plant performance changes with plant size. Plant size should therefore explicitly be included as an axis of variation in functional analyses, to better understand the relationship between functional traits and demographic rates.

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APPENDICES

Online Resource 1. Functional traits and demographic parameters r_1, r_2, m_1 and m_2 of 59 studied species. Scientific name, family, total number of stems (Ntrees), number of dead trees (Ndead) after five years of monitoring in 8-ha Brazilian dry forests, 95-percentile maximum stem diameter (D_{max}; cm), wood density (WD; g.cm^{-3}), leaf area (LA; cm^{2}), specific leaf area (SLA; mm^{2}.mg^{-1}), seed mass (SM; mg) and species-specific allometric parameters for each tree architecture variables (height [H; m], first branch height [FBH; m] and crown width [CW; m]). Allometric regressions parameters for tree architecture are based on the logarithmic equation of H~DBH, FBH~DBH and CW~DBH [e.g. $H = h_1 + h_2 \ln(DBH)$]. NA = not available. For the traits that we measured in the field (LA, SLA, FBH and CW) we provide the coefficient of variation of these traits for each species.

Species	Family	Ntrees	Ndead	D_{max}	WD	LA	SLA	SM	h1	h2	fbh1	fbh2	cw1	cw2
Amaioua guianensis	Rubiaceae	34	4	16	0.63	63.4 (0.22)	12.1 (0.16)	8	-2.66	5.62	-1.35	2.87 (0.25)	-0.98	2.08 (0.22)
Anadenanthera colubrina	Fabaceae	67	6	49.1	0.87	34.6 (0.36)	7.4 (0.19)	97.1	-2.47	5.98	-3.96	3.88 (0.25)	-4.43	4.35 (0.27)
Apuleia leiocarpa	Fabaceae	72	5	60.2	0.8	71.5 (0.38)	17.9 (0.25)	48.1	-2.47	5.98	-1.10	3.22 (0.17)	-1.19	3.48 (0.28)
Aspidosperma discolor	Apocynaceae	189	10	42.9	0.76	29 (0.32)	10.4 (0.22)	166.7	-1.37	5.39	-0.73	2.86 (0.33)	-0.37	1.46 (0.34)
Aspidosperma parvifolium	Apocynaceae	36	1	51.4	0.78	22.5 (0.26)	15.5 (0.18)	200	-8.01	7.55	-3.7	3.48 (0.18)	-4.50	4.23 (0.21)
Astronium nelson-rosae	Anacardiaceae	169	5	26.3	0.87	275 (0.41)	11.3 (0.14)	28.2	-3.06	6.75	-1.75	3.85 (0.38)	-0.89	1.96 (0.15)
Campomanesia vellutina	Myrtaceae	54	14	13.5	0.82	26.4 (0.35)	22.6 (0.25)	NA	0.95	2.59	0.49	1.35 (0.38)	0.45	1.25 (0.3)
Cariniana estrellensis	Lecythidaceae	51	2	169.7	0.64	42.9 (0.28)	9.2 (0.18)	83.3	-6.39	7.42	-2.82	3.95 (0.37)	-4.67	5.42 (0.28)
Casearia gossypiosperma	Salicaceae	91	8	25.6	0.67	27.1 (0.18)	18.4 (0.34)	NA	-2.47	5.98	-6.33	6.23 (0.18)	-4.11	4.05 (0.36)
Casearia grandiflora	Salicaceae	108	33	15.2	0.77	24.8 (0.25)	12.8 (0.21)	11.9	-2.47	5.98	1.95	1.68 (0.33)	1.20	1.03 (0.21)
Casearia sylvestris	Salicaceae	62	27	14.2	0.72	16.3 (0.23)	20 (0.14)	11.9	-2.56	5.21	-1.50	3.03 (0.44)	-0.80	1.62 (0.26)
Cheiloclinium cognatum	Celastraceae	325	23	20.4	0.77	62.6 (0.3)	12.8 (0.19)	1818.2	0.66	3.24	0.15	0.71 (0.16)	0.41	2.00 (0.37)
Chrysophyllum gonocarpum	Sapotaceae	68	4	18.7	0.67	61.4 (0.38)	13.9 (0.18)	245.7	-0.96	4.23	-0.37	1.65 (0.2)	-0.50	2.2 (0.35)
Chrysophyllum marginatum	Sapotaceae	163	33	20.3	0.7	19.9 (0.22)	16.3 (0.14)	181.8	-0.82	4.05	-0.36	1.74 (0.38)	-0.31	1.54 (0.33)
Copaifera langsdorffii	Fabaceae	68	1	89.8	0.65	41.2 (0.27)	11.2 (0.15)	581.4	-2.47	5.98	-1.11	2.69 (0.19)	-1.95	4.72 (0.2)
Cordiera sessilis	Rubiaceae	239	33	10.4	0.88	53.8 (0.41)	12 (0.19)	40	0.20	3.39	0.08	1.39 (0.22)	0.10	1.90 (0.26)
Cryptocarya aschersoniana	Lauraceae	210	17	62	0.57	39 (0.25)	11.8 (0.16)	1851.9	-2.41	5.85	-1.11	2.69 (0.28)	-0.99	2.4 (0.35)

Cupania vernalis	Sapindaceae	78	13	19.9	0.66	333.2 (0.54)	10.5 (0.14)	387.6	-0.82	4.45	-0.33	1.74 (0.12)	-0.38	2.01 (0.24)
Diospyros hispida	Ebenaceae	88	10	24.1	0.62	36.7 (0.25)	12.5 (0.18)	909.1	-1.58	4.99	-0.84	2.65 (0.36)	-0.60	1.90 (0.39)
Duguetia lanceolata	Annonaceae	181	9	24.3	0.87	39.8 (0.31)	12.6 (0.2)	625	-3.27	6.44	-1.15	2.26 (0.25)	-1.47	2.90 (0.28)
Eugenia florida	Myrtaceae	188	28	20.7	0.68	26.4 (0.3)	16.2 (0.19)	833.3	-5.30	6.1	-2.28	2.62 (0.22)	-2.81	3.23 (0.11)
Eugenia involucrata	Myrtaceae	41	3	14.7	0.76	10.1 (0.22)	16.6 (0.11)	133.3	-3.99	5.55	-1.69	2.34 (0.06)	-1.93	2.67 (0.12)
Eugenia ligustrina	Myrtaceae	28	1	11.1	0.76	9.4 (0.22)	14.9 (0.21)	NA	1.75	2.50	0.52	0.75 (0.12)	1.13	1.63 (0.18)
Faramea hyacinthina	Rubiaceae	58	5	20.8	0.58	39.7 (0.31)	12.8 (0.18)	NA	-1.13	4.26	-0.45	1.7 (0.21)	-0.63	2.38 (0.24)
Galipea jasminiflora	Rutaceae	142	20	12.1	0.75	58 (0.29)	22.8 (0.15)	31.3	-2.32	4.8	-0.85	1.73 (0.2)	-1.56	3.18 (0.11)
Garcinia gardneriana	Clusiaceae	62	9	20.6	0.72	53.3 (0.26)	10.7 (0.08)	3225.8	-3.19	5.25	-1.50	2.47 (0.21)	-1.53	2.52 (0.17)
Guatteria australis	Annonaceae	28	1	21.2	0.54	80.1 (0.19)	14.9 (0.11)	625	-3.80	6.56	-1.85	3.21 (0.2)	-1.40	2.42 (0.17)
Guazuma ulmifolia	Malvaceae	49	13	25	0.51	52.5 (0.33)	13.8 (0.2)	6.1	-2.91	5.43	-1.75	3.26 (0.17)	-1.11	2.07 (0.32)
Heisteria ovata	Olacaceae	83	4	27.3	0.7	59.8 (0.19)	9.7 (0.15)	NA	-0.96	4.70	-0.3	1.46 (0.11)	-0.61	2.96 (0.13)
Hirtella glandulosa	Chrysobalanaceae	52	3	42.1	0.93	72.9 (0.37)	10.7 (0.12)	105.3	-2.74	5.65	-1.04	2.15 (0.33)	-1.26	2.6 (0.37)
Inga vera	Fabaceae	112	9	23.5	0.58	146.5 (0.3)	14.1 (0.15)	1315.8	-0.78	5.57	-0.38	2.78 (0.12)	-0.32	2.34 (0.16)
Ixora brevifolia	Rubiaceae	106	3	21.6	0.88	50.6 (0.47)	12.2 (0.3)	NA	-0.03	3.71	-0.01	0.89 (0.45)	-0.01	2.22 (0.18)
Luehea grandiflora	Malvaceae	46	4	28.3	0.54	123.7 (0.32)	19.4 (0.17)	6.1	-2.56	4.68	-1.44	2.63 (0.33)	-1.31	2.39 (0.21)
Machaerium villosum	Fabaceae	44	4	35.8	0.78	202 (0.39)	18.9 (0.12)	476.2	-2.27	6.11	-1.18	3.17 (0.2)	-0.70	1.89 (0.27)
Matayba elaeagnoides	Sapindaceae	39	4	19.7	0.75	169.1 (0.46)	12 (0.11)	307.7	-1.05	4.71	-0.39	1.74 (0.25)	-0.56	2.5 (0.23)
Matayba guianensis	Sapindaceae	98	14	19.7	0.82	337.9 (0.38)	11.9 (0.15)	208.3	-3.18	5.91	-1.45	2.66 (0.43)	-1.42	2.61 (0.19)
Maytenus floribunda	Celastraceae	74	2	21.3	0.72	20.5 (0.37)	10.6 (0.11)	NA	-1.70	4.68	-0.97	2.67 (0.17)	-0.58	1.59 (0.10)
Micrandra elata	Euphorbiaceae	118	5	109.6	0.72	30.3 (0.47)	19.8 (0.19)	129.9	-6.7	7.54	-2.68	3.02 (0.21)	-4.43	4.98 (0.15)
Nectandra cissiflora	Lauraceae	44	5	30.5	0.59	151.1 (0.29)	9.5 (0.14)	1333.3	-2.47	6.28	-2.52	4.02 (0.29)	-1.85	2.95 (0.31)
Nectandra membranacea	Lauraceae	80	11	32.8	0.59	52.5 (0.35)	12.8 (0.17)	769.2	-2.47	5.98	1.74	1.9 (0.18)	1.39	1.52 (0.23)
Ocotea corymbosa	Lauraceae	142	9	55.8	0.53	20.1 (0.38)	10.2 (0.27)	285.7	-2.47	5.98	0.20	2.13 (0.13)	0.27	2.93 (0.37)
Ocotea spixiana	Lauraceae	51	3	37.4	0.66	42 (0.3)	9 (0.24)	606.1	-2.47	5.98	1.38	1.26 (0.2)	1.87	1.71 (0.10)
Platycyamus regnellii	Fabaceae	50	1	46.8	0.81	460.6 (0.27)	16.4 (0.22)	555.6	-5.44	7.58	-2.89	4.02 (0.21)	-2.18	3.03 (0.29)
Pouteria gardneri	Sapotaceae	28	2	27.6	0.78	116.6 (0.34)	12.8 (0.15)	250	-5.81	7.30	-2.32	2.92 (0.19)	-2.67	3.35 (0.23)
Pouteria torta	Sapotaceae	125	2	37.9	0.77	116.6 (0.48)	12.8 (0.13)	3030.3	2.04	4.30	0.92	1.94 (0.22)	1.15	2.41 (0.30)
Protium heptaphyllum	Burseraceae	235	18	34	0.63	221.2 (0.28)	11.5 (0.25)	90.9	-1.59	5.48	-0.60	2.08 (0.18)	-0.84	2.91 (0.20)
Siparuna guianensis	Siparunaceae	388	139	8.9	0.65	47.5 (0.42)	18.3 (0.18)	16	1.96	2.81	0.90	1.3 (0.31)	1.13	1.63 (0.37)

Siphoneugena densiflora	Myrtaceae	122	15	19.5	0.91	35 (0.29)	9.3 (0.21)	153.8	-4.01	6.11	-1.73	2.63 (0.23)	-2.13	3.24 (0.36)
Sweetia fruticosa	Fabaceae	45	1	56.5	0.78	34.6 (0.15)	12.5 (0.14)	196.1	-9.14	8.59	-4.47	4.21 (0.15)	-3.83	3.61 (0.34)
Tapirira obtusa	Anacardiaceae	85	13	58.9	0.46	264.1 (0.46)	11.9 (0.13)	196.1	-2.47	5.98	-0.91	2.03 (0.23)	-2.63	2.50 (0.21)
Terminalia glabrescens	Combretaceae	137	12	39.1	0.77	38.2 (0.28)	11.4 (0.25)	3.4	-3.83	6.12	-1.68	2.69 (0.26)	-1.34	2.14 (0.44)
Terminalia phaeocarpa	Combretaceae	57	6	48.8	0.7	102.1 (0.29)	12.9 (0.29)	NA	-5.08	6.82	-2.45	3.28 (0.13)	-2.09	2.80 (0.20)
Trichilia catigua	Meliaceae	120	12	20.3	0.69	114 (0.36)	14.1 (0.14)	128.2	-1.34	4.84	-0.49	1.74 (0.14)	-0.67	2.42 (0.07)
Trichilia clausseni	Meliaceae	129	11	19.9	0.66	142 (0.4)	15.1 (0.19)	161.3	-2.57	5.49	-0.85	1.81 (0.16)	-1.65	3.51 (0.31)
Trichilia elegans	Meliaceae	53	6	20.8	0.66	140.5 (0.24)	16.9 (0.16)	NA	-1.38	4.44	-0.47	1.51 (0.13)	-0.78	2.53 (0.34)
Unonopsis guatterioides	Annonaceae	102	9	21.7	0.52	72.8 (0.33)	16 (0.15)	NA	-3.9	5.70	-0.58	0.85 (0.05)	-1.59	2.33 (0.18)
Virola sebifera	Myristicaceae	123	13	29.9	0.46	144 (0.35)	9.5 (0.23)	588.2	-2.26	6.34	-1.49	4.19 (0.35)	-0.75	2.09 (0.29)
Vochysia magnifica	Vochysiaceae	113	21	51.4	0.78	69.2 (0.33)	10 (0.33)	117.6	-2.47	5.98	-4.34	4.55 (0.23)	-2.63	2.76 (0.26)
Xylopia brasiliensis	Annonaceae	38	7	18	0.7	27.5 (0.29)	9.3 (0.25)	73	-1.24	5.58	-0.78	3.47 (0.31)	-0.34	1.51 (0.39)

Online Resource 2. Species-specific demographic parameters r_1, r_2, m_1 and m_2 were summarized as medians and 95% confidence intervals for 59 species. Scientific name, total number of stems (Ntrees), number of dead trees (Ndead) after five years of monitoring in 8-ha Brazilian dry forests. The predicted demographics parameters refers to species-specific logarithmic regression for relative diameter growth rate ($RGR_{ij} = r_{1j} + r_{2j} \ln(DBH_{1i})$) and logistic binary for mortality rate ($\ln\left(MR_{ij}\right) = m_{1j} + m_{2j}\, DBH_{1i}$)

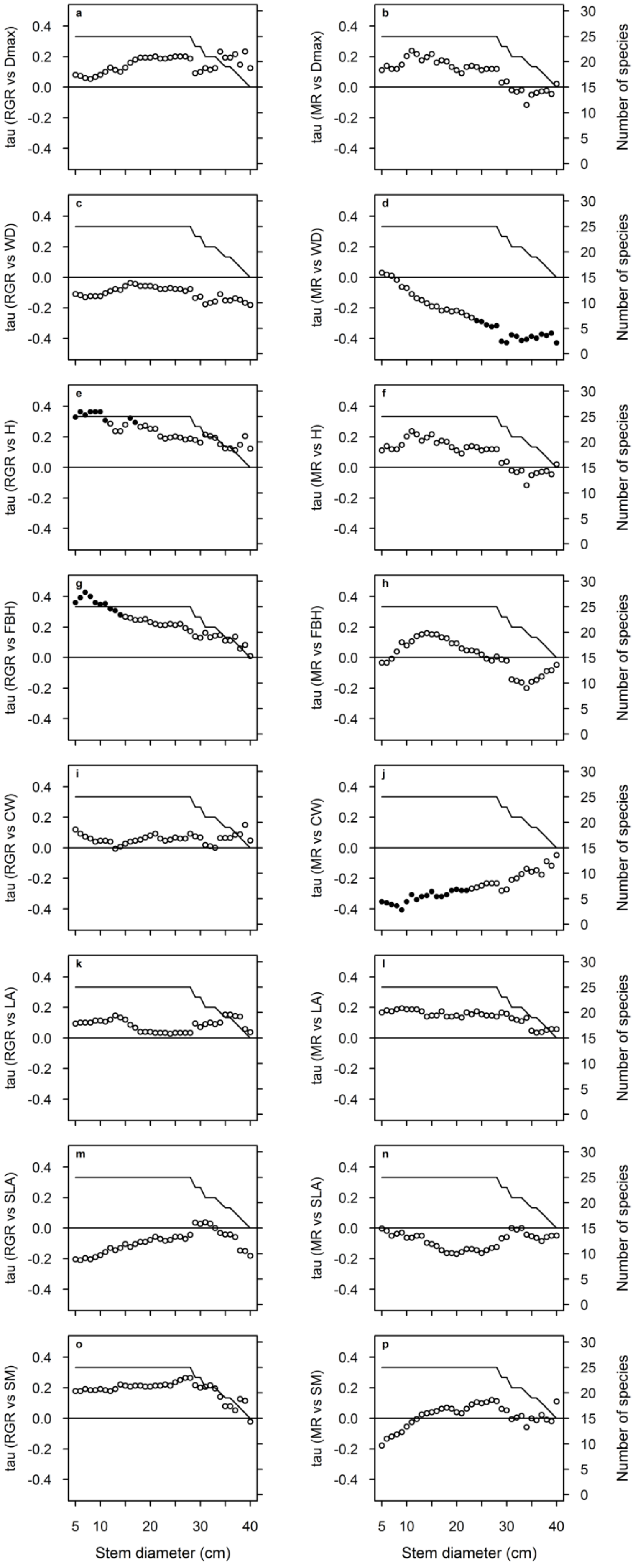
Species	Ntrees	Ndead	r1	r1 95%CI	r2	r2 95%CI	m1	m1 95%CI	m2	m2 95%CI
Amaioua guianensis	34	4	0.022	[0.008, 0.036]	-0.007	[-0.013, -0.001]	-0.871	[-23.019, 21.277]	0.388	[-2.914, 3.690]
Anadenanthera colubrina	67	6	0.011	[0.002, 0.020]	-0.002	[-0.005, 0.001]	1.133	[-11.907, 14.173]	0.062	[-0.620, 0.744]
Apuleia leiocarpa	72	5	0.018	[0.012, 0.023]	-0.004	[-0.006, -0.002]	1.528	[-12.613, 15.669]	0.061	[-0.784, 0.906]
Aspidosperma discolor	189	10	0.02	[0.016, 0.025]	-0.004	[-0.006, -0.002]	1.511	[-17.641, 20.663]	0.119	[-1.691, 1.929]
Aspidosperma parvifolium	36	1	0.006	[-0.003, 0.015]	0.000	[-0.004, 0.003]	2.807	[-18.798, 24.412]	0.054	[-1.507, 1.615]
Astronium nelson-rosae	169	5	0.016	[0.010, 0.022]	-0.003	[-0.006, -0.001]	3.426	[-19.844, 26.696]	0.005	[-1.695, 1.705]
Campomanesia vellutina	54	14	0.007	[0.001, 0.013]	-0.002	[-0.005, -0.001]	1.527	[-10.913, 13.967]	-0.052	[-1.290, 1.186]
Cariniana estrellensis	51	2	0.025	[0.017, 0.034]	-0.005	[-0.008, -0.003]	3.958	[-12.692, 20.608]	-0.014	[-0.210, 0.182]
Casearia gossypiosperma	91	8	0.016	[0.008, 0.025]	-0.003	[-0.008, 0.001]	1.676	[-14.009, 17.361]	0.079	[-1.772, 1.930]
Casearia grandiflora	108	33	0.018	[0.007, 0.029]	-0.005	[-0.010, 0.001]	1.193	[-10.773, 13.159]	-0.044	[-1.350, 1.262]
Casearia sylvestris	62	27	0.003	[-0.016, 0.023]	0.001	[-0.008, 0.011]	1.15	[-10.960, 13.260]	-0.099	[-1.370, 1.172]
Cheiloclinium cognatum	325	23	0.022	[0.018, 0.026]	-0.007	[-0.008, -0.005]	3.249	[-14.022, 20.520]	-0.053	[-1.181, 1.075]
Chrysophyllum gonocarpum	68	4	0.03	[0.018, 0.042]	-0.009	[-0.015, -0.004]	3.054	[-17.342, 23.450]	-0.029	[-1.908, 1.850]
Chrysophyllum marginatum	163	33	0.005	[0.001, 0.010]	-0.001	[-0.003, 0.001]	0.748	[-10.958, 12.454]	0.054	[-0.912, 1.020]
Copaifera langsdorffii	68	1	0.02	[0.014, 0.026]	-0.004	[-0.006, -0.003]	4.152	[-29.909, 38.213]	-0.022	[-0.609, 0.565]
Cordiera sessilis	239	33	0.031	[0.022, 0.039]	-0.012	[-0.016, -0.007]	0.506	[-24.716, 25.728]	0.203	[-3.670, 4.076]
Cryptocarya aschersoniana	210	17	0.015	[0.012, 0.018]	-0.003	[-0.004, -0.002]	2.13	[-9.417, 13.677]	0.015	[-0.481, 0.511]
Cupania vernalis	78	13	0.01	[0.003, 0.018]	-0.002	[-0.005, 0.001]	1.465	[-9.754, 12.684]	0.013	[-0.858, 0.884]
Diospyros hispida	88	10	0.004	[-0.001, 0.010]	0.000	[-0.002, 0.002]	1.568	[-12.963, 16.099]	0.033	[-0.893, 0.959]
Duguetia lanceolata	181	9	0.02	[0.015, 0.025]	-0.005	[-0.007, -0.003]	3.155	[-11.995, 18.305]	-0.019	[-1.069, 1.031]
Eugenia florida	188	28	0.009	[0.005, 0.013]	-0.003	[-0.004, -0.001]	1.332	[-12.562, 15.226]	0.034	[-1.050, 1.118]

Eugenia involucrata	41	3	0.01	[-0.011, 0.032]	-0.002	[-0.013, 0.009]	4.079	[-10.261, 18.419]	-0.133	[-1.087, 0.821]
Eugenia ligustrina	28	1	0.044	[0.027, 0.061]	-0.018	[-0.027, -0.010]	-4.726	[-29.995, 20.543]	0.978	[-3.417, 5.373]
Faramea hyacinthina	58	5	0.026	[0.014, 0.039]	-0.008	[-0.014, -0.002]	2.887	[-14.148, 19.922]	-0.05	[-1.467, 1.367]
Galipea jasminifolia	142	20	0.02	[0.009, 0.030]	-0.007	[-0.012, -0.001]	3.07	[-14.181, 20.321]	-0.166	[-2.209, 1.877]
Garcinia gardneriana	62	9	0.015	[0.006, 0.024]	-0.004	[-0.008, 0.001]	2.376	[-9.253, 14.005]	-0.059	[-1.008, 0.890]
Guatteria australis	28	1	0.031	[0.011, 0.051]	-0.009	[-0.018, 0.000]	2.249	[-36.179, 40.677]	0.108	[-3.884, 4.100]
Guazuma ulmifolia	49	13	0.018	[-0.001, 0.035]	-0.005	[-0.012, 0.002]	0.712	[-10.901, 12.325]	0.024	[-0.827, 0.875]
Heisteria ovata	83	4	0.025	[0.017, 0.033]	-0.007	[-0.010, -0.004]	3.719	[-15.748, 23.186]	-0.048	[-1.052, 0.956]
Hirtella glandulosa	52	3	0.02	[0.011, 0.028]	-0.005	[-0.008, -0.002]	-2.325	[-37.236, 32.586]	0.565	[-4.696, 5.826]
Inga vera	112	9	0.017	[0.009, 0.025]	-0.004	[-0.007, -0.001]	3.006	[-13.450, 19.462]	-0.043	[-1.104, 1.018]
Ixora brevifolia	106	3	0.03	[0.022, 0.038]	-0.009	[-0.013, -0.006]	4.653	[-18.730, 28.036]	-0.085	[-1.370, 1.200]
Luehea grandiflora	46	4	0.006	[-0.002, 0.013]	-0.001	[-0.005, 0.002]	0.02	[-24.916, 24.956]	0.275	[-2.885, 3.435]
Machaerium villosum	44	4	0.02	[0.006, 0.035]	-0.004	[-0.009, -0.001]	1.304	[-12.173, 14.781]	0.061	[-0.743, 0.865]
Matayba elaeagnoides	39	4	0.016	[0.001, 0.030]	-0.004	[-0.010, 0.003]	0.159	[-20.739, 21.057]	0.252	[-2.566, 3.070]
Matayba guianensis	98	14	0.029	[0.016, 0.042]	-0.008	[-0.014, -0.003]	1.17	[-13.043, 15.383]	0.069	[-1.453, 1.591]
Maytenus floribunda	74	2	0.003	[-0.003, 0.010]	0.001	[-0.002, 0.004]	4.616	[-21.564, 30.796]	-0.106	[-2.188, 1.976]
Micrandra elata	118	5	0.023	[0.019, 0.028]	-0.005	[-0.007, -0.004]	2.64	[-11.328, 16.608]	0.015	[-0.362, 0.392]
Nectandra cissiflora	44	5	0.026	[0.010, 0.042]	-0.005	[-0.011, 0.001]	1.362	[-10.960, 13.684]	0.057	[-0.902, 1.016]
Nectandra membranacea	80	11	0.016	[0.003, 0.029]	-0.003	[-0.008, 0.002]	1.818	[-8.936, 12.572]	0.001	[-0.490, 0.492]
Ocotea corymbosa	142	9	0.013	[0.008, 0.018]	-0.003	[-0.004, -0.001]	3.188	[-13.829, 20.205]	-0.016	[-0.459, 0.427]
Ocotea spixiana	51	3	0.021	[0.003, 0.039]	-0.005	[-0.011, 0.001]	2.821	[-17.900, 23.542]	-0.002	[-0.797, 0.793]
Platycyamus regnellii	50	1	0.018	[0.006, 0.029]	-0.003	[-0.008, 0.001]	3.274	[-19.493, 26.041]	0.037	[-1.236, 1.310]
Pouteria gardneri	28	2	0.009	[-0.003, 0.021]	-0.002	[-0.006, 0.003]	2.702	[-14.702, 20.106]	-0.009	[-1.020, 1.002]
Pouteria torta	125	2	0.015	[0.008, 0.022]	-0.003	[-0.006, -0.001]	5.006	[-25.544, 35.556]	-0.041	[-1.078, 0.996]
Protium heptaphyllum	235	18	0.017	[0.013, 0.021]	-0.004	[-0.006, -0.002]	3.03	[-12.052, 18.112]	-0.032	[-0.748, 0.684]
Siparuna guianensis	388	139	0.031	[0.020, 0.042]	-0.012	[-0.018, -0.006]	1.643	[-17.679, 20.965]	-0.169	[-3.162, 2.824]
Siphoneugena densiflora	122	15	0.014	[0.008, 0.021]	-0.004	[-0.006, -0.001]	1.239	[-13.965, 16.443]	0.071	[-1.384, 1.526]
Sweetia fruticosa	45	1	0.015	[0.006, 0.024]	-0.004	[-0.007, 0.000]	2.42	[-29.664, 34.504]	0.14	[-3.507, 3.787]
Tapirira obtusa	85	13	0.013	[0.005, 0.021]	-0.002	[-0.004, 0.001]	0.524	[-10.182, 11.23]	0.058	[-0.475, 0.591]
Terminalia glabrescens	137	12	0.013	[0.006, 0.020]	-0.003	[-0.006, -0.001]	2.424	[-12.036, 16.884]	-0.004	[-0.613, 0.605]

Terminalia phaeocarpa	57	6	0.019	[0.010, 0.027]	-0.004	[-0.007, -0.001]	2.886	[-8.270, 14.042]	-0.026	[-0.299, 0.247]
Trichilia catigua	120	12	0.024	[0.016, 0.033]	-0.007	[-0.012, -0.003]	2.088	[-11.091, 15.267]	0.014	[-1.462, 1.490]
Trichilia clausseni	129	11	0.031	[0.023, 0.040]	-0.009	[-0.013, -0.005]	1.758	[-15.615, 19.131]	0.08	[-2.135, 2.295]
Trichilia elegans	53	6	0.034	[0.020, 0.049]	-0.010	[-0.016, -0.003]	0.095	[-19.413, 19.603]	0.248	[-2.396, 2.892]
Unonopsis guatterioides	102	9	0.02	[0.012, 0.027]	-0.006	[-0.009, -0.003]	3.203	[-16.594, 23.004]	-0.066	[-1.414, 1.282]
Virola sebifera	123	13	0.032	[0.023, 0.042]	-0.009	[-0.013, -0.006]	2.609	[-12.252, 17.470]	-0.035	[-0.990, 0.920]
Vochysia magnifica	113	21	0.021	[0.014, 0.027]	-0.005	[-0.007, -0.002]	1.144	[-6.991, 9.279]	0.027	[-0.541, 0.595]
Xylopia brasiliensis	38	7	0.013	[-0.006, 0.031]	-0.002	[-0.010, 0.007]	1.859	[-11.971, 15.689]	-0.037	[-1.304, 1.230]

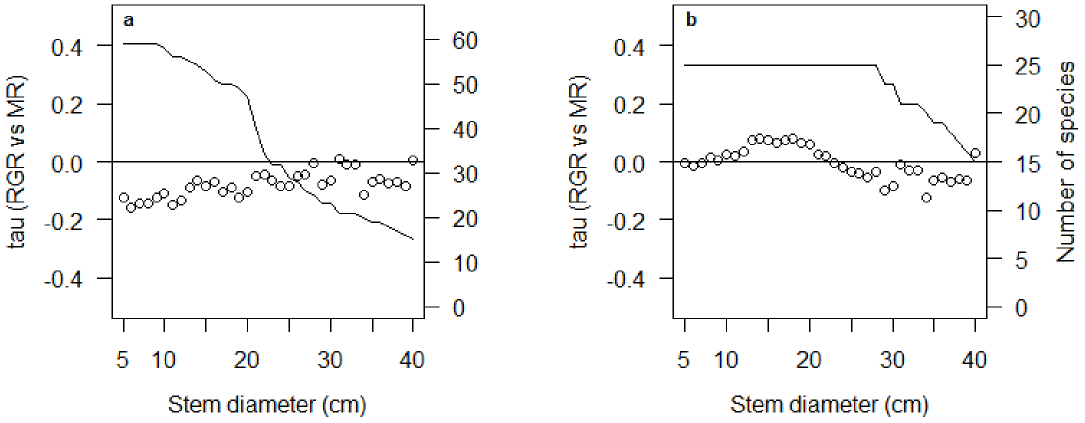
Online Resource 3. Kendall's correlation coefficient between maximum diameter (D_{max}) and wood density (WD) versus tree architecture variables (tree height [H], first branch height [FBH] and crown width [CW]), leaf traits (leaf area [LA] and specific leaf area [SLA]) and seed mass (SM). The number of species (NS) declines with increasing stem diameter since their D_{max} is lower than reference stem diameter. As tree architecture varies with stem diameter, we examined these correlations at different reference diameters (5, 10, 15, 20 and 25 cm), where most of species were included. * P < 0.05 and ** P < 0.01

Stem diameter (cm)	NS		WD	H	FBH	CW	LA	SLA	SM
5	59	D_{max}	-0,07	0,21*	0,15	0,01	0,08	-0,20*	0,03
10	58			0,35**	0,27**	0,21*			
15	53			0,30**	0,23*	0,24*			
20	47			0,39**	0,30**	0,21*			
25	29			0,11	-0,05	0,28*			
5	59	WD		-0,10	-0,15	-0,05	-0,08	-0,01	-0.07
10	58			-0,07	-0,07	0,04			
15	53			0,05	0,01	0,08			
20	47			0,04	0,02	0,10			
25	29			0,12	0,12	0,09			



Online Resource 4. Size-dependent changes in correlation coefficients (Kendall's tau) between demographic rates (RGR and MR) and maximum diameter (a,b) and wood density (c,d), height (e,f), first branch height (g,h), crown width (i,j), leaf area (k,l) specific leaf area (m,n) and seed mass (o,p) across the 25 largest dry forest tree species. Correlations are shown between relative stem diameter growth rate (RGR) and mortality rate (MR) vs. functional traits at different reference stem diameters, from 5 to 40 cm. Solid symbols indicate significant correlations ($p < 0,05$), and open symbols indicate nonsignificant correlations ($p > 0,05$). Solid gray lines show a decline in the number of species with increasing stem diameter from 25 species at the smallest reference diameter (5 cm) to 15 species at the largest reference diameter (40 cm).

Online Resource 5. Size-dependent changes in correlation coefficients between relative growth rate (RGR) and mortality rate (MR) (a) across 59 species controlling the effect of D_{max}(Kendall’s partial correlation), and (b) across the 25 largest species. Symbols show medians of distributions of Kendall’s correlation coefficients between probability distributions of RGR vs MR at different reference stem diameters, from 5 to 40 cm. Solid symbols indicate significant correlations ($p < 0,05$) and open symbols indicate non-significant correlations ($p > 0,05$). Solid gray line shows a decline in the number of species with increasing stem diameter from 59 (a) and 25 species (b) at the smallest reference diameter (5 cm) to 15 (a,b) species at the largest reference diameter (40 cm), respectively.



CAPÍTULO 3

NEIGHBOURHOOD INTERACTIONS MEDIATED BY FUNCTIONAL TRAITS DETERMINES LOCAL DOMINANCE AND COEXISTENCE OF SPECIES AT THE SAME TIME

Neighbourhood interactions mediated by functional traits determines local dominance and coexistence of species at the same time

ABSTRACT

Interspecific differences in relative fitness can cause local dominance by a single species. However, stabilizing interspecific niche differences can promote local diversity. Understanding these mechanisms requires that we simultaneously quantify their effects on demography and link these effects to community dynamics. Here, we present a five-year period dataset of eight tropical dry forest dynamics to disentangle how three key functional traits (wood density, specific leaf area and maximum diameter) mediate focal tree demographic processes (growth, survival and recruitment). processes drive community dynamics. We tested five alternative hypotheses (trait-direct effect, trait-independent effect, trait competitive effect, trait competitive response and trait similarity effect). We found strong support for the trait-direct effect, indicating that traits of focal tree, independent of its neighbourhood, are the main driver of trees demographic processes. The influence of neighbours "quantity" and "quality" were also supported, with some traits values increasing competition and others favouring tolerance to neighbours crowding. Our results indicate that interspecific traits can simultaneously promote local dominance by a group of species with suitable traits (species showing high growth and survival), at the same time that neighbourhood traits variation and recruitment (a demographic process less evaluated) can stabilize interspecific niche differences and promote local diversity.

Keywords: competition, neighbour trees, niche differentiation, trait similarity.

INTRODUCTION

Tropical forests diversity is recognized by two main patterns: at the same time that they show the richest assemblages of plant species on Earth, it is observed a very low uniformity in species density, with few species accounting for most of local individuals and most species showing very low densities (Wright 2002, Gourlet-Fleury et al. 2005). Studies in Amazonian forest, for example, estimated a total number of tree species to be about 16.000, while 227 species (1.4%) account for half of all individual trees (ter Steege et al. 2013). Evaluating the relative importance of which mechanisms drive these diversity patterns remains a central challenge in ecology.

A tendency that can help us to understand both diversity patterns is based on the niche differentiation theory (Kraft et al. 2008). Since species with contrasting niches exploit the resources in different ways, they are able to coexist in small areas, reducing competition and using available resources more efficiently (Reich et al. 2003). By contrast, species with suitable niche for the local environmental conditions are better competitors, and therefore, have higher performance and present local dominance (Wright *et al.* 2010). Many studies have evaluated competition via species, most of than with low number of species in controlled conditions (Poorter and Remkes 1990; Kitajima 1994, Sterck et al. 2003). Modelling competition by interspecific traits rather than species might overcome species because of functionality and allow general relationships to major scales (Uriarte *et al.* 2010).

Interspecific traits may mediate niche and performance differences in at least four ways (Lasky *et al.* 2014): 1) *trait-direct effect* – interspecific trait variation can be correlated with performance independent of neighbour density/traits. Thus, increased performance is expected for acquisitive traits (e.g. low wood density and high specific leaf area) when resources availability is high, and for conservative species (e.g. high wood density and low specific leaf area) when resources are scarce (Reich 2003); 2) *trait competitive effect* – negative density effect of neighbors may be asymmetric between species and dependent on traits hierarchies (Uriarte *et al.* 2010). Thus, neighbors with acquisitive traits, that capture the resources more rapidly, should have a higher negative effect on focal tree, 3) *trait competitive response* – traits may be associated with species tolerance to neighbor's density. As a result, certain trait values may have relatively higher fitness under high neighbors crowding (Lasky *et al.* 2014); 4) *trait similarity effect* – high trait differences between neighbour and focal tree reduces competition and promote better use of resources, and it is considered one of the most important driver of species competition in plant ecology (Kunstler *et al.* 2016).

. Here, we present a five-year period dataset of eight tropical dry forest dynamics to disentangle how trait-mediated processes drive community dynamics. We evaluate how these four mechanisms are mediated by three key functional traits that are associated with different plant strategies: wood density (an indicator of a trade-off between growth and survival), specific leaf area (an indicator of a trade-off in leaves with high light net gain and shade tolerance), and maximum diameter (an indicator of a trade-off between growth and early reproduction). We analysed how demographic processes (growth, survival and recruitment) of each individual tree was influenced by the abundance of competitors in its local neighbourhood, accounting for both traits of focal tree and its competitors.

METHODS

Study areas and data sampling

This study was conducted in eight tropical dry forests (18º29’ to 19º40’ S and 47º30’ to 48º24’ W) in Southeastern Brazil. The region experiences a seasonal climate characterized by rainy summers and dry winters. Mean annual rainfall ranges from 1160 to 1460 mm, dry season length from four to six months of drought (with less than 100 mm rainfall during the dry season) and mean annual temperature from 23 to 25º C. The study areas are secondary forests that experienced different disturbance (e.g., logging and grazing) for several years before abandonment (see Lopes *et al.* 2012 for further information about research sites).

We monitored 200 permanent sample plots (20 x 20 m) totalling 8 ha over a five-year period. In the first census, which was carried out at different time periods for each forest (t_0, 2006-2009), all trees with stem diameter at breast height (DBH, 1.30 m) ≥ 5 cm were tagged, their diameter was measured, height estimated, and identified to species level. In the second census, after five years for each forest (t_1, 2011–2014), all trees were re-measured and growth, survival and recruitment rates were evaluated. A total of 8699 trees (6913 alive, 953 dead and 853 recruited) were measured, belonging to 235 species.

Functional traits

We evaluated three key functional traits that are good predictors of species growth and survival rates (Westoby 1998; Poorter *et al.* 2008; Reich 2014): a whole plant trait (maximum stem diameter D_{max}), a stem trait (wood density WD), and a leaf trait (specific leaf area SLA). We used species maximum stem diameter rather than species maximum height because stem diameter was measured more precisely, and height estimations are especially difficult in tropical forests, where there is a large error for large trees (Iida *et al.* 2014). Maximum stem diameter was calculated for each species as the upper 95-percentile stem diameter for those trees whose diameter was equal to or greater than 10% of the observed maximum diameter of a population (King, Davies & Noor 2006). This method reduces the probability of underestimating the potential maximum size for a specific population with a large proportion of small individuals (King, Davies & Noor 2006). We used the diameter dataset of the first census (t_0) to determine species D_{max}.

Species wood density were obtained from a global wood density database (Zanne *et al.* 2009), filtering from the South America tropical region in the database to reduce region-specific differences as much as possible. When species-level wood density values were not available, then genus-level wood density values were used, since wood density is a trait that is phylogenetically conserved (Chave *et al.* 2006).

SLA was measured from fully expanded sun and shade leaves, with no obvious symptoms of pathogen or herbivory. Ten leaves were collected from 5-10 (average 7.8) adult trees (with diameter near to D_{max}) for each species (Pérez-Harguindeguy *et al.* 2013).

Traits were evaluated for most of sampled species (D_{max}, WD and SLA of 171, 232 and 106 species), covering a large proportion of initial basal area of each plot (average 96%, range from 41-100%). The neighbourhood framework models used in this study require the traits of focal tree and of all competitors present in the same plot. Therefore, our analyses were restricted to plots where the percentage of trees basal area with available trait data was at least 80% (200 plots for WD, 198 for D_{max} and 164 for SLA).

We acknowledge that many species do show plastic trait responses to environmental conditions (Poorter *et al.* 2012), and that traits vary during ontogeny (Sendall & Reich 2013). Yet, the variation explained by intraspecific trait differences is in general smaller compared to interspecific differences (Rozendaal, Hurtado & Poorter 2006; Hulshof & Swenson 2010), and across species, seedling traits and adult traits are strongly correlated (Poorter 2008), indicating that plastic trait changes will confound our results only to a limited extend.

Demographic models

To evaluate how traits mediate species performance and competition we used a neighbourhood modelling framework (Lasky *et al.* 2014) to estimate trees growth, survival and recruitment. Neighbourhood was defined as all trees belonging to the same plot (20 x 20 m), because coordinates of individual trees were not available and trees maximum interaction occurs in a radius of 20 m (Uriarte *et al.* 2004; Uriarte *et al.* 2010). Models were fitted for each trait separately, and estimate the growth (eq. 1), survival (eq. 2) and recruitment (eq. 3) of an individual tree *i* of focal species *f*, competitors *c*, on plot *p* and site *s*, as follow:

$$G_{i,f,p,s} = \alpha_0 + \alpha_1 T_f + \alpha_2 BA_c + \alpha_3(CWM_c) + \alpha_4(BA_c T_f) + \alpha_5/CWM_c\text{-}T_f/ + \alpha_6(DBH_i) \text{ (eq. 1)}$$

where $G_{i,f,p,s}$ is the basal area growth of individual tree; α_0 is the species average growth (model-intercept for all species); α_1 is the *trait-direct effect*, and gives the effect of species trait (T_f) on species-specific average growth (positive value indicates that high trait values increase species-specific average growth); α_2 is the *trait-independent effect*, and gives the crowding effect of neighbours basal area (BA_c) on focal tree growth, independent of their traits (negative value indicate that high basal area of neighbours reduce growth via competition); α_3 is the *trait competitive effect*, and indicates how the traits of neighbour trees weighted by their basal area (CWM_c) affect the growth of focal tree (positive values indicate that high CWM_c increases growth of focal tree); α_4 is the *trait competitive response*, and gives the response of focal tree to neighbours crowding based on focal tree trait (positive values indicates that trees with high trait values have lower growth reduction from neighbours crowding, i.e. have high tolerance to competition); α_5 is the *trait similarity effect*, and indicates how differences between CWM_c and focal tree trait affect growth (positive values indicates that high absolute differences between CWM_c and T_f increases growth); and α_6 is the size-dependent growth effect, and indicates how growth changes with stem diameter.

All parameters where modelled with a normally distributed random effect of species *f* (ε_f), plot *p* (ε_p), and site *s* (ε_s).

$$S_{i,f,p,s} = \beta_0 + \beta_1 T_f + \beta_2 BA_c + \beta_3(CWM_c) + \beta_4(BA_c T_f) + \beta_5/CWM_c\text{-}T_f/ + \beta_6(DBH_i) \quad \text{(eq. 2)}$$

where $S_{i,f,p,s}$ is the parameter for a binary logistic regression, determining expected survival of individual tree; β_0 is the species average survival (model-intercept for all species); β_1 (*trait-direct effect*), β_2 (*trait-independent effect*), β_3 (*trait competitive effect*), β_4 (*trait competitive response*), β_5 (*trait similarity effect*), and β_6 (size-dependent effect), are related to the same hypothesis tested in the growth model (eq. 1), but tested for focal tree survival.

$$R_{i,f,p,s} = \gamma_0 + \gamma_1 T_f + \gamma_2 BAc + \gamma_3(CWM_c) + \gamma_4(BA_c T_f) + + \gamma_5/CWM_c\text{-}T_f/ + \gamma_6(DBH_i) \quad \text{(eq. 3)}$$

where $R_{i,f,p,s}$ is the parameter for a binary logistic regression, determining expected recruitment of individual tree; β_0 is the species average recruitment (model-intercept for all species); β_1 (*trait-direct effect*), β_2 (*trait-independent effect*), β_3 (*trait competitive effect*), β_4 (*trait competitive response*), β_5 (*trait similarity effect*), and β_6 (size-dependent effect), are related to the same hypothesis tested in the growth model (eq. 1), but tested for focal tree recruitment.

Statistical analyses

Neighbourhood framework models (eq. 1, 2 and 3) were performed using generalized mixed models including sites, plots within sites and species as random effects (to account for normally distributed random effect of species, plots, and sites). Models were fitted for each trait separately. We used all subsets multiple regression analysis and selected the models that had lowest Akaike Information Criterion (AIC). Models were considered to be equally supported if the difference in AIC was less than two units (Burnham & Anderson 2002). When models were equally supported, we selected the most parsimonious model (with lowest number of predictors). When necessary, data were $\log_{10}$ or square root-transformed prior to analysis, to meet the assumptions of normality, homoscedasticity, reduce the effect of outliers and to account for possible nonlinear relationships between variables. We evaluated the relative importance of each ecological hypothesis (*trait-direct effect, trait-independent effect, trait competitive effect, trait competitive response and trait similarity effect*) on demographic processes (growth, survival and recruitment) by comparing the standardized regression coefficients of predictors retained in the best multiple regression model. Mixed-effects models were performed using the “lme4” package (Bates et al. 2011) and all subsets regression analyses using the “MuMIn” package (Burnham & Anderson 2002). All analyses were performed using R 3.1.2 (R Development Core Team 2013).

RESULTS

Growth, survival and recruitment were mostly driven by the traits of focal tree independent of neighbourhood competition (*trait-direct effect*, Table 1). Average growth rates were higher for species with lower wood density (α_1 = -0.026) and specific leaf area (α_1 = -0.062), and higher maximum stem diameter (α_1 = 0.068). Average survival rates were higher for species with higher wood density (β_1 = 0.250) and maximum stem diameter (β_1 = 0.234), and lower specific leaf area (β_1 = -0.565). Average recruitment rates were higher for species with higher specific leaf area (γ_1 = 0.280) and lower maximum stem diameter (γ_1 = -0.249), but was not affected by species wood density.

Growth and recruitment decreased with increases in neighbours' basal area independent of their traits (α_2 and γ_2, *trait-independent effect*), while survival was not affected (β_2, Table 1). The effect of neighbours' basal area weighted by their traits (*trait competitive effect*) was negative for SLA growth (α_3 = -0.041) and SLA recruitment (γ_3 = -0.220) models, indicating that growth and recruitment are higher when neighbours have lower SLA (Table 1). The tolerance to neighbours crowding (*trait competitive response*) was positive for SLA survival model (β_4 = 0.480), indicating that species with higher SLA have higher survival rates under higher neighbours crowding (Table 1). Absolute differences between neighbours and focal tree traits (*trait similarity effect*) was positive for WD recruitment (γ_5 = 0.159) and D_{max} recruitment (γ_5 = 0.164) models, and negative for SLA survival model (β_5 = -0.141), indicating that higher differences between WD and D_{max} of neighbours and focal tree increase recruitment, but for SLA reduce survival (Table 1).

Table 1. Best models (lowest AIC) retained for growth, survival and recruitment based on five trait-mediated competition hypotheses (trait-direct effect, trait-independent effect, trait competitive effect, trait competitive response, trait similarity effect), obtained from a series of multiple regression analyses. Models were fitted for each trait separately using generalized linear mixed models and including areas, plots within areas, and species as a random effect. Standardized regression coefficients and hypothesized relationship directions are given. Greek letters (α, β, γ) and hypotheses numbers (1-5) corresponds to equations 1-3 in methods.

Model	**Trait**	**Trait direct (1)**		**Trait-independent (2)**		**Competitive effect (3)**		**Competitive response (4)**		**Trait-similarity (5)**	
		Coef.	Hyp.	Coef.	Hyp.	Coef.	Hyp.	Coef.	Hyp.	Coef.	Hyp.
Growth (α)	WD	-0.026	-	-0.018	-		-		+		+
	SLA	-0.062	+	-0.021	-	-0.041	+		-		+
	D_{max}	0.068	+	-0.018	-		-		+		+
Survival (β)	WD	0.25	+		-		-		+		+
	SLA	-0.565	-		-		+	0.48	-	-0.141	+
	D_{max}	0.234	+		-		-		+		+
Recruitment (γ)	WD		-	-0.141	-		-		+	0.159	+
	SLA	0.28	+	-0.147	-	-0.22	+		-		+
	D_{max}	-0.249	-	-0.186	-		-		+	0.164	+

DISCUSSION

We assessed how interspecific traits mediate interactions between a focal tree and its neighbours, and determine trees growth, survival and recruitment. We tested five alternative hypotheses (*trait-direct effect, trait-independent effect, trait competitive effect, trait competitive response and trait similarity effect*). We found strong support for the trait-direct effect, indicating that traits of focal tree, independent of its neighbourhood, are the main driver of trees demographic processes. The influence of neighbours "quantity" and "quality" were also supported, with some traits values increasing competition and others favouring tolerance to neighbours crowding. Our results indicate that interspecific traits can simultaneously promote local dominance by a group of species with suitable traits (species showing high growth and survival), at the same time that neighbourhood traits variation and recruitment (a demographic process less evaluated) can stabilize interspecific niche differences and promote local diversity.

The classical wood density trade-off

As we hypothesized, species with lower wood density showed higher growth and lower survival rates (trait-direct effect, Table 1). Wood density represents the biomass per unit wood volume constructed and therefore, lower WD can contribute to higher stem growth rate because more wood volume is produced per unit biomass invested (Santiago *et al.* 2004). Conversely, lower wood density tends to be constructed of bigger cells with thinner walls and limited intercellular space, making stems less resistant to breakage, to fungal and pathogen attack and drought stress, contributing to reduce trees survival (Chave *et al.* 2009). This classical trade-off is thought to contribute to species coexistence and, therefore, to the maintenance of forest diversity in tropical forests (Poorter *et al.* 2008; Wright *et al.* 2010). Recruitment was not direct related to species wood density, but was higher when recruiting tree wood density were less similar to neighbours wood density (trait similarity effect, Table

1), suggesting that recruitment is supressed by niche similarity. The relationship between community basal area and WD was not significant, indicating that the wood density growth and survival trade-off seems to stabilize interspecific niche and performance differences, and associated with higher recruitment in less similar neighbourhood, promotes local diversity.

Lower specific leaf area promotes higher growth and survival but implicates in lower recruitment, tolerance to neighbours crowding and reduces competition

We hypothesized that species with higher specific leaf area have higher growth and recruitment because of higher interception of light, photosynthesis and carbon net gain, whereas they have higher mortality because of higher respiratory costs, herbivory and pathogen attack (Evans & Poorter 2001; Poorter & Bongers 2006). Surprisingly, lower SLA species showed high performance, with higher growth and survival rates (trait-direct effect). Species with lower SLA have lower transpiration costs (Poorter & Bongers 2006; Sterck *et al.* 2011), and produce leaves with smaller cells and thicker cell walls, decreasing cell elasticity and allowing plants to reduce leaf water potential and continue plant functioning during the onset of the dry period (Baltzer *et al.* 2008; Klein 2014). This improved water balance is especially important in dry forests, and seems to enhance performance of species with lower specific leaf area. Conversely, as we hypothesized, we found higher recruitment for species with higher SLA. The shaded conditions of understory represents an important filter for forest regeneration (Chazdon *et al.* 2007), and therefore, species with higher SLA may have favoured recruitment since they have higher interception of light per unit leaf biomass invested, maximizing photosynthetic carbon net gain under shaded conditions (Evans & Poorter 2001; Valladares & Niinemets 2008). High SLA was also related to high tolerance to neighbours crowding, increasing species survival (trait competitive response). Later in succession, forest stands are closed and the light availability is reduced, increasing performance of species that can optimize photosynthesis under low light. We found that lower SLA of neighbours increase survival and recruitment (trait competitive effect). We found that survival was higher when focal tree SLA was similar to neighbours SLA (trait similarity effect). Our results indicate that although species with lower SLA have high performance, with higher growth and survival rates, they have lower recruitment rates, are less tolerant to neighbours crowding and have weaker negative effect on others tree performance, which balance interspecific fitness variation and promote local diversity.

Maximum stem diameter expresses the life strategies dichotomy between large and small statured species

We hypothesized that species with higher maximum diameter have higher growth and survival, and lower recruitment (trait direct effect). Larger species would grow faster than small species to rapidly attain their large reproductive size and to attain the higher light conditions in the canopy at which can become reproductive (Thomas 2011). Conversely, small species may grow slowly because they allocate resources to early reproduction rather than growth (Mencuccini et al. 2005; Thomas 2011). Our results evidence the dichotomy between large and small statured species based on life-history theory. While larger trees are relatively K-selected and should have large offspring and long life span, showing high survival and low recruitment, small species are R-selected, with high investment in reproduction but with a shorter life span (Pianka 1970). Recruitment was higher when recruiting tree D_{max} were less similar to neighbours D^{max} (trait similarity effect, Table 1), suggesting that recruitment is supressed by niche similarity.

Hyperdominance in tropical forests flora vs. high number of coexisting species

We hypothesized that traits of focal tree play an important role in species growth, survival and recruitment, because they are strongly related to differences in life strategies and to ecological trade-offs (e.g. acquisitive and conservative spectrum) (Wright *et al.* 2004; Reich 2014). Our results showed that indeed traits of focal tree independent of neighbours are the main driver of demographic processes. However, instead of the classical growth-survival trade-off, we found a trade-on for two of three traits evaluated, with species with suitable traits (lower SLA and higher Dmax) showing high growth and survival. From a demographic point of view, they are superperformers species that combine high growth with high survival, thus outcompeting other species, and potentially leading to their hyperdominance and reducing species diversity.

At the same time, the trade-off between growth and survival of species wood density, the higher recruitment of species with higher specific leaf area and lower maximum stem diameter, associated with the higher tolerance to neighbours crowding of species with higher specific leaf area, lower competition effect of species with lower specific leaf area, and higher recruitment of species with wood density and maximum stem diameter with traits different from neighbours traits, promote local diversity. Our results help the understanding of the floristic patterns of tropical forests, where at the same time we find the occurrence of a small number of high density species and a large number of species with low density, promoted by a group of species with suitable traits (species showing high growth and survival), and a high number of species coexisting at a small area, promoted by interspecific traits difference that allows different exploitation of resources.

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CONSIDERAÇÕES FINAIS

Esta tese buscou avaliar como os traços funcionais de plantas direcionam o funcionamento e a dinâmica de florestas estacionais tropicais em diferentes níveis ecológicos: comunidades, populações e indivíduos arbóreos.

No primeiro capítulo, foram testadas diferentes hipóteses ecológicas atuam simultaneamente na produtividade das florestas estacionais tropicais, e os resultados comparados com o que é reportado na literatura para florestas tropicais úmidas. Nossos resultados mostraram que a produtividade de biomassa destas florestas é impulsionada principalmente pela quantidade de vegetação inicial (sendo maior em florestas com maior biomassa inicial) e pela distribuição dos traços funcionais entre as espécies (maior em florestas com traços funcionais conservativos). Surpreendentemente, a produtividade não esteve ligada à complementariedade de nichos, e negativamente à fertilidade solo. Estes resultados realçam o paradoxo que existe entre as florestas estacionais e florestas úmidas. Nas florestas tropicais úmidas, onde a disponibilidade de luz é um forte filtro ambiental, traços aquisitivos como baixa densidade de madeira e alta área foliar específica estão associados à maior produtividade. Já em florestas estacionais, onde a disponibilidade de água é um filtro ambiental mais forte, traços conservativos como alta densidade de madeira e baixa área foliar específica estão associados à maior produtividade florestal. Estes resultados sugerem que a falta de padrões globalmente consistentes na influência dos traços funcionais sobre na produtividade florestal pode ser causada pelas diferenças entre os tipos florestais. Além disso, nosso estudo aumenta a compreensão sobre as relações de produtividade de biomassa em florestas estacionais tropicais, e pode ajudar a prever como as florestas tropicais devem responder a futuros aumentos de estresse hídrico, mudando as relações globais traços de produtividade em todo o mundo e o espectro econômico dos traços funcionais.

No segundo capítulo foi avaliado como o crescimento e a mortalidade das espécies é direcionada pelos seus traços funcionais, e como estas relações mudam com sua ontogenia. Nos observamos que, de fato, os traços funcionais afetam diretamente as taxas demográficas das espécies, e que essa influência varia ao longo da ontogenia arbórea. Em indivíduos de estatura menor, traços funcionais relacionados ao aumento da captura de luz, como maior área foliar e área de copa, aumentam as taxas de crescimento e/ou reduzem as taxas de mortalidade. Em indivíduos maiores, traços funcionais que aumentam a tolerância à seca, como a maior densidade de madeira, reduzem as taxas de mortalidade. Verificamos também que a luz continua a ser um fator limitante para o desenvolvimento das espécies no sub-bosque de florestas estacionais tropicais, o que comumente não é reportado por outros estudos. Novamente mostramos que, de um ponto de vista funcional, as florestas estacionais tropicais apresentam relações diferentes entre os traços e as taxas demográficas, comparadas às florestas tropicais úmidas. Enquanto a maior densidade de madeira e menor área foliar específica estão intimamente relacionadas à tolerância à sombra em florestas úmidas, e reduzindo o crescimento das espécies, estes traços parecem estar relacionados à tolerância à seca em florestas estacionais, o que aumentando o crescimento e reduzindo a mortalidade das espécies. Os resultados indicaram também que, em tamanhos menores, não observa-se o trade-off entre crescimento e sobrevivência, comumente observado em florestas úmidas, mas até mesmo um trade-on, com espécies apresentando traços funcionais que ao mesmo tempo aumentam seu crescimento e a sobrevivência. Teoricamente, este trade-on pode ser responsável pela diminuição da diversidade em florestas estacionais tropicais, que de fato apresentam menor diversidade em relação às florestas tropicais úmidas. Além disso, estes resultados enfatizam que o tamanho da planta deve ser incluído como um eixo de variação na análise funcional, para melhor compreensão das relação entre as características funcionais e as taxas demográficas.

No terceiro capítulo, avaliamos como as interações entre indivíduos arbóreos vizinhos, mediadas pelos seus traços funcionais, determinam o crescimento, sobrevivência e/ou recrutamento de uma determinada árvore focal. Testamos cinco hipóteses alternativas e observamos que o efeito direto dos traços da árvore focal, independente de seus vizinhos, é o principal componente que influencia nos processos demográficos. Mesmo assim, a influência da "quantidade" e da "qualidade" dos vizinhos também foi suportada, sendo que alguns traços funcionais aumentaram a competição e outros aumentarão a tolerância à maior concentração de árvores vizinhas. Nossos resultados indicam que os traços interespecíficos pode promover simultaneamente o dominância local por um grupo de espécies com características favoráveis (espécies apresentando alto crescimento e sobrevivência), mas que ao mesmo tempo é balanceada com a maior tolerância e recrutamento de outros traços, o que permite estabilizar as diferenças entre os nichos e promover a diversidade local.