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Running head: Competition effects in tropical forests

Title: Competition influences tree growth, but not mortality, across environmental gradients in Amazonia and tropical Africa

Authors: Danaë M.A. Rozendaal[1,2,3,4,5*], Oliver L. Phillips[6], Simon L. Lewis[6,7], Kofi Affum-Baffoe[8], Esteban Alvarez Dávila[9,10], Ana Andrade[11], Luiz E.O.C. Aragão[12], Alejandro Araujo-Murakami[13], Timothy R. Baker[6], Olaf Bánki[14], Roel J.W. Brienen[6], José Luis C. Camargo[15], James A. Comiskey[16,17], Marie Noel Djuikouo K.[18], Sophie Fauset[19], Ted R. Feldpausch[12], Timothy J. Killeen[20], William F. Laurance[21], Susan G.W. Laurance[21], Thomas Lovejoy[22], Yadvinder Malhi[23], Beatriz S. Marimon[24], Ben-Hur Marimon Junior[24], Andrew R. Marshall[25,26,27], David A. Neill[28], Percy Núñez Vargas[29], Nigel C.A. Pitman[30,31], Lourens Poorter[3], Jan Reitsma[32], Marcos Silveira[33], Bonaventure Sonké[34], Terry Sunderland[35,36], Hermann Taedoumg[34], Hans ter Steege[14,37], John W. Terborgh[38,21], Ricardo K. Umetsu[24], Geertje M.F. van der Heijden[39], Emilio Vilanova[40], Vincent Vos[41,42], Lee J.T. White[43,44,45], Simon Willcock[46], Lise Zemagho[34], and Mark C. Vanderwel[1]

[1]Department of Biology, University of Regina, Regina, SK, Canada; [2]Laboratory of Geo-Information Science and Remote Sensing, Wageningen University, Wageningen, the Netherlands; [3]Forest Ecology and Forest Management Group, Wageningen University, Wageningen, the Netherlands; [4]Plant Production Systems Group, Wageningen University, Wageningen, the Netherlands; [5]Centre for Crop Systems Analysis, Wageningen University, Wageningen, the Netherlands; [6]School of Geography, University of Leeds, Leeds, UK; [7]Department of Geography, University College London, London, UK; [8]Mensuration Unit, Forestry Commission of Ghana, Kumasi, Ghana; [9]Escuela ECAPMA, UNAD, Calle 14 Sur No. 14-23, Bogotá, Colombia; [10]Fundación Con Vida, Avenida del Río # 20-114, Medellín,

Colombia; [11]Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil; [12]Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, UK; [13]Museo de Historia Natural Noel Kempff Mercado, Universidad Autónoma Gabriel Rene Moreno, Santa Cruz, Bolivia; [14]Naturalis Biodiversity Center, Leiden, the Netherlands; [15]Instituto Nacional de Pesquisas da Amazônia, Projeto Dinâmica Biológica de Fragmentos Florestais, Manaus, Brazil; [16]Inventory & Monitoring Program, National Park Service, Fredericksburg, VA, USA; [17]Smithsonian Institution, Washington, DC, USA; [18]Department of Botany & Plant Physiology, Faculty of Science, University of Buea, Buea, Cameroon; [19]School of Geography, Earth and Environmental Sciences, University of Plymouth, Plymouth, UK; [20]Agteca-Amazonica, Santa Cruz, Bolivia; [21]Centre for Tropical Environmental and Sustainability Science and College of Science and Engineering, James Cook University, Cairns, Australia; [22]Department of Environmental Science and Policy, George Mason University, Fairfax, VA, USA; [23]School of Geography and the Environment, University of Oxford, Oxford, UK; [24]Universidade do Estado de Mato Grosso, Nova Xavantina, Brazil; [25]Tropical Forests and People Research Centre, University of the Sunshine Coast, Australia; [26]Department of Environment and Geography, University of York, York, UK; [27]Flamingo Land Ltd., North Yorkshire, UK; [28]Facultad de Ingeniería Ambiental, Universidad Estatal Amazónica, Puyo, Pastaza, Ecuador; [29]Universidad Nacional de San Antonio Abad del Cusco, Cusco, Peru; [30]Science and Education, The Field Museum, Chicago, IL, USA; [31]Center for Tropical Conservation, Nicholas School of the Environment, Duke University, Durham, NC, USA; [32]Bureau Waardenburg, Culemborg, the Netherlands; [33]Museu Universitário, Universidade Federal do Acre, Brazil; [34]Plant Systematic and Ecology Laboratory, University of Yaounde I, Cameroon; [35]CIFOR, Bogor, Indonesia; [36]College of Marine and Environmental Sciences, James Cook University, Cairns, Australia;

[37]Systems Ecology, Free University, Amsterdam, Netherlands; [38]Department of Biology and Florida Museum of Natural History, University of Florida, Gainesville, FL, USA; [39]School of Geography, University of Nottingham, Nottingham, UK; [40]Instituto de Investigaciones para el Desarrollo Forestal, Universidad de Los Andes, Mérida, Venezuela; [41]Universidad Autónoma de Beni, Riberalta, Beni, Bolivia; [42]Centro de Investigación y Promoción del Campesinado, Riberalta, Beni, Bolivia; [43]Agence Nationale des Parcs Nationaux, Libreville, Gabon; [44]Institut de Recherche en Ecologie Tropicale, Libreville, Gabon; [45]School of Natural Sciences, University of Stirling, Stirling, UK; [46]School of Natural Sciences, Bangor University, Bangor, UK.

*Corresponding author: Danaë M.A. Rozendaal, Plant Production Systems Group, Wageningen University, P.O. Box 430, 6700 AK Wageningen, the Netherlands. Telephone: +31 317 485321, E-mail: danae.rozendaal@wur.nl

Abstract

Competition among trees is an important driver of community structure and dynamics in tropical forests. Neighboring trees may impact an individual tree's growth rate and probability of mortality, but large-scale geographic and environmental variation in these competitive effects has yet to be evaluated across the tropical forest biome. We quantified effects of competition on tree-level basal area growth and mortality for trees ≥ 10 cm diameter across 151 ~1-ha plots in mature tropical forests in Amazonia and tropical Africa by developing non-linear models that accounted for wood density, tree size and neighborhood crowding. Using these models, we assessed how water availability (i.e., climatic water deficit) and soil fertility influenced the predicted plot-level strength of competition (i.e., the extent to which growth is reduced, or mortality is increased, by competition across all individual trees). On both continents, tree basal area growth decreased with wood density, and increased with tree size. Growth decreased with neighborhood crowding, which suggests that competition is important. Tree mortality decreased with wood density and generally increased with tree size, but was apparently unaffected by neighborhood crowding. Across plots, variation in the plot-level strength of competition was most strongly related to plot basal area (i.e., the sum of the basal area of all trees in a plot), with greater reductions in growth occurring in forests with high basal area, but in Amazonia the strength of competition also varied with plot-level wood density. In Amazonia, the strength of competition increased with water availability because of the greater basal area of wetter forests, but was only weakly related to soil fertility. In Africa, competition was weakly related to soil fertility, and invariant across the shorter water availability gradient. Overall, our results suggest that competition influences the structure and dynamics of tropical forests primarily through effects on individual tree growth rather than mortality, and that the strength of competition largely depends on environment-mediated variation in basal area.

Key words: climatic water deficit; competition; forest dynamics; tree growth; mortality; neighborhood effects; soil fertility; trait-based models; tropical forest; wood density.

Introduction

Competition is an important driver of community structure and dynamics in forests worldwide (Kunstler et al. 2016), particularly in closed-canopy forests such as mature, undisturbed tropical forests, where low light levels under the canopy typically limit tree growth. Generally, competition with neighboring trees is expected to decrease growth and increase the probability of mortality of individual tropical trees (Uriarte et al. 2004, Lasky et al. 2015). However, effects of competition on growth and mortality of individual trees have only been quantified within single tropical forest sites to date (e.g. Uriarte et al. 2004, Baribault et al. 2012). Whether strong effects of competition on demographic rates are pervasive, and whether they vary across environmental gradients in the tropics remains unresolved.

Better knowledge of the effects of competition on tropical tree growth and mortality, and the geographic variation thereof, is essential for enhancing understanding of the global terrestrial carbon balance. Mature tropical forests have increased in biomass over recent decades (Lewis et al. 2009), and those in Amazonia have become more dynamic (McDowell et al. 2018). Mortality rates have a key role in controlling biomass in tropical forests (Johnson et al. 2016), as increases in mortality over time are influencing the carbon balance of Amazon forests (Brienen et al. 2015). Changes in the average strength of competition in forests might be one of the driving factors of such dynamic changes, since increased biomass (i.e., increased neighborhood crowding) leads to enhanced competition, with expected impacts in turn in decreased growth and increased mortality. More generally, the underlying causes of tree mortality in the tropics are still actively debated (e.g., McDowell et al. 2018), and quantifying their effects on the terrestrial carbon balance is a key challenge for ecologists and global change scientists. In addition to mortality that results from competition, trees may die from a range of other processes, including hydraulic failure in response to drought (large trees in particular; Phillips et al. 2010, Bennett et al. 2015, Rowland et al. 2015), from senescence (although effects are weak; Mencuccini et al. 2005), and from large-scale wind disturbance (Espírito-Santo et al. 2014), but which process(es) dominate(s) remains poorly understood.

Environmental conditions vary considerably across tropical forest sites, and this variation is known to strongly influence forest structure and dynamics. Across the Amazon basin, for example, water availability generally decreases from north to south, while soil fertility increases from east to west (ter Steege et al. 2006). Drier forests generally have a lower stature, lower aboveground biomass and basal area, and a more open canopy than wet forests (Quesada et al. 2012), with typically lower rates of tree growth (Toledo et al. 2011) and stem turnover (Quesada et al. 2012). Forests are more dynamic on the high-fertility soils of western Amazonia, with higher coarse woody productivity (Malhi et al. 2004, Baker et al. 2009), higher stem mortality (Johnson et al. 2016), lower basal area and aboveground biomass, and lower mean wood density (WD) than eastern Amazonia (Baker et al. 2004, Malhi et al. 2006, ter Steege et al. 2006, Quesada et al. 2012). Environmental gradients are also found across African tropical forests, where basal area decreases with both rainfall seasonality and soil fertility (sum of bases; Lewis et al. 2013).

Effects of competition on tree growth and mortality are expected to vary across continental environmental gradients in Amazonia and tropical Africa because water and soil nutrient availability influence forest structure and understory light availability. Competition has been hypothesized to intensify with resource availability because high resource levels lead to rapid growth and resource depletion, whereas plant growth is generally low in stressful habitats (Grime 1979). In tropical forests, competition is likely to be strongest at high resource (water and/or soil nutrient availability) levels, which support a higher basal area. Then, the resulting crowding leads to stronger competition because of reduced light availability to individual trees.

The response of any given focal tree to competition will likely depend not only on the degree of crowding in its local neighborhood, but also on its size and functional traits. Smaller trees are more strongly affected by competition (Uriarte et al. 2004) because they are more heavily shaded by taller neighbors, and likely suffer from greater belowground competition. Shade-intolerant tree species, which typically have low wood density (WD; van Gelder et al. 2006), respond more strongly to changes in light availability than shade-tolerant species (Bazzaz 1979), and thus are likely to be more strongly affected by competition. Indeed, shade-intolerant (Hubbell et al. 2001, Canham et al. 2006, Kunstler et al. 2011) and low WD tree species (Kunstler et al. 2016) often show greater growth decreases in response to neighborhood crowding. Hence, variation in the plot-level strength of competition (i.e., the extent to which growth is reduced, or mortality is increased, by competition across all individual trees in a plot) across environmental gradients may not only depend on forest basal area, but also on tree size distributions and mean wood density. Nevertheless, forest basal area is expected to have the largest effect, because the basal area of neighbor trees directly influences resource availability to a focal tree.

In this study, we quantify the effects of neighborhood crowding on tree growth and mortality across gradients of moisture and soil nutrient availability in Amazonia and tropical Africa. Neighborhood crowding likely reflects competition for light (although competition for water and soil nutrients may also play a role), as light is typically the main factor limiting tree growth in closed-canopy forests. We use data from 151 ~1 ha-plots to fit non-linear growth and mortality models based on tree WD, size, and neighborhood crowding. We use these models to estimate the predicted plot-level strength of competition, i.e., to what extent growth across all trees is reduced compared to a low level of neighborhood crowding, and assess how water availability and soil fertility influence the strength of competition through relationships with average tree size, plot basal area and plot wood density. Specifically, we test the following predictions: (1) tree growth will decrease, and mortality increase, with neighborhood crowding; (2) low WD species will be most strongly affected by neighborhood crowding; (3) variation in the plot-level strength of competition will be more strongly related to plot basal area than to wood density or mean tree size; (4) the plot-level strength of competition will intensify with increasing climatic water availability through relationships with plot basal area on both continents; and (5) the predicted plot-level strength of competition will be negatively related to soil fertility in Africa because of decreasing basal area with increasing soil fertility (sum of bases; Lewis et al. 2013), but be largely independent of soil fertility in Amazonia because of weak correlations between soil fertility and basal area (Quesada et al. 2012).

Methods

Plot data

We used data from 102 permanent plots in Amazonia from the RAINFOR network and 49 in tropical Africa from the AfriTRON network, curated at ForestPlots.net (Lopez-Gonzalez et al. 2009, 2011; Fig. 1), to span the environmental gradients in each tropical lowland forest region. Plots were all below 500 m a.s.l., non-flooded, closed-canopy forests, with a five-fold range of mean annual precipitation in Amazonia (855-4273 mm) and two-fold range in Africa (1377-2716 mm). Soil fertility, estimated by soil total exchange bases (in cmol(+) kg^{-1}), varied from 0.5-13.2 cmol(+) kg^{-1} in Amazonia, and from 2-13.5 cmol(+) kg^{-1} in Africa. Most plots were 1 ha in size, but plot size ranged from 0.25 to 9 ha (Appendix S1: Table S1). Trees $\geq$ 10 cm diameter at breast height (dbh), or above buttresses, were measured for their diameter, identified to species, and either mapped or assigned to 0.04 ha subplots. Across all plots, 2,947 species and 73,100 trees were included in Amazonia, and 695 species and 20,705 trees in Africa. For each plot, we included data from two censuses with an average interval length of 6.3 years (range: 3.0-12.7 years; Appendix S1: Table S1) and an average starting year of 1994 (range: 1971-2008), and calculated annual basal area growth (in cm^2 yr^{-1}) for trees that were present in both censuses. We excluded monocotyledonous species (palms and *Strelitziaceae*) from the growth models, as they do not have secondary growth. Neighborhood crowding was expressed as the total basal area of neighbor trees within a 0.04-ha subplot (BA_{neigh}) in the first census. We defined neighborhoods based on subplots instead of on a fixed radius around each focal tree, to allow inclusion of plots for which individual trees were not mapped (Appendix S2). We found that BA_{neigh} accurately captured local effects of competition (Appendix S2). Neighborhood crowding likely reflects competition for light, although competition for water and soil nutrients may also occur. Other processes, for example pathogen accumulation at high densities of conspecific trees that increase mortality (negative density-dependence; NDD), may also contribute, but effects of NDD are typically weak for large trees (Zhu et al. 2015).

Environmental conditions and wood density

Average annual rainfall (in mm yr^{-1}) for each of the plots was obtained from WorldClim 2 (Fick and Hijmans 2017). Climatic water deficit (CWD; in mm yr^{-1}; Chave et al. 2014) was obtained from http://chave.ups-tlse.fr/pantropical_allometry.htm. CWD is defined as the cumulative amount of water lost by the environment during months in which evapotranspiration exceeds rainfall. CWD is negative for sites that experience seasonal drought stress; a CWD of 0 indicates absence of seasonal drought stress. Topsoil total exchange bases (TEB; in cmol(+) kg^{-1}) was included as an indicator of soil fertility, and was obtained from the World Harmonized Soil Database (FAO/IIASA/ISRIC/ISS-CAS/JRC 2012). Wood density (WD) data were obtained from a global database (Chave et al. 2009, Zanne et al. 2009). In cases where a species-specific WD value was not available, we used genus- or family-level mean WD (Baker et al. 2004). Genus-level WD was used for 1578 (out of 2947) and for 233 (out of 695) species in Amazonia and Africa, respectively. Family-level WD was used for 235 and 186 species in Amazonia and Africa, respectively. For stems that remained unidentified, or for which family-level mean WD was unavailable (for 37 species in Amazonia and 31 in Africa), we used the mean WD across all stems in the plot.

Modeling approach

We used a combination of (modeling) approaches to evaluate whether the predicted strength of competition varied across environmental gradients in Amazonia and Africa. Firstly, we used the plot data from both continents to construct non-linear models of individual tree growth and mortality as functions of tree size (dbh), neighborhood crowding, and WD. Separate models were fitted for Amazonia and tropical Africa. Secondly, we used the estimated parameters of the fitted growth models to calculate the strength of competition (C_{plot}) at the plot level (mortality was excluded because competition effects on mortality were very weak; see Results). As a last step, we assessed (1) whether C_{plot} varied with water availability and soil fertility, and (2) how C_{plot} was influenced by variation in plot basal area, plot-level WD, and average tree size. Variation in C_{plot} could arise from plot-to-plot differences in average neighborhood crowding (i.e., plot basal area), average WD, or average tree size, as each of these influenced the modeled effect of competition on individual tree growth. We describe each of these steps in greater detail below.

We modeled the annual basal area growth (G) and the annual probability of mortality (M) for individual trees on each continent as follows:

$$G = a_{\mathrm{G}} \times p_{\mathrm{G}} \times S_{\mathrm{G}} \times C_{\mathrm{G}}$$

$$M = [1 + a_{\mathrm{M}} \times p_{\mathrm{M}} \times S_{\mathrm{M}} \times C_{\mathrm{M}}]^{-1}$$

where a_{G} and a_{M} are constants, p_{G} and p_{M} are plot-level random effects, and S and C (each subscripted for growth and mortality) are non-linear functions that capture effects of tree size and competition, respectively:

$$S = \mathrm{dbh}^{s_1} \times \exp\,(-s_2 \times \mathrm{dbh})$$

$$C = \exp\,(-c_1 \times \mathrm{dbh}^{c_2} \times \mathrm{BA}_{\mathrm{neigh}})$$

where s_1, s_2, c_1, and c_2 control the shape of the functions and have separate values for growth and mortality. S has a flexible form that can produce either an intermediate peak or a continuous increase in tree growth with tree size (dbh; Coomes et al. 2014). For mortality, S can produce a U-shaped response where mortality both decreases with size for small trees and increases with size for larger trees (Rüger et al. 2011, Iida et al. 2014). C is a decreasing function that can produce lower growth and higher mortality in trees with greater neighborhood crowding. The sensitivity of growth and mortality to competition may vary with tree size (as determined by c_2), as large trees may be less susceptible to competition than small trees.

We applied a trait-based approach to account for taxonomic variation in growth and mortality, as a species-level approach was not feasible given the huge diversity of tree species in the tropics (e.g., an estimated 15,000 tree species in the Amazon basin; ter Steege et al. 2015). WD is known to be a good predictor of tropical tree growth and mortality (e.g., Chao et al. 2008, Poorter et al. 2008, Wright et al. 2010, Rüger et al. 2012; Aleixo et al. 2019), therefore we defined model parameters a, s_1, s_2, c_1 and c_2 as linear functions of WD. As such, WD could influence growth and mortality directly, as well as indirectly through effects on size relationships and responses to competition (e.g., Hérault et al. 2011, Iida et al. 2014, Kunstler et al. 2016). Models were fit using a hierarchical Bayesian approach (Appendix S2, Data S1: Model_script.R).

Using the fitted growth models, we calculated the strength of competition for each plot (C_{plot}) as the percent reduction in plot-level basal area growth due to competition compared to a low, baseline level of neighborhood crowding by assessing to what extent growth was reduced for each individual tree:

$$C_{\text{plot}} = \left(1 - \left(\frac{\sum_{i=1}^{n} G_i^{<c>}}{\sum_{i=1}^{n} G_i^{<lc>}}\right)\right) \times 100$$

where for tree i, $G_i^{<c>}$ represents predicted basal area growth with the observed level of competition, and $G_i^{<lc>}$ represents its potential growth at a low, baseline level of competition. Quantifying plot-level competition based on the growth reduction compared to potential growth in the absence of competition may be unrealistic, because a BA_{neigh} of zero is rarely found. Per continent, we calculated the 10th percentile of the plot-level 10th percentile values of BA_{neigh} (11.3 $\text{m}^2\ \text{ha}^{-1}$ for Amazonia; 9.8 $\text{m}^2\ \text{ha}^{-1}$ for Africa). We therefore calculated the strength of competition based on a general baseline level of $\text{BA}_{\text{neigh}} = 10\ \text{m}^2\ \text{ha}^{-1}$ for both continents. Thus, C_{plot} was calculated by comparing predicted plot-level growth (based on all individual trees) with competition to growth at a BA_{neigh} of 10 m^2 ha^{-1}. Growth predictions were based on the posterior means of the model parameters.

For each continent, we examined whether C_{plot} was correlated with water availability (CWD) or soil fertility (TEB). To assess whether variation in C_{plot} was driven by variation in plot basal area, plot-level WD (basal area-weighted mean), or average tree size (the diameter of a tree with mean basal area; $\sqrt{(\sum dbh^2)/n}$)), we modeled C_{plot} as a function of plot BA, plot-level WD, and average tree size using linear regression. In order to compare effect sizes among the three predictors, predictors were standardized by subtracting the mean and dividing the difference by the standard deviation. All analyses were performed in R 3.1.2 (R Core Team 2014).

Results

Overall responses to competition

Individual tree growth was strongly affected by competition (Fig. 2; Appendix S1: Table S2), but competition effects were stronger in Amazonian than African tropical forests. For example, for a 20 cm diameter tree with a WD of 0.6 gr cm^{-3}, growth decreased by 34% in Amazonia (Fig. 2e,g) and 17% in Africa (Fig. 2f,h) as BA_{neigh} increased from 10 to 50 m^2 ha^{-1}. Further, even though plot-level basal area was on average slightly lower in Amazonia (25.9 ± 0.44 m^2 ha^{-1}; mean ± SE) than in Africa (28.7 ± 0.64 m^2 ha^{-1}), the stronger response of trees to competition in Amazonia resulted in greater predicted decreases in plot-level wood production than in Africa. Competition reduced plot-level basal area growth (compared to a baseline, low BA_{neigh} value of 10 m^2 ha^{-1}) by, on average, 31.1% (range: 4.5-25.2%; Fig. 3a,c) in Amazonia, and by 7.4% in Africa (range: 5.3-11.7%; Fig. 3b,d).

In contrast to effects on growth, competition with neighboring trees had little or no effect on the probability of mortality. Nevertheless, the mortality model that included competition performed better than the no-competition model for Amazonia (Appendix S1: Table S2). The predicted probability of mortality for a 20-cm dbh tree with a WD of 0.6 gr cm^{-3} remained constant at 1.4% (Fig. 2m,o) and 1.0% (Fig. 2n,p) per year as BA_{neigh} increased from 10 to 50 m^2 ha^{-1} in Amazonia and Africa, respectively.

Effects of wood density and tree size

Tree basal area growth decreased with increasing WD on both continents (Fig. 2a,b). In Amazonia, a 20-cm tree with low WD (0.3 g cm^{-3}) grew more than twice as fast as a high WD (0.9 g cm^{-3}) tree of the same size (Fig. 2a). In Africa, the growth decrease with increasing WD was less pronounced (Fig. 2b). Growth increased with tree size on both continents (Fig. 2c,d), with low WD species exhibiting stronger size-related increases in growth.

On both continents, small trees were more strongly affected by competition than large trees (Fig. 2e,f). In Amazonia, growth of a 10 cm-tree and a 30 cm-tree decreased by 49% and 27%, respectively, as neighbor basal area increased from 10 to 50 m^2 ha^{-1} (Fig. 2e). Similar growth decreases were found in Africa, with a 28% and 18% growth decrease for a 10-cm and a 30-cm tree, respectively (Fig. 2f). Amazonian trees with different WD showed similar absolute decreases in growth resulting from competition, but on a proportional basis high WD species expressed greater decreases than low WD species (48% and 17%, respectively) as BA_{neigh} increased from 10 to 50 m^2 ha^{-1} (Fig. 2g). Conversely, the growth of high WD species in Africa was less affected by competition than that of low WD species (decreases of 14% and 28%, respectively; Fig. 2h).

The probability of mortality decreased with WD on both continents (Fig. 2i,j), but the decline was more pronounced and more consistent in Amazonia than in Africa. Mortality generally increased with tree size (Fig. 2k,l), particularly for trees > 50 cm dbh, although low abundances increased uncertainty for large trees. Small trees with low WD had higher mortality than mid-sized trees (7% and 23% higher mortality at 10 cm dbh than at 50 cm dbh in Amazonia and tropical Africa, respectively), leading to a U-shaped size-mortality relationship. Effects of competition on mortality were very weak on both continents, regardless of WD or tree size (Fig. 2m,n,o,p).

Variation in the strength of competition

In Amazonia, the plot-level strength of competition (C_{plot}) was strongly and positively correlated with CWD, but negatively correlated with TEB, particularly after accounting for variation in CWD (Fig. 3a,b). Plot basal area had the largest effect on C_{plot}, followed by a positive effect of plot WD, and a small negative effect of mean tree size (Fig. 3e). In Africa, C_{plot} was not correlated with CWD, and just weakly, positively correlated with TEB (Fig. 3c,d). Like in Amazonia, C_{plot} was largely driven by a positive effect of plot basal area. Unlike Amazonia, plot-level WD had little influence on C_{plot} in tropical Africa (Fig. 3f).

Discussion

Large variation in the strength of competition on tree growth across environmental gradients

Across two continents, we found that competition is an important driver of tropical tree growth, but unexpectedly not of mortality. Variation in the plot-level strength of competition across tropical forests was large for both continents. As expected, individual tree growth was most strongly affected by competition in forests with high basal area, although in Amazonia competition was also strong in high WD forests. In Amazonia, as expected, the strength of competition on tree growth increased with water availability (CWD), likely because of higher plot basal area in wetter forests (Appendix S1: Fig. S1). However, the strength of competition declined slightly with soil fertility (TEB) likely because of lower plot-level WD at high soil fertility (Appendix S1: Table S3), and because low WD species in Amazonia appeared to be less susceptible to competition. Unexpectedly, the strength of competition did not vary with water availability, nor with soil fertility, in Africa. This may have been due to the shorter water availability and soil fertility gradients compared to Amazonia in our study, which likely partly explains the lack of relationships with environmental conditions in tropical Africa. Given these differences, we must be careful in drawing general conclusions across continents. Across the same range in environmental conditions (based on Africa, excluding two outliers; Fig. 3b,d), the relationship between the strength of competition and CWD was stronger in Amazonia (Pearson's $r = 0.40$, $n = 38$ plots) than in Africa ($r = -0.12$). The relationship between the strength of competition and TEB was somewhat stronger for Africa due to outlier exclusion ($r = 0.23$) than for Amazonia ($r = 0.10$, $n = 41$ plots). Overall, our results are partly consistent with Grime's (1979) hypothesis that competition is strongest in resource-rich environments because of the increased strength of competition under high water availability in Amazonia.

Effects of WD and tree size on growth and mortality

In contrast, effects of WD and tree size on individual tree growth and mortality were largely consistent between Amazonia and tropical Africa. In general, our results confirmed findings of previous studies that were based on a single, or a few, tropical forest sites, and indicated that these attributes control growth and mortality across most of the tropical forest biome. Tree growth and mortality both decreased with WD, as reported by smaller-scale Neotropical studies (e.g., Chao et al. 2008, Keeling et al. 2008, Poorter et al. 2008, Wright et al. 2010, Rüger et al.

2012). Low WD is associated with an acquisitive strategy that confers rapid growth, but that comes at the cost of high mortality because of lower tolerance to stress and damage compared to high WD species (Wright et al. 2010). Basal area growth increased with tree size, presumably because larger trees have more resources and/or leaf area available to support assimilation of carbon (Stephenson et al. 2014). The ontogenetic increase in growth was strongest for low WD species (Fig. 2c,d), probably because of the low construction cost of low-density wood. These findings are consistent with single-site studies that found that low WD tropical tree species had the strongest increase in diameter growth at intermediate tree size (King et al. 2006, Hérault et al. 2011, but see Rüger et al. 2012).

Our study is one of the first to show a clearly U-shaped size-mortality relationship (cf. Rüger et al. 2011, Iida et al. 2014, Pillet et al. 2018), which we found for low WD species. For trees ≥ 30 cm dbh, and for high WD trees in general, the risk of death increased nearly monotonically with size. Small trees, particularly those with low WD, may be most susceptible to physical damage in the understory (Clark and Clark 1991). The higher mortality risk for large trees may be a result of the stronger risk of hydraulic failure for large trees (Rowland et al. 2015) rather than senescence (Mencuccini et al. 2005).

Competition decreased tree growth but did not influence mortality

Our results show that growth decreases with increased neighborhood crowding across tropical forests on two continents, particularly for small trees. This provides large-scale confirmation that results reported to date for single neotropical forest sites in Costa Rica, Ecuador, Panama and Puerto Rico (Uriarte et al. 2004, Baribault et al. 2012, Grote et al. 2013, Lasky et al. 2015, Fortunel et al. 2016) are typical of the biome. We also expected that low WD species would be most strongly affected by competition. Low WD species were indeed most affected by competition in Africa, consistent with earlier findings of strong growth responses of low WD species to competition (Kunstler et al. 2016) and light availability (Rüger et al. 2012), which supports the notion that shade intolerant tree species respond more strongly to changes in resource levels. However, it remains unclear why high WD species in Amazonia were more susceptible to competition. The mean and range of neighborhood crowding levels did not vary across WD classes (< 0.35 g cm^{-3}; 0.35-0.75 g cm^{-3}; > 0.75 g cm^{-3}; results not shown), thus effects of competition were not weaker because low WD species were confined to areas with low neighborhood crowding.

Our results suggest that competition does not strongly influence tree mortality in either Amazonia or tropical Africa. The lack of evidence for impacts of competition on mortality could be partly due to only including trees ≥ 10 cm dbh in our study. Generally, mortality rates are highest for seedlings and saplings (trees < 10 cm dbh; Clark and Clark 1992, Condit et al. 1995) because of the low-light conditions in the understory, and mortality resulting from negative density-dependent effects (Zhu et al. 2015). Those studies that have found clear effects of competition on tropical tree mortality included trees < 10 cm dbh, and likely included a larger range of resource levels by focusing on forests in recovery from disturbances such as agricultural use (Lasky et al. 2014) and hurricanes (Uriarte et al. 2004). Our findings suggest that competition is not a widespread and important driver of mortality for trees ≥ 10 cm dbh in mature tropical forests. Instead, it appears that processes such as hydraulic failure (e.g., Rowland et al. 2015) and more stochastic wind-disturbances (Espírito-Santo et al. 2014; Aleixo et al. 2019) may be the dominant causes of mortality, while accelerated growth may eventually increase mortality by ensuring that trees reach larger sizes more quickly (cf. Brienen et al. 2015, McDowell et al. 2018). Nevertheless, the effects of competition on growth may still indirectly lead to an increased risk of mortality, as suppressed trees will be less likely to escape from suppression because of their slow growth, and thus accumulate mortality risk over a longer period of time.

Implications for projecting the tropical forest carbon sink

Our results provide some insights into how competition may influence ongoing and future changes in the tropical forest carbon sink. First, we found that the decrease in basal area growth due to competition increased strongly with forest basal area. Hence, when forests gain basal area over time, greater competition between trees is likely to reduce tree growth, which might explain why long-term increases in productivity in Amazonia have leveled off since 2000 (Brienen et al. 2015). Secondly, we found that, particularly in Amazonia, effects of competition are also influenced by stand-level WD. Changes in WD over time (e.g., van der Sande et al. 2016) may not only influence standing biomass (Baker et al. 2004), but also alter the strength of competition.

Competition effects should be appropriately incorporated into models that are used for projecting future dynamics of tropical forests. In individual-based forest dynamics models, effects of competition are typically included (Fyllas et al. 2014), but models could be further improved by also including effects of WD, and tree size, on the strength of competition. These changes are relatively easy to implement, as direct effects of tree size are already included, and WD data are available for many species (Chave et al. 2009). In Dynamic Global Vegetation Models that are applied over broad geographical scales, inclusion of forest basal area as a measure of neighborhood crowding will mostly account for geographical variation in the strength of competition. Such models could be improved further by including average plot WD.

In conclusion, our study revealed that in 151 forest plots distributed across Amazonia and tropical Africa competition is an important driver of individual tree growth rates, but not of the probability of tree mortality. This is, to our knowledge, the first study to evaluate the effects of competition on tropical tree growth and mortality at such a broad geographical scale. Given that geographic variation in the strength of competition is mainly driven by forest basal area (i.e., neighborhood crowding), we anticipate that wood production might decrease as tropical forests accrue higher basal area.

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Figure Legends

Fig. 1. Maps of the plot locations across gradients in climatic water deficit (CWD) and soil total exchange bases (TEB). (a) Amazonia (102 plots); (b) tropical Africa (49 plots).

Fig. 2. Effects of wood density (WD), tree size, and competition (subplot neighbor basal area; BA_{neigh}) on predicted annual basal area growth and mortality across Amazonia (n = 102 plots) and tropical Africa (n = 49). Solid lines and symbols indicate predicted effects based on the posterior means; shaded areas indicate the 95% credible interval. Boxplots indicate the distribution of the variable on the x-axis. BA_{neigh} was kept constant at the mean for quantifying effects of WD and tree size on growth and mortality; tree size was kept constant at 20 cm diameter for quantifying effects of WD and BA_{neigh}.

Fig. 3. Relationships between the strength of competition on basal area growth (C_{plot}: reduction in plot-level basal area growth by competition based on a reference value of 10 m^2 ha^{-1}) and climatic water deficit (CWD), soil total exchange bases (TEB), plot basal area (BA), plot wood density (WD), and mean tree size in Amazonia (n = 102 plots) and tropical Africa (n = 49 plots). (a-d) Grey bars represent 95% credible intervals; Pearson's correlation (r) and partial (r_{part}) correlation coefficients are indicated; (e,f) standardized regression coefficients with 95% confidence intervals are indicated.

Figure 1

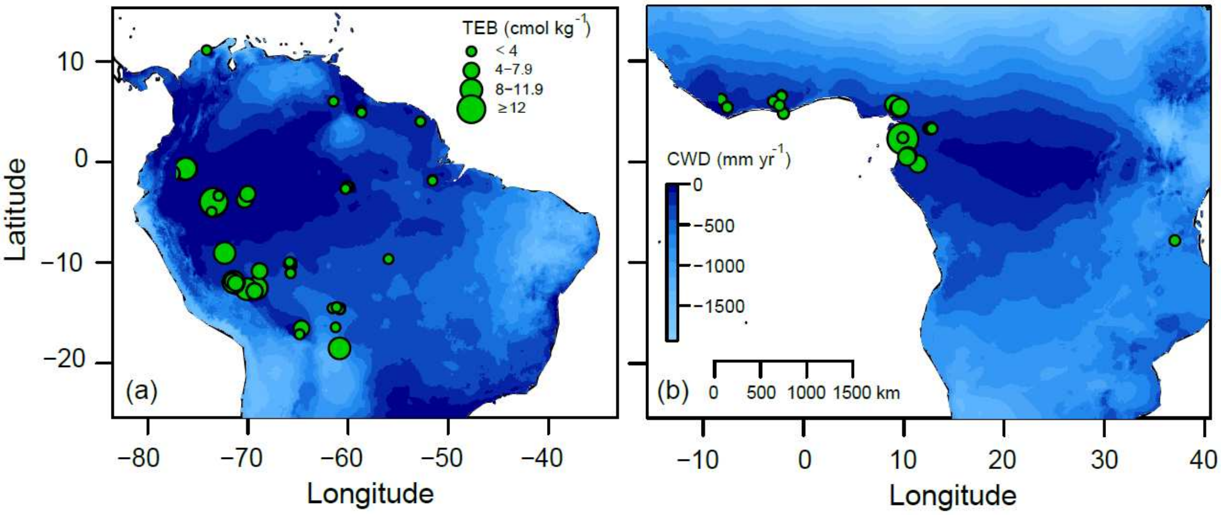

TEB (cmol kg^{-1})
< 4
4−7.9
8−11.9
≥12
10
0
−10
−20
Latitude
(a)
−80
−70
−60
−50
−40
Longitude
CWD (mm yr^{-1})
0
−500
−1000
−1500
0
500
1000
1500 km
(b)
−10
0
10
20
30
40
Longitude

Figure 2

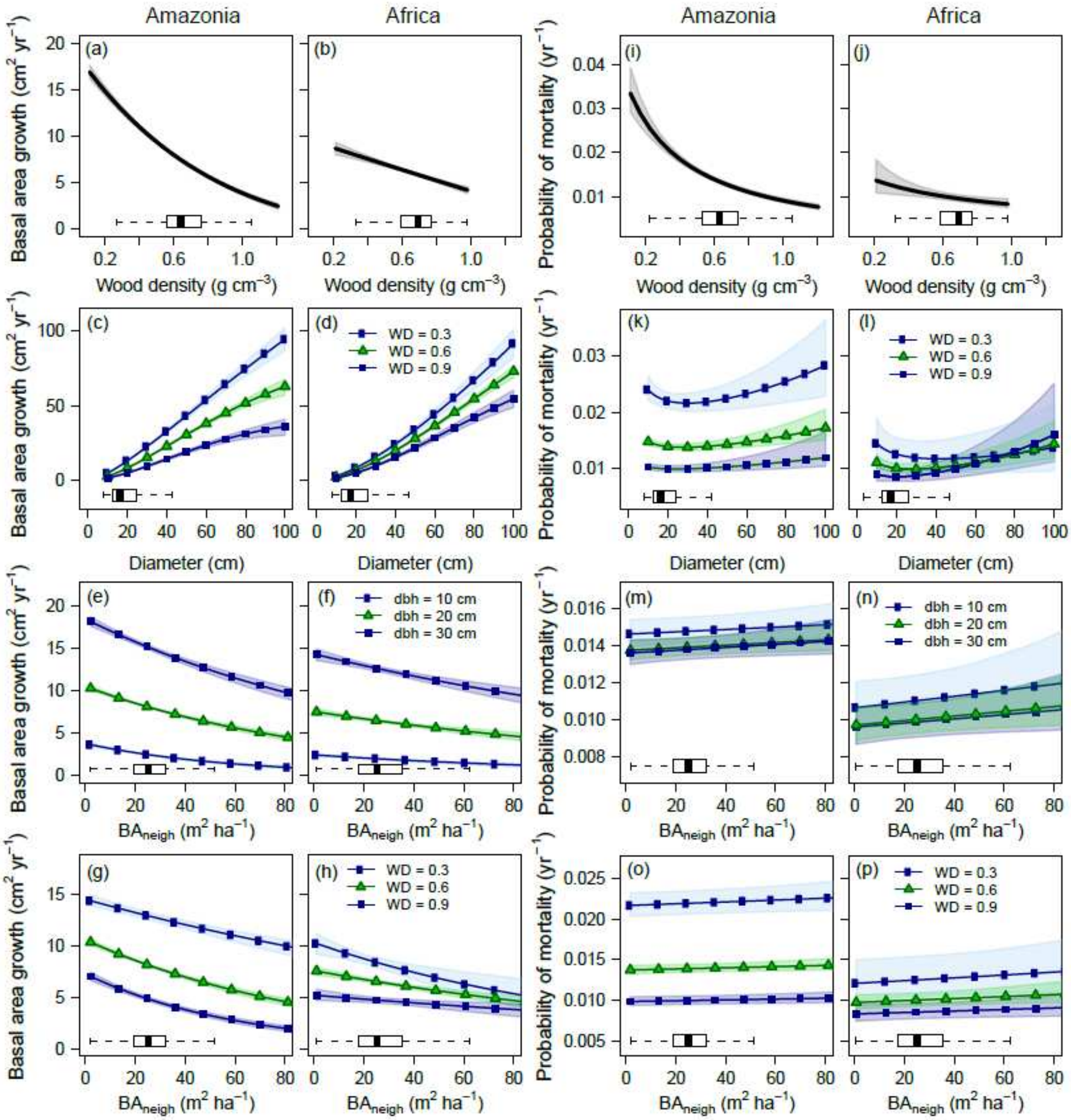
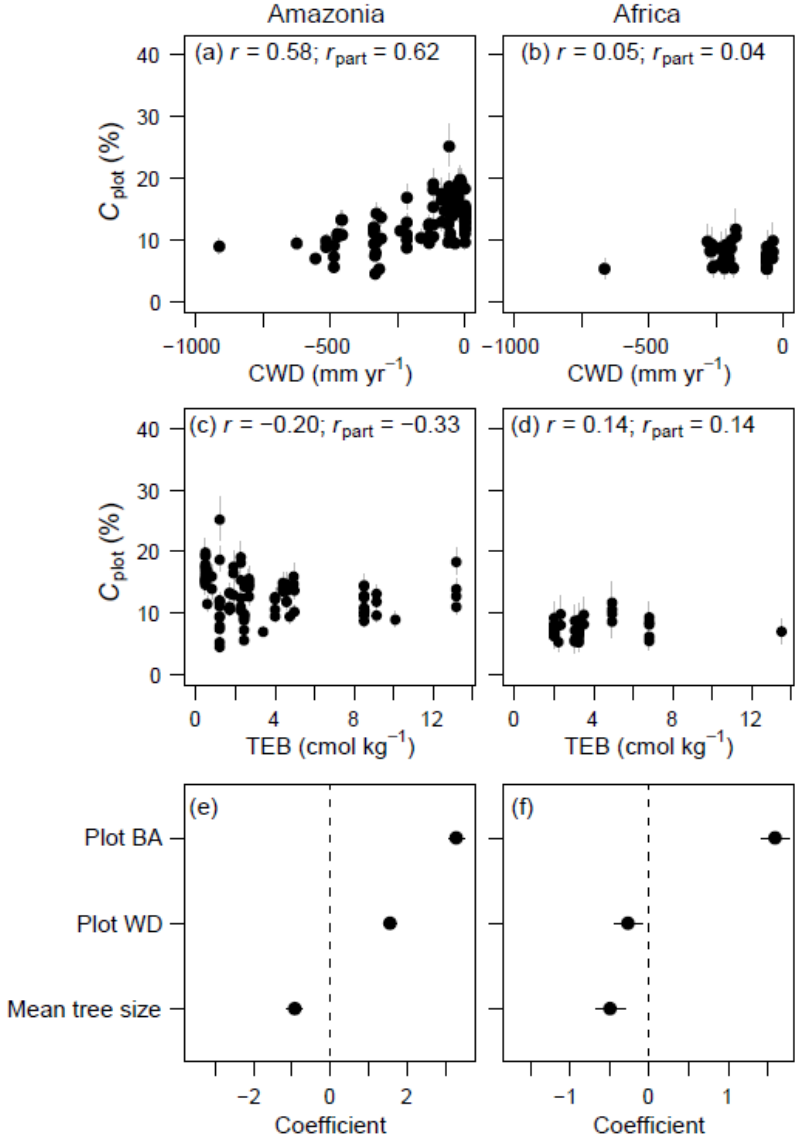

Amazonia
Africa
Amazonia
Africa
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
(m)
(n)
(o)
(p)
Basal area growth (cm^2 yr^{-1})
Probability of mortality (yr^{-1})
Wood density (g cm^{-3})
Diameter (cm)
BA_{neigh} (m^2 ha^{-1})
WD = 0.3
WD = 0.6
WD = 0.9
dbh = 10 cm
dbh = 20 cm
dbh = 30 cm
0
5
10
15
20
50
100
0.2
0.6
1.0
20
40
60
80
100
0.01
0.02
0.03
0.04
0.008
0.010
0.012
0.014
0.016
0.005
0.010
0.015
0.020
0.025

Figure 3


Amazonia
Africa
(a) r = 0.58; r_{part} = 0.62
(b) r = 0.05; r_{part} = 0.04
C_{plot} (%)
40
30
20
10
0
−1000
−500
0
CWD (mm yr^{-1})
(c) r = −0.20; r_{part} = −0.33
(d) r = 0.14; r_{part} = 0.14
TEB (cmol kg^{-1})
0
4
8
12
(e)
(f)
Plot BA
Plot WD
Mean tree size
−2
0
2
−1
1
Coefficient

Supplementary Information. Danaë M.A. Rozendaal, Oliver L. Phillips, Simon L. Lewis, Kofi Affum-Baffoe, Esteban Alvarez Dávila, Ana Andrade, Luiz E.O.C. Aragão, Alejandro Araujo-Murakami, Timothy R. Baker, Olaf Bánki, Roel J.W. Brienen, José Luis C. Camargo, James A. Comiskey, Marie Noel Djuikouo K., Sophie Fauset, Ted R. Feldpausch, Timothy J. Killeen, William F. Laurance, Susan G.W. Laurance, Thomas Lovejoy, Yadvinder Malhi, Beatriz S. Marimon, Ben-Hur Marimon Junior, Andrew R. Marshall, David A. Neill, Percy Núñez Vargas, Nigel C.A. Pitman, Lourens Poorter, Jan Reitsma, Marcos Silveira, Bonaventure Sonké, Terry Sunderland, Hermann Taedoumg, Hans ter Steege, John W. Terborgh, Ricardo K. Umetsu, Geertje M.F. van der Heijden, Emilio Vilanova, Vincent Vos, Lee J.T. White, Simon Willcock, Lise Zemagho, and Mark C. Vanderwel. Competition influences tree growth, but not mortality, across environmental gradients in Amazonia and tropical Africa. *Ecology*.

Appendix S1

Table S1. List of included plots.

Continent	Country	Plot name	Plot code	Trees mapped / subplots	Plot area (ha)	Latitude	Longitude
Amazon	Bolivia	BEEM plot 5	BEE-05	mapped	1	-16.5	-64.6
Amazon	Bolivia	Chore 1	CHO-01	0.04 ha subplots	1	-14.4	-61.1
Amazon	Bolivia	Cerro Pelao 1	CRP-01	0.04 ha subplots	1	-14.5	-61.5
Amazon	Bolivia	Cerro Pelao 2	CRP-02	mapped	1	-14.5	-61.5
Amazon	Bolivia	Huanchaca Dos, plot 1	HCC-21	0.04 ha subplots	1	-14.5	-60.7
Amazon	Bolivia	Huanchaca Dos, plot 2	HCC-22	0.04 ha subplots	1	-14.5	-60.7
Amazon	Bolivia	Isla Huanchaca, plot 1	HCC-23	0.04 ha subplots	1	-14.6	-60.7
Amazon	Bolivia	Los Fierros Bosque I	LFB-01	0.04 ha subplots	1	-14.6	-60.8
Amazon	Bolivia	Los Fierros Bosque II	LFB-02	0.04 ha subplots	1	-14.6	-60.8
Amazon	Bolivia	Las Londras, plot 1	LSL-01	0.04 ha subplots	1	-14.4	-61.1
Amazon	Bolivia	Las Londras, plot 2	LSL-02	0.04 ha subplots	1	-14.4	-61.1
Amazon	Bolivia	Mabet plot 1	MBT-01	mapped	1	-10.1	-65.9
Amazon	Bolivia	Mabet plot 4	MBT-04	mapped	1	-10.3	-65.6
Amazon	Bolivia	Mabet plot 5	MBT-05	mapped	1	-10.0	-65.6
Amazon	Bolivia	Mabet plot 6	MBT-06	mapped	1	-10.0	-65.6
Amazon	Bolivia	Mabet plot 7	MBT-07	mapped	1	-9.9	-65.7
Amazon	Bolivia	Mabet plot 8	MBT-08	mapped	1	-9.9	-65.8
Amazon	Bolivia	Ottavio Ranch, Bolivia, plot 1, forest	OTT-01	mapped	1	-16.4	-61.2
Amazon	Bolivia	Reserva El Tigre 05	RET-05	mapped	1	-11.0	-65.7
Amazon	Bolivia	Reserva El Tigre 06	RET-06	mapped	1	-11.0	-65.7
Amazon	Bolivia	Reserva El Tigre 08	RET-08	mapped	1	-11.0	-65.7
Amazon	Bolivia	Reserva El Tigre 09	RET-09	mapped	1	-11.0	-65.7
Amazon	Bolivia	Sacta plot 1	SCT-01	0.04 ha subplots	1	-17.1	-64.8
Amazon	Bolivia	Sacta plot 6	SCT-06	mapped	1	-17.1	-64.8
Amazon	Bolivia	Tucavaca plot 1, forest	TUC-01	0.04 ha subplots	1	-18.5	-60.8
Amazon	Brazil	Alta Floresta plot 1	ALF-01	0.04 ha subplots	1	-9.6	-55.9
Amazon	Brazil	Alta Floresta plot 2	ALF-02	mapped	1	-9.6	-55.9
Amazon	Brazil	BDFFP, 2303 Dimona 5-6	BDF-01	0.04 ha subplots	2	-2.3	-60.1

Amazon	Brazil	BDFFP, 1101 Gaviao	BDF-03	0.04 ha subplots	1	-2.4	-59.9
Amazon	Brazil	BDFFP, 1102 Gaviao	BDF-04	0.04 ha subplots	1	-2.4	-59.9
Amazon	Brazil	BDFFP, 1103 Gaviao	BDF-05	0.04 ha subplots	1	-2.4	-59.9
Amazon	Brazil	BDFFP, 1201 Gaviao	BDF-06	0.04 ha subplots	3	-2.4	-59.9
Amazon	Brazil	BDFFP, 1105 Gaviao	BDF-07	0.04 ha subplots	1	-2.4	-59.9
Amazon	Brazil	BDFFP, 1109 Gaviao	BDF-08	0.04 ha subplots	1	-2.4	-59.9
Amazon	Brazil	BDFFP, 1113 Florestal	BDF-09	0.04 ha subplots	1	-2.4	-59.8
Amazon	Brazil	BDFFP, 1301 Florestal 1= plot 1301.1 and 1301.3	BDF-10	0.04 ha subplots	2	-2.4	-59.9
Amazon	Brazil	BDFFP, 1301 Florestal 2= plots 1301.4,5,6	BDF-11	0.04 ha subplots	3	-2.4	-59.8
Amazon	Brazil	BDFFP, 1301 Florestal 3=plots 1301.7,8	BDF-12	0.04 ha subplots	2	-2.4	-59.9
Amazon	Brazil	BDFFP, 3402 Cabo Frio	BDF-13	0.04 ha subplots	9	-2.4	-59.9
Amazon	Brazil	BDFFP, 3304 Porto Alegre	BDF-14	0.04 ha subplots	1	-2.4	-60.0
Amazon	Brazil	Bionte 1	BNT-01	mapped	1	-2.6	-60.2
Amazon	Brazil	Bionte 02	BNT-02	mapped	1	-2.6	-60.2
Amazon	Brazil	Bionte 4	BNT-04	mapped	1	-2.6	-60.2
Amazon	Brazil	TORRE Caxiuana	CAX-06	0.04 ha subplots	1	-1.7	-51.5
Amazon	Brazil	Caxiuana Terra Preta	CAX-08	0.04 ha subplots	1	-1.8	-51.5
Amazon	Brazil	Jacaranda, norte-sul (north-south), plots 1-5	JAC-01	0.04 ha subplots	5	-2.6	-60.2
Amazon	Brazil	Jacaranda, leste-oeste (east-west), plots 6-10	JAC-02	0.04 ha subplots	5	-2.6	-60.2
Amazon	Brazil	RESEX Chico Mendes: Seringal Porongaba 1	POR-01	0.04 ha subplots	1	-10.8	-68.8
Amazon	Brazil	RESEX Chico Mendes: Seringal Porongaba 2	POR-02	0.04 ha subplots	1	-10.8	-68.8
Amazon	Brazil	Alto Jurua	RST-01	0.04 ha subplots	1	-9.0	-72.3
Amazon	Colombia	Amacayacu: Agua Pudre E	AGP-01	0.04 ha subplots	1	-3.7	-70.3
Amazon	Colombia	Amacayacu: Agua Pudre U	AGP-02	0.04 ha subplots	1	-3.7	-70.3
Amazon	Colombia	Reserva Kalashe 1	KAL-01	0.04 ha subplots	1	11.2	-74.1
Amazon	Colombia	Amacayacu: Lorena E	LOR-01	0.04 ha subplots	1	-3.1	-70.0
Amazon	Colombia	Amacayacu: Lorena U subplot 1-13	LOR-02	0.04 ha subplots	0.52	-3.1	-70.0
Amazon	Ecuador	Jatun Sacha 2	JAS-02	0.04 ha subplots	1	-1.1	-77.6
Amazon	Ecuador	Jatun Sacha 3	JAS-03	0.04 ha subplots	1	-1.1	-77.6
Amazon	Ecuador	Jatun Sacha 4 Full plot	JAS-04	0.04 ha subplots	0.96	-1.1	-77.6
Amazon	Ecuador	Jatun Sacha 5, till 2002	JAS-05	0.04 ha subplots	1	-1.1	-77.6
Amazon	Ecuador	Tiputini 1	TIP-01	0.04 ha subplots	1	-0.7	-76.4
Amazon	Ecuador	Tiputini 2	TIP-02	0.04 ha subplots	0.8	-0.6	-76.1
Amazon	Ecuador	Tiputini 3	TIP-03	mapped	1	-0.6	-76.2
Amazon	French Guiana	Nouragues Grand Plateau 11L	NOU-02	mapped	1	4.1	-52.7
Amazon	French Guiana	Nouragues Grand Plateau 12L	NOU-03	mapped	1	4.1	-52.7
Amazon	French Guiana	Nouragues Grand Plateau 17L	NOU-08	mapped	1	4.1	-52.7

Amazon	French Guiana	Nouragues Grand Plateau 19L	NOU-10	mapped	1	4.1	-52.7
Amazon	French Guiana	Nouragues Petit Plateau 20H	NOU-11	mapped	1	4.1	-52.7
Amazon	Guyana	Forest reserve Mabura hill 01	FMH-01	mapped	1	5.2	-58.7
Amazon	Guyana	Forest reserve Mabura hill 01	FMH-03	mapped	1	5.2	-58.7
Amazon	Guyana	Pibiri 05	PIB-05	mapped	1	5.0	-58.6
Amazon	Guyana	Pibiri 06	PIB-06	mapped	1	5.0	-58.6
Amazon	Guyana	Pibiri 12	PIB-12	mapped	1	5.0	-58.6
Amazon	Peru	Altos de Maizal	ALM-01	mapped	2	-11.8	-71.5
Amazon	Peru	Allpahuayo A	ALP-01	0.04 ha subplots	1	-3.9	-73.4
Amazon	Peru	Allpahuayo B	ALP-02	0.04 ha subplots	1	-4.0	-73.4
Amazon	Peru	Allpahuayo C	ALP-30	mapped	1	-4.0	-73.4
Amazon	Peru	Allpahuayo D	ALP-40	mapped	1	-3.9	-73.4
Amazon	Peru	Cuzco Amazonico, CUZAM1E	CUZ-01	0.04 ha subplots	1	-12.5	-69.1
Amazon	Peru	Cuzco Amazonico, CUZAM1U	CUZ-02	0.04 ha subplots	1	-12.5	-69.1
Amazon	Peru	Cuzco Amazonico, CUZAM2E	CUZ-03	0.04 ha subplots	1	-12.5	-69.1
Amazon	Peru	Cuzco Amazonico, CUZAM2U	CUZ-04	0.04 ha subplots	1	-12.5	-69.1
Amazon	Peru	Jenaro Herrera A Terraza Alta	JEN-11	mapped	1	-4.9	-73.6
Amazon	Peru	Jenaro Herrera B Varillal	JEN-12	0.04 ha subplots	1	-4.9	-73.6
Amazon	Peru	Jacaratia Los Amigos	LAS-02	mapped	1	-12.6	-70.1
Amazon	Peru	Manu, alluvial Cocha Cashu Trail 3, M1	MNU-01	mapped	2.25	-11.9	-71.4
Amazon	Peru	Manu, terra firme terrace, M3	MNU-03	mapped	2	-11.9	-71.4
Amazon	Peru	Manu, terra firme ravine, M4	MNU-04	mapped	1	-11.9	-71.4
Amazon	Peru	Manu, alluvial Cocha Cashu Trail 12	MNU-05	mapped	2	-11.9	-71.4
Amazon	Peru	Manu, alluvial Cocha Cashu Trail 2 & 31	MNU-06	mapped	2.25	-11.9	-71.4
Amazon	Peru	Cocha Salvador Manu, mature floodplain	MNU-08	mapped	2	-12.0	-71.2
Amazon	Peru	Sucusari A	SUC-01	0.04 ha subplots	1	-3.3	-72.9
Amazon	Peru	Sucusari B	SUC-02	0.04 ha subplots	1	-3.2	-72.9
Amazon	Peru	Sucusari C	SUC-03	0.04 ha subplots	1	-3.2	-72.9
Amazon	Peru	Sucusari D	SUC-04	mapped	1	-3.3	-72.9
Amazon	Peru	Sucusari E	SUC-05	mapped	1	-3.3	-72.9
Amazon	Peru	Tambopata plot zero	TAM-01	0.04 ha subplots	1	-12.8	-69.3
Amazon	Peru	Tambopata plot one	TAM-02	0.04 ha subplots	1	-12.8	-69.3
Amazon	Peru	Tambopata plot three	TAM-05	0.04 ha subplots	1	-12.8	-69.3
Amazon	Peru	Tambopata plot six	TAM-07	0.04 ha subplots	1	-12.8	-69.3
Amazon	Peru	Tambopata plot seven	TAM-08	0.04 ha subplots	1	-12.8	-69.3
Amazon	Venezuela	El Dorado, KM93, plotGl, ED1	ELD-01	mapped	0.25	6.1	-61.4

Amazon	Venezuela	El Dorado, KM93, plotG2, ED1	ELD-02	mapped	0.25	6.1	-61.4
Africa	Cameroon	Bissombo 1	BIS-01	mapped	1	3.3	12.5
Africa	Cameroon	Bissombo 2	BIS-02	mapped	1	3.3	12.5
Africa	Cameroon	Bissombo 3	BIS-03	mapped	1	3.3	12.5
Africa	Cameroon	Bissombo 4	BIS-04	mapped	1	3.3	12.5
Africa	Cameroon	Bissombo 5	BIS-05	mapped	1	3.3	12.5
Africa	Cameroon	Bissombo 6	BIS-06	mapped	1	3.3	12.5
Africa	Cameroon	Campo Ma'an 1	CAM-01	0.04 ha subplots	1	2.4	9.9
Africa	Cameroon	Campo Ma'an 2	CAM-02	0.04 ha subplots	1	2.3	9.9
Africa	Cameroon	Campo Ma'an 3	CAM-03	0.04 ha subplots	1	2.4	9.9
Africa	Cameroon	Dja Somolomo 1	DJK-01	mapped	1	3.3	12.7
Africa	Cameroon	Dja Somolomo 2	DJK-02	mapped	1	3.3	12.7
Africa	Cameroon	Dja Somolomo 3	DJK-03	mapped	1	3.4	12.7
Africa	Cameroon	Dja Somolomo 4	DJK-04	mapped	1	3.4	12.7
Africa	Cameroon	Dja Somolomo 5	DJK-05	mapped	1	3.3	12.8
Africa	Cameroon	Dja Somolomo 6	DJK-06	mapped	1	3.3	12.8
Africa	Cameroon	Edjagham, plot 4	EJA-04	0.04 ha subplots	1	5.7	9.0
Africa	Cameroon	Edjagham, plot 5	EJA-05	0.04 ha subplots	1	5.7	9.0
Africa	Cameroon	Nguti plot 1	NGI-01	mapped	1	5.3	9.5
Africa	Cameroon	Nguti plot 2	NGI-02	mapped	1	5.3	9.5
Africa	Cameroon	Nguti plot 3	NGI-03	mapped	1	5.4	9.6
Africa	Gabon	Lope Reitsma	LOP-01	mapped	1	-0.2	11.4
Africa	Gabon	Monts de Cristal, plot 2	MDC-02	mapped	1	0.6	10.4
Africa	Gabon	Monts de Cristal, plot 3	MDC-03	mapped	1	0.6	10.4
Africa	Gabon	Monts de Cristal, plot 4	MDC-04	mapped	1	0.5	10.3
Africa	Ghana	Asenanyo F.R. 2	ASN-02	mapped	0.6	6.6	-2.2
Africa	Ghana	Asenanyo F.R. 4	ASN-04	mapped	0.92	6.5	-2.2
Africa	Ghana	Cape Three Points Plot 9	CAP-09	mapped	1	4.9	-2.0
Africa	Ghana	Cape Three Points Plot 10	CAP-10	mapped	1	4.8	-2.0
Africa	Ghana	Dadieso 3, occasionally flooded	DAD-31	0.04 ha subplots	0.56	6.0	-3.0
Africa	Ghana	Dadieso 4, terra firme	DAD-42	mapped	0.72	6.0	-3.0
Africa	Ghana	Fure Headwaters 7	FUR-07	mapped	1	5.6	-2.4
Africa	Liberia	Cavalla 1	CVL-01	mapped	1	6.2	-8.2
Africa	Liberia	Cavalla 8	CVL-08	mapped	1	6.2	-8.2
Africa	Liberia	Cavalla 10	CVL-10	mapped	1	6.2	-8.2
Africa	Liberia	Cavalla 11	CVL-11	mapped	1	6.2	-8.2
Africa	Liberia	Grebo F.R.1	GBO-01	mapped	1	5.4	-7.6
Africa	Liberia	Grebo F.R.2	GBO-02	mapped	1	5.4	-7.6
Africa	Liberia	Grebo F.R.3	GBO-03	mapped	1	5.4	-7.6
Africa	Liberia	Grebo F.R.4	GBO-04	mapped	1	5.4	-7.6
Africa	Liberia	Grebo F.R.8	GBO-08	mapped	1	5.4	-7.6
Africa	Liberia	Grebo F.R.10	GBO-10	mapped	1	5.4	-7.6
Africa	Liberia	Grebo F.R.11	GBO-11	mapped	1	5.4	-7.6
Africa	Liberia	Grebo F.R.13	GBO-13	mapped	1	5.4	-7.6
Africa	Liberia	Grebo F.R.14	GBO-14	mapped	1	5.4	-7.6
Africa	Liberia	Grebo F.R.15	GBO-15	mapped	1	5.4	-7.6

Africa	Liberia	Grebo F.R.16	GBO-16	mapped	1	5.4	-7.6
Africa	Liberia	Grebo F.R.18	GBO-18	mapped	1	5.4	-7.6
Africa	Liberia	Grebo F.R.19	GBO-19	mapped	1	5.4	-7.6
Africa	Tanzania	VTA-ARM-1	VTA-01	0.04 ha subplots	1	-7.8	37.0

Table S2. Comparison of individual-based tree growth and mortality models with and without effects of competition for 151 plots in Amazonia and tropical Africa. Effects of neighborhood crowding were expressed as the basal area of neighbor trees per 0.04 ha subplot (BA_{neigh}). Models were compared based on the Watanabe-Akaike Information Criterion (WAIC), with the difference from the best model (ΔWAIC) shown. Best models are indicated in bold.

	Amazon		Africa	
	growth	mortality	growth	mortality
Competition index	ΔWAIC	ΔWAIC	ΔWAIC	ΔWAIC
none	5942	2310	913	**0**
BA_{neigh}	**0**	**0**	**0**	98

Table S3. Correlations (Pearson's *r*) between the plot-level strength of competition (C_{plot}), climatic water deficit (CWD), total exchange bases (TEB), plot basal area (BA), plot wood density (WD), and mean tree size in Amazonia (*n* = 102 plots) and tropical Africa (*n* = 49 plots).

	C_{plot}	CWD	TEB	Plot BA	Plot WD
Amazonia					
CWD	0.58				
TEB	-0.20	0.12			
Plot BA	0.84	0.54	-0.09		
Plot WD	0.53	0.12	-0.48	0.12	
Mean tree size	0.31	0.17	-0.18	0.56	0.13
Africa					
CWD	0.05				
TEB	0.14	0.07			
Plot BA	0.86	0.16	0.12		
Plot WD	0.04	-0.01	0.11	0.36	
Mean tree size	0.10	0.06	-0.17	0.49	0.51

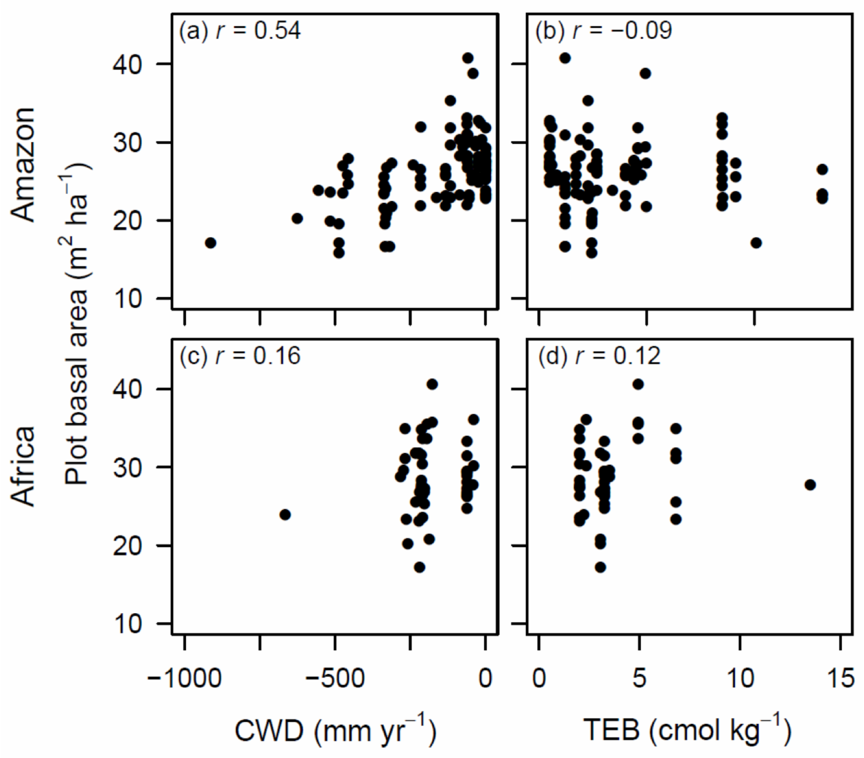


Fig. S1. Plot basal area across gradients in climatic water deficit (CWD) and soil total exchange bases (TEB) in the Amazon (*n* = 102 plots) and tropical Africa (*n* = 49 plots). Pearson's correlation coefficients (*r)* are indicated.

Supplementary Information. Danaë M.A. Rozendaal, Oliver L. Phillips, Simon L. Lewis, Kofi Affum-Baffoe, Esteban Alvarez Dávila, Ana Andrade, Luiz E.O.C. Aragão, Alejandro Araujo-Murakami, Timothy R. Baker, Olaf Bánki, Roel J.W. Brienen, José Luis C. Camargo, James A. Comiskey, Marie Noel Djuikouo K., Sophie Fauset, Ted R. Feldpausch, Timothy J. Killeen, William F. Laurance, Susan G.W. Laurance, Thomas Lovejoy, Yadvinder Malhi, Beatriz S. Marimon, Ben-Hur Marimon Junior, Andrew R. Marshall, David A. Neill, Percy Núñez Vargas, Nigel C.A. Pitman, Lourens Poorter, Jan Reitsma, Marcos Silveira, Bonaventure Sonké, Terry Sunderland, Hermann Taedoumg, Hans ter Steege, John W. Terborgh, Ricardo K. Umetsu, Geertje M.F. van der Heijden, Emilio Vilanova, Vincent Vos, Lee J.T. White, Simon Willcock, Lise Zemagho, and Mark C. Vanderwel. Competition influences tree growth, but not mortality, across environmental gradients in Amazonia and tropical Africa. *Ecology*.

Detailed description of individual growth and mortality models

Appendix S2

Individual growth and mortality models

We modelled tree growth and mortality as a function of size, competition and wood density for each continent (Amazonia, tropical Africa), using non-linear hierarchical models. Annual basal area growth (G) and annual probability of mortality (M) for a tree were modeled as follows:

$$G = a_G \times p_G \times S_G \times C_G$$
$$M = [1 + a_M \times p_M \times S_M \times C_M]^{-1}$$

where a_G and a_M are constants, and p_G and p_M are plot-level random effects. S and C (for growth and mortality) are non-linear functions that capture effects of tree size and competition:

$$S = \text{dbh}^{s_1} \times \exp\left(-s_2 \times \text{dbh}\right)$$
$$C = \exp\left(-c_1 \times \text{dbh}^{c_2} \times \text{BA}_{\text{neigh}}\right)$$

where dbh indicates diameter at breast height of a tree, and BA_{neigh} its neighbor basal area. s_1, s_2, c_1 and c_2 control the shape of the functions and have separate values for growth and mortality. To aid model fitting, we re-scaled dbh and BA_{neigh} by dividing them by numbers close to their observed means.

We accounted for species-to-species variation in growth and mortality by constructing models based on WD. To incorporate WD effects, we defined a, s_1, s_2, c_1 and c_2 as linear functions of WD. For each of these (here θ), we estimated parameters $\theta_{\min}$ and $\theta_{\max}$ to define their values at the minimum and maximum WD that was observed among species ($\text{WD}_{\min}$ and $\text{WD}_{\max}$, respectively). We used linear interpolation to estimate θ for each stem as:

$$\theta = w\theta_{\min} + (1-w)\theta_{\max}$$

where weighting coefficient w is calculated as:

$$w = \frac{\text{WD}_{\max} - \text{WD}}{\text{WD}_{\max} - \text{WD}_{\min}}$$

We used hierarchical Bayesian modeling to estimate the posterior distribution of the parameters for each model. Annual basal area growth (ΔBA) of individual trees was modeled by a normal distribution, with a standard deviation that increased as a linear function of dbh. Observations of tree survival (D=0) or death (D=1) over the census interval were modeled by a Bernoulli distribution whose mean was the compounded probability of mortality over a census interval of y years. Plot effects on tree growth and mortality were considered to be normally distributed with a mean of one:

$$\Delta\mathrm{BA} \sim \mathrm{N}(G, \sigma_0 + \sigma_{\mathrm{dbh}} \times \mathrm{dbh})$$
$$D \sim \mathrm{Bern}(1 - (1 - M)^y)$$
$$p_{\mathrm{G}} \sim \mathrm{N}(1, \sigma_{\mathrm{G}})$$
$$p_{\mathrm{M}} \sim \mathrm{N}(1, \sigma_{\mathrm{M}})$$

where σ_0, σ_{dbh}, σ_{G}, and σ_{M} are estimated parameters. All model parameters were assigned uninformative priors. We performed Markov chain Monte Carlo sampling with four chains, with per chain 750 000 burn-in and 500 000 sampling iterations. We thinned chains by retaining every 100th sample, and assessed convergence using the Gelman-Rubin criterion (Gelman and Rubin 1992). To assess whether competition influenced growth and mortality, we compared the model with effects of competition with a model that excluded competition by fixing either C_{G} or C_{M} at 1, based on the Watanabe-Akaike Information Criterion (WAIC; Watanabe 2013, Hooten and Hobbs 2015).

All analyses were performed in R 3.1.2 (R Core Team 2014). MCMC sampling was performed using the ‘Filzbach’ sampler, as implemented in the ‘filzbach’ package (Lyutsarev and Purves 2013). The Gelman-Rubin criterion was calculated using the ‘coda’ package (Plummer et al. 2006).

Comparison of indices of competition

To assess whether $\mathrm{BA}_{\mathrm{neigh}}$ accurately captured local effects of competition, we also fit models with a neighborhood crowding index (NCI; see Uriarte et al. 2004) instead of $\mathrm{BA}_{\mathrm{neigh}}$ for a subset of 86 plots for which at least 90 % of the trees were mapped. We randomly assigned coordinates to trees that were not mapped within the corresponding 0.04 ha subplot. All trees within 10 m of the edge of the plot were excluded from analysis, as their neighborhood is partially undefined. NCI is considered to be a good proxy for light availability to an individual tree (Grote et al. 2013). NCI is based on the size of and distance to, neighbor trees within a 10 m radius of the focal tree:

$$\mathrm{NCI} = \sum_{j=1, i \neq j}^{J} \frac{\mathrm{dbh}_j^2}{\mathrm{dist}_{ij}^2}$$

where dist is the distance between focal tree i and neighbor tree j for a total of J neighbor trees. For both continents, growth models that included NCI were not better supported than models with $\mathrm{BA}_{\mathrm{neigh}}$ (Table S1). A mortality model that included NCI performed better than a model with $\mathrm{BA}_{\mathrm{neigh}}$ for Africa, but for Amazonia the mortality model without competition was best supported (Table S1). Thus, $\mathrm{BA}_{\mathrm{neigh}}$ generally captured local effects of competition, but not for tree mortality in Africa. Nevertheless, also in models based on NCI, effects of competition on mortality were negligible (results not shown). We therefore included results for models that included BA_{neigh} only, based on data from all 151 plots.

Table S1. Comparison of individual-based tree growth and mortality models that varied in competition index for 86 plots in Amazonia (*n* = 44) and tropical Africa (*n* = 42) for which trees were mapped. Models were compared based on the Watanabe-Akaike Information Criterion (WAIC), with the difference from the best model (ΔWAIC) shown. Best models are indicated in bold. NCI = neighborhood crowding index; BA_{neigh} = basal area of neighbor trees per 0.04 ha subplot.

	Amazon		Africa	
	growth	mortality	growth	mortality
Competition index	ΔWAIC	ΔWAIC	ΔWAIC	ΔWAIC
none	1566	**0**	1079	384
NCI	177	437	761	**0**
BA_{neigh}	**0**	331	**0**	295

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