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Elias, F, Marimon, BS, Marimon-Junior, BH et al. (5 more authors) (2018) Idiosyncratic soil-tree species associations and their relationships with drought in a monodominant Amazon forest. Acta Oecologica. pp. 127-136. ISSN 1146-609X

https://doi.org/10.1016/j.actao.2018.07.004

Idiosyncratic soil-tree species associations and their relationships with drought in a monodominant Amazon forest

Fernando Elias[1]; Beatriz Schwantes Marimon[1,2,3]*; Ben Hur Marimon-Junior[1,2,3]; Jean Carlos Budke[4]; Adriane Esquivel-Muelbert[5]; Paulo Sérgio Morandi[3]; Simone Matias Reis[3] and Oliver L. Phillips[5]

[1]Universidade do Estado de Mato Grosso, Programa de Pós-Graduação em Ecologia e Conservação, 78690-000, Nova Xavantina, Mato Grosso, Brasil.

[2]Universidade do Estado de Mato Grosso, Faculdade de Ciências Agrárias, Biológicas e Sociais Aplicadas, 78690-000, Nova Xavantina, Mato Grosso, Brasil.

[3]Rede Bionorte, Doutorado em Biodiversidade e Biotecnologia, Universidade do Estado de Mato Grosso, 78690-000, Nova Xavantina, Mato Grosso, Brasil.

[4]Universidade Regional Integrada do Alto Uruguai e das Missões, Programa de Pós-Graduação em Ecologia, 99700-000, Erechim-RS, Brasil.

[5]School of Geography, University of Leeds, LS2 9JT, Leeds, UK.

*Corresponding author: B.S. Marimon, Universidade do Estado de Mato Grosso, Programa de Pós-Graduação em Ecologia e Conservação, Caixa Postal 08, 78690-000, Nova Xavantina, Mato Grosso, Brasil. Phone +55 66 3438 1224. E-mail: biamarimon@unemat.br

E-mail addresses: fernandoeliasbio@gmail.com (F. Elias), biamarimon@unemat.br (B.S. Marimon), bhmarimon@unemat.br (B.H. Marimon-Junior), jean@uricer.edu.br (J.C. Budke), adriane.esquivel@gmail.com (A. Esquivel-Muelbert), morandibio@gmail.com (P.S. Morandi), simonematiasreis@gmail.com (S.M. Reis), O.Phillips@leeds.ac.uk (O.L. Phillips).

Abstract

Monodominant forests are characterized by the strong influence of a single species on the structure and diversity of the community. In the tropics, monodominant forests are rare exceptions within the generally highly diverse tropical forest biome. Some studies have shown that tree monodominance may be a transient state caused by successional and demographic variation among species over time. Working in a Brosimum rubescens Taub. (Moraceae) monodominant forest at the southern edge of Amazonia, we tested the hypotheses that local-scale variation in intra- and interspecific spatial patterns of dominant tree species is affected by i) demographic rates of recruitment and mortality following severe droughts, ii) local variation in edaphic properties, and iii) occupation of species in the vertical layer of the forest. We quantified intra- and interspecific spatial patterns and edaphic associations of the five most abundant species using aggregation and association distance indices, and examined changes over time. We found some support for all hypotheses. Thus, intra- and interspecific spatial patterns of most species varied over time, principally after severe drought, emphasizing species-level variability and their interactions in sensitivity to this disturbance, even as B. rubescens monodominance was maintained. While positive and negative spatial associations with edaphic properties provide evidence of habitat specialization, the absence of negative spatial associations of B. rubescens with edaphic properties indicates that this species experiences little environmental restriction, and this may be one of the factors that explain its monodominance. Spatial repulsion and attraction between species in the same and in different vertical layers, respectively, indicates niche overlap and differentiation, while changes over time indicate that the relationships between species are dynamic and affected by drought disturbance.

Keywords: Brosimum rubescens; Competition; Janzen-Connell; Niche; Spatial patterns.

1. Introduction

Tropical forest plant communities are usually characterized by very high diversity (Gentry, 1988; Clinebell et al., 1995). Yet, many tropical forests are dominated by an ‘oligarchic suite’ of relatively few tree species at local scales (e.g., Pitman et al., 2013) even when regional floras run to thousands of species (ter Steege et al., 2013). These dominance patterns have been tentatively related to climatic and edaphic conditions (ter Steege et al., 2013; Lloyd et al., 2015), as well as to the competitive ability of particular species (Pitman et al., 2001). A particular extreme case of dominance in tropical forests is found across the transition zone between Cerrado and the Amazon rainforest biomes, where continuous forest patches with monodominance of Brosimum rubescens Taub. (Moraceae) are occasionally found (Marimon et al., 2001a, 2001b), particularly in the eastern part of Mato Grosso state in Brazil. In these monodominant patches, diversity and species richness is extremely low when compared to the adjacent forests (Marimon et al., 2016). Up to 80% of the aboveground biomass is found within the single dominant taxon, and fewer than ten species together make up to 90% of biomass (Marimon et al., 2001a, 2001b).

The exact causes of tropical monodominance remain elusive, in spite of considerable effort (Torti et al., 2001; Peh et al., 2011a, 2011b; Marimon et al., 2016). Nevertheless, a potentially key finding may be that monodominance emerges when normal processes of ecological succession and recovery of alpha diversity are greatly slowed (Peh et al., 2011a; Newberry et al., 2013). In this case, the monodominance can persist for a long period of time even in periods of marked disturbances (Ibanez and Birnbaum, 2014), although why this may be is unclear. Within Amazonia and potentially throughout the tropics, drought is a major disturbance driver, with important consequences for forest structure and dynamics (Phillips et al., 2009; Bennett et al., 2015; Brienen et al., 2015; Doughty et al., 2015; Feldpausch et al., 2016) - and potentially also for species diversity as most moist forest species do not tolerate long dry seasons (Clinebell et al., 1995; Esquivel-Muelbert et al., 2016, 2017). Most notably over the past decade at least two major droughts have affected southern Amazonia (in 2005 and 2010, cf. Phillips et al., 2009; Lewis et al., 2011; Marengo et al., 2011), with additional unusual drying in Mato Grosso during 2007/2008 (Brando et al., 2008). These droughts have driven increases in mortality in Amazonia and elsewhere (e.g., Phillips et al., 2009, 2010; Brienen et al., 2015), and periodic drying may also be partly responsible for the 'hyperdynamic' nature of forests at the southern Amazon margin (Marimon et al., 2014). However, very little is known on how intra- and interspecific spatial patterns of species in monodominant forests respond over time to tropical drought. Here, evaluation of the spatial patterns of tree species might help to understand intrinsic demographic processes in these communities, as spatial patterns reflect different factors that act upon the survival of individuals (Getzin et al., 2014; Luo and Chen, 2015; Xie et al., 2015). For example, if monodominance is promoted by moisture stress (because relatively few tropical moist species thrive in more seasonal forests), then we would expect the dominants in these forests to respond positively to drought - or at least to be less adversely affected than their neighbours.

Drought is not the only factor capable of strongly impacting tropical tree distributions. For instance, the traditional Janzen-Connell (J-C) model proposes that after the initial establishment of species, density-dependent biotic processes reduce survival and intraspecific aggregation, thus tending towards spatial regularity of individuals and enhancing overall community diversity (Janzen, 1970; Connell, 1971). However, in tropical communities, these "J-C processes" might be disguised by the effect of environmental conditions and niche separation among life stages (Soliveres et al., 2010; Zhu et al., 2013; Xie et al., 2015), as habitat specialization and tolerance limits means that intraspecific aggregations of tree species are also determined by the spatial structuring of resources (Arieira et al., 2016). Notably, edaphic conditions comprise one of the most variable axes of the spatial niche, and are among the best predictors of distribution patterns of tree species (e.g., Harms et al., 2001; Phillips et al., 2003; Getzin et al., 2008). For instance, the ability to accumulate toxic elements such as aluminum and manganese in leaves can provide a localized competitive advantage for some species at sites with higher abundance of these elements (Haridasan, 2000), while species intolerant to those elements are likely to have distributions anti-correlated with the distribution of toxic metals and of metal-tolerators (Malavolta et al., 1997).

Naturally, as well as showing differing tolerances of stress factors, plant species compete with each other for essential resources needed for plant establishment, development, and reproduction, notably water, light, nutrients, and space (Barot and Gignoux, 2004). Therefore, for prolonged coexistence to occur there must be differentiation in some niche dimensions (Amarasekare, 2003), because niche similarity intensifies interspecific competition and consequently reinforces negative interactions among species (Zhang et al., 2010; Sühs and Budke, 2011). The separation of the species among vertical layers in forests indicates niche differentiation, since occupation of each layer is related to the functional characteristics of species, such as photosynthetic capacity (Ellsworth and Reich, 1993), leaf traits (Bündchen et al., 2015), growth (Enquist et al., 2011) and pollinator vectors (Yamamoto et al., 2007). Thus, species that occupy the same layer are more likely to compete with one-another and hence may be more likely to separate spatially in the horizontal dimension (Sühs and Budke, 2011). Conversely, if stochastic community processes such as extinction, speciation and limitation of dispersion then species patterns of spatial distribution are more likely to be stochastic in time and space (Chave and Leigh Jr., 2002; Hubbell, 2005).

Thus, assessing these multiple factors and their interactions over time is essential for understanding better the ecological patterns that regulate the distribution of species at different spatial scales in tropical forests. This study evaluates the effects of severe drought and of edaphic properties on intra- and interspecific spatial patterns of tree species over time in a monodominant forest in southern Amazonia. We tested the hypotheses that i) demographic rates (recruitment and mortality) after severe droughts, ii) spatial structure of edaphic properties, and iii) occupation of species in the vertical layer of the forest may each account for variation in intra- and interspecific spatial patterns of dominant tree species at the local scale.

2. Material and Methods

2.1. Study Area

This study was conducted in a semideciduous seasonal forest located at 14°50’47” S and 52°08’37” W, in the locality of Fazenda Veracruz, close to Nova Xavantina, in the eastern region of the state of Mato Grosso. This forest has been monitored using permanent plots since 1996, and is characterized by the monodominance of Brosimum rubescens Taub. (Moraceae), which locally dominates the forest biomass (Marimon et al., 2001a). The monodominant patch is found within the wider transition zone between the Amazon rainforest and Cerrado biomes (Marimon et al., 2001a, 2014).

The climate of the region is tropical with dry winter (Aw in the Köppen classification), with strong precipitation seasonality and two well-defined periods, rainy from October to March and dry from April to September (Alvares et al., 2013). Mean annual rainfall and temperature are ~1,500 mm and 24.7° C, respectively, and altitude ranges from 190 to 280 m (Marimon et al., 2001a). Severe droughts were experienced in the study area in 1998, 2005, 2007 and 2010 (Zeng et al., 2008; Lewis et al., 2011; Feldpausch et al., 2016).

The soil in the forest is a plintosol, being dystrophic, acidic, shallow, and with low cation-exchange capacity, base saturation, and Ca/Mg ratio (1:3). Gravel fraction is around 28% down to 10-cm depth, with intermediate K levels, and high proportion of Fe (Marimon et al., 2001a).

2.2. Data collection

In 1996, Marimon et al. (2001a) established 60 contiguous subplots of 10 x 10 m (0.6 ha) in the Brosimum rubescens patch, where all individuals with diameter at breast height ≥ 5 cm were measured and identified. In 2001, 2004, 2010, and 2013, all individuals were remeasured and those that reached the minimum limits (DBH ≥ 5 cm) were included in the sampling. Identification was performed in the field and by comparing samples to herbarium vouchers from Herbarium NX (UNEMAT-Nova Xavantina), UB (Universidade de Brasília), and from virtual herbaria (The New York Botanic Garden, Kew Garden, and CRIA). Nomenclature of taxa was reviewed according to the List of Flora Species of Brazil (BFG, 2015), and botanical classification followed the APG IV (2016). Data used in this study are stored in 'ForestPlots.net' digital platform (Lopez-Gonzalez et al., 2011).

Detailed information on the chemical and physical properties of the soil are found in Marimon et al. (2001a), who collected random samples of surface soil (0–10 cm depth) in each 10 x 10 m subplot. Percentage gravel was determined by sieving particles through a sieve with 2 mm mesh, and pH was determined by soil-water suspension (ratio soil: water 1:2.5; Anderson and Ingram, 1993). Exchangeable Ca, Mg, and Al concentrations were determined in 1 mol L^{-1} KCl (Sumner and Miller, 1996) and P, K, Fe, Mn, Cu, and Zn contents in Mehlich-I solution (0.0125 mol L^{-1} + HCl 0.05 mol L^{-1}; Nelson et al., 1953).

2.3. Data analysis

We selected the five tree species with the highest absolute density in the first inventory (1996) distributed between the overstory (Brosimum rubescens Taub. – Moraceae and Tetragastris altissima (Aubl.) Swart – Burseraceae) and understory strata (Amaioua guianensis Aubl. – Rubiaceae, Cheiloclinium cognatum (Miers) A.C.Sm. – Celastraceae, and Protium pilosissimum Engl. – Burseraceae). We compared the density of these species among inventories

(1996, 2001, 2004, 2010, and 2013) using ANOVA of repeated measures and using Tukey's multiple comparison as a post hoc (Zar, 2010) in the R program using the 'stats' package (R Development Core Team, 2016). Assumptions of residual normality and variance homogeneity were checked using the Shapiro-Wilk’s and Bartlett’s tests, respectively (Zar, 2010).

To assess variation in demographic rates in each species among inventories, we calculated mean annual mortality and recruitment rates - hereafter mortality and recruitment - based on the abundance of species for different diameter classes (Sheil et al., 1995). We standardize the best interval between the diameter classes by the formula IC = A/K (A= amplitude of values; K= Sturges’ constant) (Spiegel, 1976). Here, the formula guarantees proportionality in the distribution of individuals among diameter classes. We square-root transformed mortality and recruitment values among diameter classes and subsequently plotted them in frequency histograms. We compared mean annual mortality and recruitment rates of diameter classes for each species (1996-2001, 2001-2004, 2004-2010, and 2010-2013) using the Wilcoxon test, and between periods using Friedman’s and Dunn’s as post hoc tests (Zar, 2010) in the R program using package ‘stats’ (R Development Core Team, 2016). To evaluate the influence of density (fixed effect) of each species on the mortality rate over time, we use linear mixed effect models (GLMM) (Zuur et al., 2009) in the R program using ‘lme4’ package (Bates et al., 2013). Outliers that exceeded the maximum limit of 3 SD (standard deviation) were excluded from the model using ‘outliers’ package (Komsta, 2015). Because they are measures repeated in space and time, we use the subplots as a random effect in the GLMM models. The assumptions of the GLMM were verified by graphical analysis (Zuur et al., 2009).

We described the intraspecific spatial patterns of species and edaphic properties among inventories using the Aggregation Index - Spatial Analysis by Distance Indices – SADIE (Perry, 1995, 1998). In order to define aggregation, the index estimates distance from regularity (D), i.e., the distance individuals from a population must travel between sampling units (subplots) so that both units have the same density. In this case, sampling units with higher D values have higher aggregation and those with lower D values have lower aggregation, and it is possible to evaluate the partial contribution of gaps and aggregates to the overall spatial pattern of the population. We performed kriging of the species spatial distribution in each inventory with the Surfer program (Golden Software, 1999). Aggregation Index values higher or lower than 1, when significant, indicate aggregation and regularity, respectively, whereas non-significant values indicate randomness (Perry, 1995, 1998).

We described interspecific spatial patterns of species (i.e., the spatial associations of each species to each other, and to edaphic properties) using the SADIE Association Index (Perry, 1997; Perry et al., 1999). Based on Pearson's correlations, this index calculates pair overlap of two datasets and varies from +1 (positive association, $p < 0.025$) to -1 (negative association, $p > 0.975$). Thus, when there is spatial association (two-tailed p-values), high values of the association index indicate a high relation between the spatial distribution of the species (or with the characteristics of the soil). Positive associations are characterized by the spatial overlap between two species, in other words, occurs when there is spatial coincidence between the aggregates and the gaps of both species. In contrast, negative associations are observed when clusters and gaps are not coincident in space and, therefore, generate negative association index values (cf. Perry et al., 1999). The significance of Aggregation and Association Indexes values was evaluated using Monte Carlo permutations (Perry, 1998). Calculations of Aggregation and Association Indices were performed using the software SADIEShell 1.2 (Perry et al., 1996; Perry, 1998). For all analyses, we used an alpha level of 5%.

3. Results

3.1. Intraspecific spatial patterns and population demography

The mortality and recruitment rates of the species in the subplots did not show significant variation over time (Figure 1). However, within diameter classes, density, mortality and recruitment rates did vary by years, mainly after the severe 2005, 2007 and 2010 droughts (Figs. 2, 3; Table 1). Thus, both Amaioua guianensis and Brosimum rubescens had significantly reduced total densities in the final two inventories (Fig. 3). Notably, the mortality rate among the diameter classes of A. guianensis exceeded recruitment in 2004-2010 and 2010-2013, excluding all individuals with diameter larger than 20.1 cm (Fig. 2). Brosimum rubescens also lost individuals over time but remained strongly dominant. The relative density of A. guianensis, B. rubescens, C. cognatum, P. pilosissimum and T. altissima in the final inventory was 6.9, 39.9, 10.3, 24.8 and 9.7%, respectively. Brosimum rubescens also had strong recruitment among almost all diameter classes in the final period (Fig. 2; Table 1). The species T. altissima and C. cognatum did not vary significantly in density between inventories (Fig. 3). However, from 2010 to 2013, mortality of C. cognatum, mainly in larger size classes, outnumbered recruitment (Fig. 2; Table 1). Mortality and recruitment rates among diameter classes of P. pilosissimum and T. altissima did not show significant variation among the periods analyzed (Fig. 2; Table 1). Yet, P. pilosissimum had the greatest proportional variation in density among inventories, with net gains of 51, 32, and 23% in the censuses of 2001, 2004, and 2010, respectively compared to the first inventory (Figs. 2, 3; Table 1). In the final inventory, after the 2010 drought, this species accumulated losses of 13% in number of individuals, mainly those of larger diameter classes (Figs. 2, 3; Table 1). In addition, mortality of all species evaluated was positively related with density in the subplots (Table A.1).

The five most abundant species varied in how their individuals are distributed locally. Brosimum rubescens and Protium pilosissimum maintained random and aggregated spatial patterns among inventories, respectively, in spite of experiencing variations in density (Figs. 3, 4, A.1). The other three species showed variations in intraspecific spatial patterns among inventories, mainly after the severe drought in 2010 (Figs. 4, A.1). Amaioua guianensis had aggregated distribution in the first four inventories, and random distribution in 2013, while Tetragastris altissima showed spatial randomness in the first three inventories and aggregation in 2010 and 2013 (Figs. 4, A.1). On the other hand, spatial distribution of Cheiloclinium cognatum was random in 1996 and 2001, and regular in 2004. After the 2005-2007 droughts, the intraspecific distribution of C. cognatum returned to the random pattern of the two first inventories (Figs. 4, A.1).

3.2. Spatial relationships of species vs. edaphic properties

We observed significant spatial associations between the dominant tree species and edaphic properties, as well as changes in these relationships over time (Table 2; Figs. A.1, A.2). The two most abundant species in the study area, Brosimum rubescens and Protium pilosissimum, were positively associated with Ca, K, Mn and Ca/Mg, and showed no negative spatial relationships with any edaphic properties. B. rubescens was exclusively associated with Al, and P. pilosissimum was associated with Mg, Cu, pH, and gravel (Table 2; Figs. A1, A.2). Amaioua guianensis showed negative association with Ca, Mg, K, Zn, Ca/Mg, and gravel, and positive association with Fe (Table 2). However, in the last inventory, after the 2010 drought, these spatial associations were not observed. Conversely, spatial associations of Cheiloclinium cognatum and Tetragastris altissima only started to occur in the last two inventories; C. cognatum showed negative associations with Ca, P, and Al, and positive associations with pH. In turn, T. altissima was positively associated with Ca, Mg, K, Mn, Cu, Zn, pH, and gravel (Table 2; Fig. A1).

3.3. Interspecific spatial patterns of species

Differences in interspecific spatial associations are related to the position of the species in the vertical layers of the forest (Table 3; Fig. A.1). For example, two typical understory species, Amaioua guianensis and Protium pilosissimum, were negatively associated in space in the first three inventories (1996, 2001, and 2004) prior to the droughts of 2005, 2007 and 2010 (Table 3; Fig. A.1). These species show distinct associations with overstory species: A. guianensis was negatively associated with Tetragastris altissima in 2010, and P. pilosissimum was positively associated with Brosimum rubescens in nearly all inventories (Table 3; Fig. A.1). Likewise, the overstory species, B. rubescens and T. altissima, were negatively associated between 2001 and 2004 (Table 3; Fig. A.1).

4. Discussion

Our results show that spatial patterns of dominant species are subject to changes according to changes in demography after intense drought events, and partly reflect spatial structure of soil properties in the habitat and the position of the species in the forest strata, providing support to each of our initial hypotheses. Nevertheless, the monodominance and spatial pattern of Brosimum rubescens were maintained over time, even with variations in density after the intense drought events of 2005 and 2010, demonstrating the strong resistance and resilience of the species. The absence of negative spatial associations of B. rubescens with edaphic characteristics indicates lack of environmental restriction here, and this may help to explain the maintenance of its monodominance in the study area.

4.1. Intraspecific spatial patterns and demography

The dominant tree species show variation in intraspecific spatial patterns over time, consistent with demographic oscillations related to severe droughts, corroborating our initial hypothesis. This result shows the heterogeneity and spatial dynamics of forest communities, as well as the different strategies used by species to occupy space, may vary over time. For instance, the decrease in aggregation towards spatial randomness of Amaioua guianensis might be related to variations in density over time and to the initial proportions of individuals among life stages. In this case, the self-thinning process which recruits experience as their life stages advance may have been intensified by severe droughts, as observed by Johnson et al. (2014) and Clyatt et al. (2016) in temperate forests. On the other hand, the fact that intraspecific spatial patterns of Brosimum rubescens and Protium pilosissimum were maintained among inventories, even while there were variations in density and demography, shows the robustness of the intraspecific distributions of these species, remaining unchanged even in the face of significant drought disturbance. Thus, the events that occurred in the study area may not have been sufficient to cause changes in the spatial distribution of these species, as observed by Elias et al. (2013) in a cerradão (savanna woodland).

The predominantly random spatial pattern of B. rubescens and the slightly decrease in total density over time is an indication that density-dependent mortality is the major determining factor of the spatial distribution of this species, and that this process has intensified over time. The unimodal height distribution of this species and its dominance in the canopy of the study area (Marimon et al., 2001a), suggest that most individuals are in the intermediate or advanced life stages, which are generally distributed randomly or regularly according to the Janzen-Connell model (Stoll and Bergius, 2005; Getzin et al., 2011; Clyatt et al., 2016). The J-C model also explains the spatial history of Cheiloclinium cognatum in the first three inventories, prior to the 2005 drought, when the species showed decrease in spatial randomness towards regularity. However, the fact that it returned to spatial randomness after the 2005 drought and that it maintained this pattern until the last inventory emphasizes the sensitivity of this species to this disturbance, as well as its recurrence over time. Similarly, the high mortality rates of C. cognatum, which exceeded recruitment over the latest periods, appear responsible for the changes and maintenance of random spatial patterns after droughts. Meanwhile, the increased recruitment of B. rubescens in the final inventories reveals a clear difference in the resilience capacity of this species and C. cognatum in the face of severe droughts. Considering the demographic dynamics of the main species and the resilience of B. rubescens after the drought events, we expect that the monodominance will be maintained in the long term even in the face of occasional disturbances.

The changes in Tetragastris altissima from random to aggregate spatial patterns after drought is an indication that this disturbance concentrated mortality at sites with higher water stress (Luo and Chen, 2015; Challis et al., 2016; Panayotov et al., 2016). This might have led to the aggregation of the surviving individuals, even under density-dependent effects, considering this pattern is more influenced by habitat than intraspecific associations (Luo et al., 2012; Arieira et al., 2016). Similar results were found by Elias et al. (2013) in a ‘savanna woodland’ in the transition zone between Amazon rainforest and Cerrado. These authors reported that droughts determine tree species aggregation over time, confirming the sensitivity of intraspecific spatial patterns to predict these disturbances, as suggested by Flugge et al. (2012).

4.2. Spatial relationships of species vs. edaphic properties

Positive spatial associations between tree species and the edaphic properties analyzed indicate the influence of habitat on spatial distribution patterns, and show that there is niche specialization among species. Positive spatial associations of Brosimum rubescens and Protium pilosissimum with Ca/Mg, Ca, K, and Mn demonstrate the wide niche range of these species and might justify their dominance in the study area. This is due to the fact that Ca and K are shown to be important modulators of tree species structure in tropical forests (Wright et al., 2011; Santiago et al., 2012; Lloyd et al., 2015), acting together with Mn in growth, carbohydrate transport, photosynthesis, gas exchanges, hormone control, and mainly, resistance to diseases (Malavolta et al., 1997). Therefore, the positive associations of species with these elements, mostly K, might favor reproductive success and high abundance in the study area. This corroborates the findings of Marimon et al. (2001b), who recorded high K and Mn concentrations in leaves of B. rubescens, which are generally consistent with concentrations at the soil level (Brady and Weil, 1996). In addition, the absence of negative associations between B. rubescens and edaphic properties indicates that the soils of the study area do not present restrictions to their establishment, and therefore favour the monodominance of the species.

Amaioua guianensis showed negative spatial association with Ca/Mg, Ca, Mg, K, and gravel indicating that its spatial distribution is independent of fertility parameters and that this species most likely prefers to occupy less drained locations. The soil A horizon in the study area is shallow (~80 cm) with high concentrations of hydromorphic laterites, which can impede drainage locally according to topographic position (Marimon-Junior, 2007). Botrel et al. (2002) also described negative relationships of species from the family Rubiaceae with soil drainage in a semi-deciduous seasonal forest of Southeastern Brazil. Hence, this result might be an indication of the sensitivity of understory species to water restrictions (Tobin et al., 1999), mainly in years of severe droughts recorded in the inventories over time (Zeng et al., 2008; Lewis et al., 2011). On the other hand, positive spatial associations of A. guianensis with Fe may indicate habitat preference linked to the benefits of this element in photosynthesis, production of leaves, and flowering (Belkhodja et al., 1998; Molassiotis et al., 2006). In this case, the positive spatial association with Fe might be a strategy to avoid reduced photosynthetic rates, since this species occurs in the understory and has restricted access to lighting. However, Protium pilosissimum (Burseraceae) shares the same forest layer with A. guianensis (Rubiaceae) and was not associated to this element. Recently, Souza et al. (2016) have shown that phylogenetic factors strongly control large-scale ecological variation in Amazon tree traits related to carbon cycling and storage (demography, size, and wood density), yet the extent to which phylogeny is a marker for variation in other nutrient processes in Amazon forests remains largely unknown. Our study suggests that, for Fe at least, marked phylogenetically-associated niche differentiation in nutritional requirements may exist at a remarkably fine spatial scale, even within the same vertical strata and hence the same light environment.

Temporal changes in spatial associations of species according to edaphic properties revealed marked spatial dynamics in the forest community, potentially related to population imbalance and niche partitioning among life stages, corroborating with our initial hypothesis. It thus appears that in our study site the relevance of edaphic properties in determining spatial patterns of tree species may depend on the ontogenetic stage of individuals. Other work in tropical ecosystems (Comita et al., 2007; Kanagaraj et al., 2011; Arieira et al., 2016) found that the relationship of tree species with habitat decreases with ontogenetic advancement due to the increase in intraspecific competition driven by density-dependent mortality. In our forest, the positive spatial associations of Tetragastris altissima with Ca, Mg, Mn, Cu, Zn, and pH, recorded only in the two last inventories, might be related to the intense demographic variations (e.g., mortality and recruitment) of this population in this period. In this case, mortality of individuals reduced intraspecific competition and led to greater spatial aggregation in the population. On the other hand, the negative spatial association of Cheiloclinium cognatum with Ca may be related to the direct competition with Protium pilosissimum and T. altissima were positively associated with this element among the inventories.

4.3. Interspecific spatial patterns

The marked negative spatial association between species of the same forest layer, such as Brosimum rubescens and Tetragastris altissima in the overstory, and Amaioua guianensis and Protium pilosissimum in the understory, is evidence of niche overlap. Elsewhere, similar lighting requirements might have induced competition among canopy species in a subtropical forest, determining spatial repulsion between their individuals (Sühs and Budke, 2011). Similarly, congeneric species in a temperate forest showed high level of interspecific competition intensified by trophic similarities between them (Zhang et al., 2010). Yet, equally, in our monodominant forest the positive association between species from different layers (e.g., B. rubescens and P. pilosissimum; T. altissima and A. guianensis) suggests local competitive exclusion. These positive and negative associations ensure that space sharing due to habitat specialization of species and is consistent with previous findings in forest ecosystems (Martínez et al., 2010; Lan et al., 2012; Liu and Slik, 2014). It is also possible that canopy species facilitate the establishment of understory species in the areas below their treetops (e.g., nurse effects), creating microenvironmental conditions that benefit positive interactions between them (Ren et al., 2008). This type of interaction is common among tree species and might be one of the determining factors of the high alpha-diversity found in tropical forests (Wright, 2002; Liu and Slik, 2014). Conversely, it has been observed that tree monodominance might also inhibit the establishment of understory species (Torti et al., 2001). In our study, the positive spatial associations between layers observed in this forest suggest that the understory species analyzed are specialists and adapted to this case of tree monodominance.

Changes in interspecific spatial associations of species among inventories might be related to growth and recruitment of individuals over time. Juveniles show higher positive spatial associations than negative compared to adults, which indicates that individuals in this life stage have a wider range of niches and higher regeneration capacity (Hao et al., 2007). This fact highlights the importance of the J-C effect, which changes interspecific spatial patterns of the species according to the size of individuals and to the scale analyzed (Hao et al., 2007; Getzin et al., 2014). Therefore, interspecific associations are subject to variations over time, according to the demographic oscillations of species (life stages), and represent the natural spatial dynamics of populations. Moreover, as observed in spatial distribution, these changes in interspecific spatial associations might be related to the droughts that occurred in the region in 2005, 2007 and 2010 (Zeng et al., 2008; Lewis et al., 2011; Feldpausch et al. 2016). Xie et al. (2015) observed that water stress increases positive associations in desert areas, and Miriti (2007) described changes in interspecific associations of bushes after a severe drought. Overall the changes in spatial associations over time suggest that drought disturbances have marked effects on the temporal and spatial relationships of tree species in Amazon forests.

5. Conclusions

Temporal changes in intra- and interspecific spatial patterns of species in a monodominant forest and their consistency with demographic variations after severe droughts emphasize the potential sensitivity of Amazon forest ecosystems to this disturbance. The spatial associations between species and edaphic properties analyzed here, as well as the maintenance of these relationships over time (e.g., Amaioua guianensis and gravel; Brosimum rubescens and K) indicate the relevance of habitat in determining intraspecific spatial patterns of tree species. However, the absence of negative spatial associations for the monodominant species B. rubescens suggests that the species is not subject to any edaphic restrictions for establishment, and this helps to explain the maintenance of the monodominance. The marked spatial repulsion and attraction between species in the same layer (e.g., A. guianensis and P. pilosissimum) and between those from different layers (e.g., B. rubescens and P. pilosissimum) suggests that structural arrangements of species assemblages in Amazon forests are determined, respectively, by niche similarity and differentiation patterns. Overall, while monodominance was not favoured by drought, the maintenance of the spatial patterns of B. rubescens and P. pilosissimum also demonstrate resilience of this system in the face of severe droughts, as their monodominance persisted.

Author contributions

FE and BSM conceived the study and wrote the manuscript. FE, BSM, BHMJr and OLP designed the study. JCB, AEM, PSM and SMR contributed to data analysis. All authors apart from JCB and AEM collected field data, and all contributed to editing, commented and approved the manuscript.

Acknowledgements

We are grateful to Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the master's scholarship granted to the first author, and to Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Fundação de Amparo à Pesquisa do Estado de Mato Grosso (FAPEMAT) for funding the Long Term Ecological Research (PELD) project (Stage I, Process 558069/2009-6; Stage II, Proc. 403725/2012-7; and Proc. 164131/2013-FAPEMAT) and PPBio (Proc. 457602/2012-0). We are also grateful to CNPq for research productivity grants (PQ-2) to BHMJ and BSM, and for Doctorate Sandwich grants (207405/2015-4; 207405/2015-8) to PSM and SMR. OP is supported by a PVE award from CNPq-CsF (Proc. 401279/2014-6 - Amazon transitions: developing a network to monitor vegetation and global change responses on-the-ground at the southern margins of Amazonia), an ERC Advanced Grant (291585, “T-FORCES”) and a Royal Society Wolfson Award.

References

Alvares, C.A., Stape, J.L., Sentelhas, P.C., de Moraes Gonçalves, J.L., Sparovek, G., 2013. Köppen’s climate classification map for Brazil. Meteorol. Zeitschrift 22, 711–728. doi:10.1127/0941-2948/2013/0507

Amarasekare, P., 2003. Competitive coexistence in spatially structured environments: A synthesis. Ecol. Lett. 6, 1109–1122. doi:10.1046/j.1461-0248.2003.00530.x

Anderson, J.M., Ingram, J.S.I., 1993. Tropical Soil Biology and Fertility: A Handbook of Methods, second ed., CAB Intern, Wallingford.

APG IV. Angiosperm Phylogeny Group., 2016. An update of the Angiosperm Phylogeny Group classification for the ordens and families of flowering plants: APG IV. Bot. J. Linn. Soc. 141, 339–436. doi:10.1046/j.1095-8339.2003.t01-1-00158.x

Arieira, J., Penha, J., Nunes da Cunha, C., Couto, E.G., 2016. Ontogenetic shifts in habitat-association of tree species in a neotropical wetland. Plant Soil 404, 219–236. doi:10.1007/s11104-016-2844-y

Barot, S., Gignoux, J., 2004. Mechanisms promoting plant coexistence: Can all the proposed processes be reconciled? Oikos 106, 185–192. doi:10.1111/j.0030-1299.2004.13038.x

Bates, D., Maechler, M., Bolker, B., Walker, S., 2013. lme4: Linear mixed-effects models using Eigen and S4.

Belkhodja, R., Sanz, M., Abad, J., 1998. Iron deficiency in peach trees: effects on leaf chlorophyll and nutrient concentrations in flowers and leaves. Plant Soil 203, 257–268. doi: 10.1023/A:1004373202458

Bennett, A.C., McDowell, N.G., Allen, C.D., Anderson-Teixeira, K.J., 2015. Larger trees suffer most during drought in forests worldwide. Nat. Plants 1, 15139. doi: 10.1038/NPLANTS.2015.139

BFG., 2015. Growing knowledge: An overview of Seed Plant diversity in Brazil. Rodriguesia 66, 1085–1113. doi:10.1590/2175-7860201566411

Botrel, R.T., Oliveira-Filho, A.T., Rodrigues, L.A., 2002. Influência do solo e topografia sobre as variações da composição florística e estrutura da comunidade arbóreo-arbustiva de uma floresta estacional semidecidual em Ingaí, MG. Rev. Bras. Bot. 25, 195–213.

Brady, N.C., Weil, R.R., 1996. The Nature and Properties of Soils, sixth ed., Prentice Hall, New Jersey.

Brando, P.M., Nepstad, D.C., Davidson, E.A., Trumbore, S.E., Ray, D., Camargo, P., 2008. Drought effects on litterfall, wood production and belowground carbon cycling in an Amazon forest: results of a throughfall reduction experiment. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 363, 1839–48. doi:10.1098/rstb.2007.0031

Brienen, R.J.W., Phillips, O.L., Feldpausch, T.R., Gloor, E., Baker, T.R., Lloyd, J., Lopez-Gonzalez, G., Monteagudo-Mendoza, A., Malhi, Y., Lewis, S.L., Vásquez Martinez, R., Alexiades, M., Álvarez Dávila, E., Alvarez-Loayza, P., Andrade, A., Aragão, L.E.O.C., Araujo-Murakami, A., Arets, E.J.M.M., Arroyo, L., Aymard C, G.A., Bánki, O.S., Baraloto, C., Barroso, J., Bonal, D., Boot, R.G.A., Camargo, J.L.C., Castilho, C. V, Chama, V., Chao, K.J., Chave, J., Comiskey, J.A., Cornejo Valverde, F., da Costa, L., de Oliveira, E.A., Di Fiore, A., Erwin, T.L., Fauset, S., Forsthofer, M., Galbraith, D.R., Grahame, E.S., Groot, N., Hérault, B., Higuchi, N., Honorio Coronado, E.N., Keeling, H., Killeen, T.J., Laurance, W.F., Laurance, S., Licona, J., Magnussen, W.E., Marimon, B.S., Marimon-Junior, B.H., Mendoza, C., Neill, D.A., Nogueira, E.M., Núñez, P., Pallqui Camacho, N.C., Parada, A., Pardo-Molina, G., Peacock, J., Peña-Claros, M., Pickavance, G.C., Pitman, N.C.A., Poorter, L., Prieto, A., Quesada, C.A., Ramírez, F., Ramírez-Angulo, H., Restrepo, Z., Roopsind, A., Rudas, A., Salomão, R.P., Schwarz, M., Silva, N., Silva-Espejo, J.E., Silveira, M., Stropp, J., Talbot, J., ter Steege, H., Teran-Aguilar, J., Terborgh, J., Thomas-Caesar, R., Toledo, M., Torello-Raventos, M., Umetsu, R.K., van der Heijden, G.M.F., van der Hout, P., Guimarães Vieira, I.C., Vieira, S.A., Vilanova, E., Vos, V.A., Zagt, R.J., 2015. Long-term decline of the Amazon carbon sink. Nature 519, 344–8. doi:10.1038/nature14283

Bündchen, M., Boeger, M.R., Reissmann, C.B., 2015. Estrutura foliar de espécies lenhosas de dossel e sub-bosque em uma fl oresta subtropical do sul do Brasil. Iheringia 70, 105–114.

Challis, A., Stevens, J.C., McGrath, G., Miller, B.P., 2016. Plant and environmental factors associated with drought-induced mortality in two facultative phreatophytic trees. Plant Soil. doi:10.1007/s11104-016-2793-5

Chave, J., Leigh Jr., E.G., 2002. A Spatially Explicit Neutral Model of b-Diversity in Tropical Forests. Theor. Popul. Biol. 62, 153–168. doi:10.1006/tpbi.2002.1597

Clinebell, R.R., Phillips, O.L., Gentry, A.H., Stark, N., Zuuring, H., 1995. Prediction of neotropical tree and liana species richness from soil and climatic data. Biodivers. Conserv. 4, 56–90. doi:10.1007/BF00115314

Clyatt, K.A., Crotteau, J.S., Schaedel, M.S., Wiggins, H.L., Kelley, H., Churchill, D.J., Larson, A.J., 2016. Historical spatial patterns and contemporary tree mortality in dry mixed-conifer forests. For. Ecol. Manage. 361, 23–37. doi:10.1016/j.foreco.2015.10.049

Comita, L.S., Condit, R., Hubbell, S.P., 2007. Developmental changes in habitat associations of tropical trees. J. Ecol. 95, 482–492. doi:10.1111/j.1365-2745.2007.01229.x

Connell, J.H., 1971: On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. in: den Boer, P.J., Gradwell, G.R. (Eds.), Dynamics of populations, Pudoc, Wageningen, pp.298–312.

Doughty, C.E., Metcalfe, D.B., Girardin, C.A.J., Amézquita, F.F., Cabrera, D.G., Huasco, W.H., Silva-Espejo, J.E., Araujo-Murakami, A., da Costa, M.C., Rocha, W., Feldpausch, T.R., Mendoza, A.L.M., da Costa, A.C.L., Meir, P., Phillips, O.L., Malhi, Y., 2015. Drought impact on forest carbon dynamics and fluxes in Amazonia. Nature 519, 78–82. doi:10.1038/nature14213

Elias, F., Marimon, B.S., Matias, S., Reis, D.A., Forsthofer, M., Morandi, P.S., Marimon-junior, B.H., 2013. Dinâmica da distribuição espacial de populações arbóreas, ao longo de uma década, em cerradão na transição Cerrado-Amazônia, Mato Grosso. Biota Amaz. 3, 1-14. doi:10.18561/2179-5746/biotaamazonia.v3n3p1-14

Ellsworth, D.S., Reich, P.B., 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. Oecologia 96, 169–178. doi:10.1007/BF00317729

Enquist, B.J., Enquist, C.A.F., 2011. Long-term change within a Neotropical forest: Assessing differential functional and floristic responses to disturbance and drought. Glob. Chang. Biol. 17, 1408–1424. doi:10.1111/j.1365-2486.2010.02326.x

Esquivel-Muelbert, A., Baker, T.R., Dexter, K.G., Lewis, S.L., ter Steege, H., Lopez-Gonzalez, G., Monteagudo Mendoza, A., Brienen, R., Feldpausch, T.R., Pitman, N., Alonso, A., van der Heijden, G., Peña-Claros, M., Ahuite, M., Alexiaides, M., Álvarez Dávila, E., Murakami, A.A., Arroyo, L., Aulestia, M., Balslev, H., Barroso, J., Boot, R., Cano, A., Chama Moscoso, V., Comiskey, J.A., Cornejo, F., Dallmeier, F., Daly, D.C., Dávila, N., Duivenvoorden, J.F., Duque Montoya, A.J., Erwin, T., Di Fiore, A., Fredericksen, T., Fuentes, A., García-Villacorta, R., Gonzales, T., Guevara Andino, J.E., Honorio Coronado, E.N., Huamantupa-Chuquimaco, I., Killeen, T.J., Malhi, Y., Mendoza, C., Mogollón, H., Jørgensen, P.M., Montero, J.C., Mostacedo, B., Nauray, W., Neill, D., Vargas, P.N., Palacios, S., Palacios Cuenca, W., Pallqui Camacho, N.C., Peacock, J., Phillips, J.F., Pickavance, G., Quesada, C.A., Ramírez-Angulo, H., Restrepo, Z., Reynel Rodriguez, C., Paredes, M.R., Sierra, R., Silveira, M., Stevenson, P., Stropp, J., Terborgh, J., Tirado, M., Toledo, M., Torres-Lezama, A., Umaña, M.N., Urrego, L.E., Vasquez Martinez, R., Gamarra, L.V., Vela, C.I.A., Vilanova Torre, E., Vos, V., von Hildebrand, P., Vriesendorp, C., Wang, O., Young, K.R., Zartman, C.E., Phillips, O.L., 2017. Seasonal drought limits tree species across the Neotropics. Ecography 40, 618–629. doi:10.1111/ecog.01904

Esquivel-Muelbert, A., Galbraith, D., Dexter, K.G., Baker, T.R., Lewis, S.L., Meir, P., Rowland, L., Costa, A.C.L. da, Nepstad, D., Phillips, O.L., 2017. Biogeographic distributions of neotropical trees reflect their directly measured drought tolerances. Sci. Rep. 7, 8334. doi:10.1038/s41598-017-08105-8

Feldpausch, T.R., Phillips, O.L., Brienen, R.J.W., Gloor, E., Lloyd, J., Lopez-Gonzalez, G., Monteagudo-Mendoza, A., Malhi, Y., Alarcón, A., Álvarez Dávila, E., Alvarez-Loayza, P., Andrade, A., Aragao, L.E.O.C., Arroyo, L., Aymard C., G.A., Baker, T.R., Baraloto, C., Barroso, J., Bonal, D., Castro, W., Chama, V., Chave, J., Domingues, T.F., Fauset, S., Groot, N., Honorio Coronado, E., Laurance, S., Laurance, W.F., Lewis, S.L., Licona, J.C., Marimon, B.S., Marimon-Junior, B.H., Mendoza Bautista, C., Neill, D.A., Oliveira, E.A., Oliveira dos Santos, C., Pallqui Camacho, N.C., Pardo-Molina, G., Prieto, A., Quesada, C.A., Ramírez, F., Ramírez-Angulo, H., Réjou-Méchain, M., Rudas, A., Saiz, G., Salomão, R.P., Silva-Espejo, J.E., Silveira, M., ter Steege, H., Stropp, J., Terborgh, J., Thomas-Caesar, R., van der Heijden, G.M.F., Vásquez Martinez, R., Vilanova, E., Vos, V.A., 2016. Amazon forest response to repeated droughts. Global Biogeochem. Cycles 30, 964–982. doi:10.1002/2015GB005133

Flügge, A.J., Olhede, S.C., Murrell, D.J., 2012. The memory of spatial patterns: changes in local abundance and aggregation in a tropical forest. Ecology 93, 1540–1549. doi:10.1890/11-1004.1

Gentry, A.H., 1988. Tree species richness of upper Amazonian forests. Proceedings of the National Academy of Sciences 85, 156–159. doi:10.1073/pnas.85.1.156

Getzin, S., Wiegand, T., Hubbell, S.P., 2014. Stochastically driven adult-recruit associations of tree species on Barro Colorado Island. Proc. Natl. Acad. Sci. 281, 20140922. doi:10.1098/rspb.2014.0922

Getzin, S., Wiegand, T., Wiegand, K., He, F., 2008. Heterogeneity influences spatial patterns and demographics in forest stands. J. Ecol. 96, 807–820. doi:10.1111/j.1365-2745.2007.0

Getzin, S., Worbes, M., Wiegand, T., Wiegand, K., 2011. Size dominance regulates tree spacing more than competition within height classes in tropical Cameroon. Journal of Tropical Ecology 27, 93–102. doi:10.1017/S0266467410000453

Golden Software, I., 1999. Surfer 7.0. Contouring and 3D surface mapping for scientist’s engineers. User’s guide.

Hao, Z., Zhang, J., Song, B., Ye, J., Li, B., 2007. Vertical structure and spatial associations of dominant tree species in an old-growth temperate forest. For. Ecol. Manage. 252, 1–11. doi:10.1016/j.foreco.2007.06.026

Haridasan, M., 2000. Nutrição mineral de plantas nativas do cerrado. Revista Brasileira de Fisiologia Vegetal 12, 54–64. doi:10.1111/j.1558-5646.2009.00942.x

Harms, K.E., Condit, R., Hubbell, S.P., Foster, R.B., 2001. Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. J. Ecol. 89, 947–959. doi:10.1046/j.0022-0477.2001.00615.x

Hubbell, S., 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. Funct. Ecol. 19, 166–172. doi:10.1111/j.0269-8463.2005.00965.x

Ibanez, T., Birnbaum, P., 2014. Monodominance at the rainforest edge: case study of Codia mackeeana (Cunoniaceae) in New Caledonia. Australian Journal of Botany 62, 4, 312–321.

Janzen, D.H., 1970. Herbivores and the number of tree species in Tropical Forests. Am. Nat. 104, 501–528. doi:10.1086/282687

Johnson, D.J., Bourg, N.A., Howe, R., McShea, W.J., Wolf, A., Clay, K., 2014. Conspecific negative density-dependent mortality and the structure of temperate forests. Ecology 95, 2493–2503. doi:10.1890/13-2098.1

Kanagaraj, R., Wiegand, T., Comita, L.S., Huth, A., 2011. Tropical tree species assemblages in topographical habitats change in time and with life stage. J. Ecol. 99, 1441–1452. doi:10.1111/j.1365-2745.2011.01878.x

Komsta, L., 2015. A collection of some tests commonly used for identifying outliers. R package version 0.14.

Lan, G., Getzin, S., Wiegand, T., Hu, Y., Xie, G., Zhu, H., Cao, M., 2012. Spatial distribution and interspecific associations of tree species in a tropical seasonal rain forest of China. PLoS One 7, e46074. doi:10.1371/journal.pone.0046074

Lewis, S.L., Brando, P.M., Phillips, O.L., van der Heijden, G.M.F., Nepstad, D., 2011. The 2010 Amazon drought. Science 331, 554. doi:10.1126/science.1200807

Liu, J.J., Slik, J.W.F., 2014. Forest fragment spatial distribution matters for tropical tree conservation. Biol. Conserv. 171, 99–106. doi:10.1016/j.biocon.2014.01.004

Lloyd, J., Domingues, T.F., Schrodt, F., Ishida, F.Y., Feldpausch, T.R., Saiz, G., Quesada, C.A., Schwarz, M., Torello-Raventos, M., Gilpin, M., Marimon, B.S., Marimon-Junior, B.H., Ratter, J.A., Grace, J., Nardoto, G.B., Veenendaal, E., Arroyo, L., Villarroel, D., Killeen, T.J., Steininger, M., Phillips, O.L., 2015. Edaphic, structural and physiological contrasts across Amazon Basin forest-savanna ecotones suggest a role for potassium as a key modulator of tropical woody vegetation structure and function. Biogeosciences 12, 6529–6571. doi:10.5194/bg-12-6529-2015

Lopez-Gonzalez, G., Lewis, S.L., Burkitt, M., Phillips, O.L., 2011. ForestPlots.net: A web application and research tool to manage and analyse tropical forest plot data. J. Veg. Sci. 22, 610–613. doi:10.1111/j.1654-1103.2011.01312.x

Luo, Y., Chen, H.Y.H., 2015. Climate change-associated tree mortality increases without decreasing water availability. Ecol. Lett. 18, 1207–1215. doi:10.1111/ele.12500

Luo, Z., Mi, X., Chen, X., Ye, Z., Ding, B., 2012. Density dependence is not very prevalent in a heterogeneous subtropical forest. Oikos 121, 1239–1250. doi:10.1111/j.1600-

Malavolta, E., Vitti, G.C., Oliveira, S.A., 1997. Avaliação do estado nutricional das plantas. second ed., Associação Brasileira para Pesquisa do Potássio e do Fosfato, Piracicaba.

Marengo, J.A., Tomasella, J., Alves, L.M., Soares, W.R., Rodriguez, D.A., 2011. The drought of 2010 in the context of historical droughts in the Amazon region. Geophys. Res. Lett. 38, L12703. doi:10.1029/2011GL047436

Marimon, B.S., Felfili, J.M., Haridasan, M., 2001a. Studies in monodominant forests in eastern Mato Grosso, Brazil: I. A forest of Brosimum rubescens Taub. Edinburgh J. Bot. 58, 123–137. doi:10.1017/S096042860100049X

Marimon, B.S., Felfili, J.M., Haridasan, M., 2001b. Studies in monodominant forests in eastern Mato Grosso, Brazil: II. A forest in the Areões Xavante Indian Reserve. Edinburgh J. Bot. 58, 483–497. doi:10.1017/S0960428601000798

Marimon, B.S., Felfili, J.M., Marimon-Junior, B.H., Fagg, C.W., da Silveira Anacleto, T.C., Umetsu, R.K., Lenza, E., Batista, J.D., Rossete, A.N., 2016. Leaf herbivory and monodominance in a Cerrado-Amazonia transitional forest, Mato Grosso, Brazil. Plant Biosystems 150, 124–130. doi: 10.1080/11263504.2014.983577

Marimon, B.S., Marimon-Junior, B.H., Feldpausch, T.R., Oliveira-Santos, C., Mews, H.A., Lopez-Gonzalez, G., Lloyd, J., Franczak, D.D., de Oliveira, E.A., Maracahipes, L., Miguel, A., Lenza, E., Phillips, O.L., 2014. Disequilibrium and hyperdynamic tree turnover at the forest–cerrado transition zone in southern Amazonia. Plant Ecol. Divers. 7, 281–292. doi:10.1080/17550874.2013.818072

Marimon-Junior, B.H., 2007. Relação entre diversidade arbórea e aspectos do ciclo biogeoquímico de uma floresta monodominante de Brosimum rubescens Taub. e uma floresta mista no leste Mato-Grossense. Universidade de Brasília, Brasília.

Miriti, M., 2007. Twenty years of changes in spatial association and community structure among desert perennials. Ecology 88, 1177–1190. doi:10.1890/06-1006

Molassiotis, A., Tanou, G., Diamantidis, G., Patakas, A., Therios, I., 2006. Effects of 4-month Fe deficiency exposure on Fe reduction mechanism, photosynthetic gas exchange, chlorophyll fluorescence and antioxidant defense in two peach rootstocks differing in Fe deficiency tolerance. J. Plant Physiol. 163, 176–185. doi:10.1016/j.jplph.2004.11.016

Nelson, W.L., Mehlich, A., Winters, E., 1953. The development, evaluation and use of soil tests for phosphorus availability. In: Pierre, W.H., Norman, A.G. (Eds.), Soil fertilizer phosphorus. Academic, New York, pp. 153–188.

Newbery, D. M., Van Der Burgt, X. M., Worbes, M., Chuyong, G. B. 2013. Transient dominance in a central African rain forest. Ecol. Mon. 83, 3, 339–382. doi:10.1890/12-1699.1

Panayotov, M., Kulakowski, D., Tsvetanov, N., Krumm, F., Berbeito, I., Bebi, P., 2016. Climate extremes during high competition contribute to mortality in unmanaged self-thinning Norway spruce stands in Bulgaria. For. Ecol. Manage. 369, 74–88. doi:10.1016/j.foreco.2016.02.033

Peh, K.S., Lewis, S.L., Lloyd, J., 2011a. Mechanisms of monodominance in diverse tropical tree-dominated systems. J. Ecol. 99, 891–898. doi:10.1111/j.1365-2745.2011.01827.x

Peh, K.S.H., Sonké, B., Lloyd, J., Quesada, C.A., Lewis, S.L., 2011b. Soil does not explain monodominance in a Central African tropical forest. PLoS One 6, 2, e16996. doi:10.1371/journal.pone.0016996

Perry, J.N., 1995. Spatial Analysis by Distance Indices. J. Anim. Ecol. 64, 303–314. doi:10.2307/5892

Perry, J.N., 1997. Spatial association for counts of two species. Acta Jutl. 72, 149–170.

Perry, J.N., 1998. Measures of spatial pattern for counts. Ecology 79, 1008–1017. doi:10.1890/0012-9658

Perry, J.N., Bell, E.D., Smith, R.H., Woiwod, I.P., 1996. SADIE: software to measure and model spatial pattern. Asp. Appl. Biol. 46, 95–102.

Perry, J.N., Winder, L., Holland, J.M., Alston, R.D., 1999. Red-blue plots for detecting clusters in count data. Ecol. Lett. 2, 106–113. doi:10.1046/j.1461-0248.1999.22057.x

Phillips, O.L., Aragao, L.E.O.C., Lewis, S.L., Fisher, J.B., Lloyd, J., Lopez-Gonzalez, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C.A., van der Heijden, G., Almeida, S., Amaral, I., Arroyo, L., Aymard, G., Baker, T.R., Banki, O., Blanc, L., Bonal, D., Brando, P., Chave, J., de Oliveira, A.C.A., Cardozo, N.D., Czimczik, C.I., Feldpausch, T.R., Freitas, M.A., Gloor, E., Higuchi, N., Jimenez, E., Lloyd, G., Meir, P., Mendoza, C., Morel, A., Neill, D.A., Nepstad, D., Patino, S., Penuela, M.C., Prieto, A., Ramirez, F., Schwarz, M., Silva, J., Silveira, M., Thomas, A.S., Steege, H. t., Stropp, J., Vasquez, R., Zelazowski, P., Davila, E.A., Andelman, S., Andrade, A., Chao, K.-J., Erwin, T., Di Fiore, A., C., E.H., Keeling, H., Killeen, T.J., Laurance, W.F., Cruz, A.P., Pitman, N.C.A., Vargas, P.N., Ramirez-Angulo, H., Rudas, A., Salamao, R., Silva, N., Terborgh, J., Torres-Lezama, A., 2009. Drought sensitivity of the Amazon rainforest. Science 80, 323, 1344–1347. doi:10.1126/science.1164033

Phillips, O.L., Núñez Vargas, P., Monteagudo, A.L., Cruz, A.P., Zans, M.E.C., Sánchez, W.G., Yli-Halla, M., Rose, S., 2003. Habitat association among Amazonian tree species: A landscape-scale approach. J. Ecol. 91, 757–775. doi:10.1046/j.1365-2745.2003.00815.x

Phillips, O.L., van der Heijden, G., Lewis, S.L., López-González, G., Aragão, L.E.O.C., Lloyd, J., Malhi, Y., Monteagudo, A., Almeida, S., Dávila, E.A., Amaral, I., Andelman, S., Andrade, A., Arroyo, L., Aymard, G., Baker, T.R., Blanc, L., Bonal, D., de Oliveira, Á.C.A., Chao, K.J., Cardozo, N.D., da Costa, L., Feldpausch, T.R., Fisher, J.B., Fyllas, N.M., Freitas, M.A., Galbraith, D., Gloor, E., Higuchi, N., Honorio, E., Jiménez, E., Keeling, H., Killeen, T.J., Lovett, J.C., Meir, P., Mendoza, C., Morel, A., Vargas, P.N., Patiño, S., Peh, K.S.H., Cruz, A.P., Prieto, A., Quesada, C.A., Ramírez, F., Ramírez, H., Rudas, A., Salamão, R., Schwarz, M., Silva, J., Silveira, M., Ferry Slik, J.W., Sonké, B., Thomas, A.S., Stropp, J., Taplin, J.R.D., Vásquez, R., Vilanova, E., 2010. Drought-mortality relationships for tropical forests. New Phytol. 187, 631–646. doi:10.1111/j.1469-8137.2010.03359.x

Pitman, N.C.A., Silman, M.R., Terborgh, J.W., 2013. Oligarchies in Amazonian tree communities: a ten-year review. Ecography 36, 114–123. doi:10.1111/j.1600-0587.2012.00083.x

Pitman, N.C.A., Terborgh, J.W., Silman, M.R., Núñez, P. V., Neill, D.A., Cerón, C.E., Palacios, W.A., Aulestia, M., 2001. Dominance and distribution of tree species in upper Amazonian terra firme forests. Ecology 82, 2101–2117. doi:10.1890/0012-9658(2001)082[2101:DADOTS]2.0.CO;2

R Development Core Team. 2016. R Development Core Team. R A Lang. Environ. Stat. Comput.

Ren, H., Yang, L., Nan, L. 2008. Nurse plant theory and its application in ecological restoration in lower subtropics of China. Progress in Natural Science 18, 137-142. doi: 10.1016/j.pnsc.2007.07.008

Santiago, L.S., Wright, S.J., Harms, K.E., Yavitt, J.B., Korine, C., Garcia, M.N., Turner, B.L., 2012. Tropical tree seedling growth responses to nitrogen, phosphorus and potassium addition. J. Ecol. 100, 309–316. doi:10.1111/j.1365-2745.2011.01904.x

Sheil, D., Burslem, D.F.R.P., Alder, D., 1995. The Interpretation and Misinterpretation of Mortality Rate Measures. J. Ecol. 83, 331–333. doi:10.2307/2261571

Soliveres, S., DeSoto, L., Maestre, F.T., Olano, J.M., 2010. Spatio-temporal heterogeneity in abiotic factors modulate multiple ontogenetic shifts between competition and facilitation. Perspectives in Plant Ecology, Evolution and Systematics 12, 227–234. doi:10.1016/j.ppees.2010.02.003

Souza, F.C., Dexter, K.G., Phillips, O.L., Brienen, R.J.W., Chave, J., Galbraith, D.R., Lopez Gonzalez, G., Monteagudo Mendoza, A., Pennington, R.T., Poorter, L., Alexiades, M., Álvarez-Dávila, E., Andrade, A., Aragão, L.E.O.C., Araujo-Murakami, A., Arets, E.J.M.M., Aymard C, G.A., Baraloto, C., Barroso, J.G., Bonal, D., Boot, R.G.A., Camargo, J.L.C., Comiskey, J.A., Valverde, F.C., de Camargo, P.B., Di Fiore, A., Elias, F., Erwin, T.L., Feldpausch, T.R., Ferreira, L., Fyllas, N.M., Gloor, E., Herault, B., Herrera, R., Higuchi, N., Honorio Coronado, E.N., Killeen, T.J., Laurance, W.F., Laurance, S., Lloyd, J., Lovejoy, T.E., Malhi, Y., Maracahipes, L., Marimon, B.S., Marimon-Junior, B.H., Mendoza, C., Morandi, P., Neill, D.A., Vargas, P.N., Oliveira, E.A., Lenza, E., Palacios, W.A., Peñuela-Mora, M.C., Pipoly, J.J., Pitman, N.C.A., Prieto, A., Quesada, C.A., Ramirez-Angulo, H., Rudas, A., Ruokolainen, K., Salomão, R.P., Silveira, M., Stropp, J., ter Steege, H., Thomas-Caesar, R., van der Hout, P., van der Heijden, G.M.F., van der Meer, P.J., Vasquez, R. V., Vieira, S.A., Vilanova, E., Vos, V.A., Wang, O., Young, K.R., Zagt, R.J., Baker, T.R., 2016. Evolutionary heritage influences Amazon tree ecology. Proc. R. Soc. B Biol. Sci. 283, 20161587. doi:10.1098/rspb.2016.1587

Spiegel, M.P., 1976. Estatística. Mc Graw-Hill, São Paulo.

Stoll, P., Bergius, E., 2005. Pattern and process: Competition causes regular spacing of individuals within plant populations. J. Ecol. 93, 395–403. doi:10.1111/j.1365-2745.2005.00989.x

Sühs, R.B., Budke, J.C., 2011. Spatial distribution, association patterns and richness of tree species in a seasonal forest from the Serra Geral formation, southern Brazil. Acta Bot. Brasilica 25, 605–617. doi:10.1590/S0102-33062011000300014

Sumner, M.E., Miller, W.P., 1996. Cation exchange capacity and exchange coefficients. in: Sparks, D.L., Page, A.L., Helmke, P.A., Loeppert, R.H., Soltanpour, P.N., Tabatabai, M.A., Johnston, C.T. (Eds.), Methods of Soil Analysis. Part. 3. Chemical Methods. Soil Science Society of America, Madison, pp. 1201–1229.

ter Steege, H., Pitman, N.C.A., Sabatier, D., Baraloto, C., Salomao, R.P., Guevara, J.E., Phillips, O.L., Castilho, C. V., Magnusson, W.E., Molino, J.-F., Monteagudo, A., Nunez Vargas, P., Montero, J.C., Feldpausch, T.R., Coronado, E.N.H., Killeen, T.J., Mostacedo, B., Vasquez, R., Assis, R.L., Terborgh, J., Wittmann, F., Andrade, A., Laurance, W.F., Laurance, S.G.W., Marimon, B.S., Marimon, B.-H., Guimaraes Vieira, I.C., Amaral, I.L., Brienen, R., Castellanos, H., Cardenas Lopez, D., Duivenvoorden, J.F., Mogollon, H.F., Matos, F.D. d. A., Davila, N., Garcia-Villacorta, R., Stevenson Diaz, P.R., Costa, F., Emilio, T., Levis, C., Schietti, J., Souza, P., Alonso, A., Dallmeier, F., Montoya, A.J.D., Fernandez Piedade, M.T., Araujo-Murakami, A., Arroyo, L., Gribel, R., Fine, P.V.A., Peres, C.A., Toledo, M., Aymard C., G.A., Baker, T.R., Ceron, C., Engel, J., Henkel, T.W., Maas, P., Petronelli, P., Stropp, J., Zartman, C.E., Daly, D., Neill, D., Silveira, M., Paredes, M.R., Chave, J., Lima Filho, D. d. A., Jorgensen, P.M., Fuentes, A., Schongart, J., Cornejo Valverde, F., Di Fiore, A., Jimenez, E.M., Penuela Mora, M.C., Phillips, J.F., Rivas, G., van Andel, T.R., von Hildebrand, P., Hoffman, B., Zent, E.L., Malhi, Y., Prieto, A., Rudas, A., Ruschell, A.R., Silva, N., Vos, V., Zent, S., Oliveira, A.A., Schutz, A.C., Gonzales, T., Trindade Nascimento, M., Ramirez-Angulo, H., Sierra, R., Tirado, M., Umana Medina, M.N., van der Heijden, G., Vela, C.I.A., Vilanova Torre, E., Vriesendorp, C., Wang, O., Young, K.R., Baider, C., Balslev, H., Ferreira, C., Mesones, I., Torres-Lezama, A., Urrego Giraldo, L.E., Zagt, R., Alexiades, M.N., Hernandez, L., Huamantupa-Chuquimaco, I., Milliken, W., Palacios Cuenca, W., Pauletto, D., Valderrama Sandoval, E., Valenzuela Gamarra, L., Dexter, K.G., Feeley, K., Lopez-Gonzalez, G., Silman, M.R., 2013. Hyperdominance in the Amazonian Tree Flora. Science 342, 1243092–1243092. doi:10.1126/science.1243092

Tobin, M.F., Lopez, O.R., Kursar, T.A, 1999. Responses of tropical understory plants to a severe drought: tolerance and avoidance of water stress. Biotropica 31, 570–578. doi:10.1111/j.1744-7429.1999.tb00404.x

Torti, S.D., Coley, P.D., Kursar, T.A. 2001. Causes and consequences of monodominance in tropical lowland forests. Am. Nat. 157, 2, 141-153. doi:10.1086/318629

Wright, S.J., 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia 130, 1–14. doi:10.1007/s004420100809

Wright, S.J., Joseph B. Yavitt, Wurzburger, N., Turner, B.L., Tanner, E.V.J., Sayer, E.J., Santiago, L.S., Kaspari, M., Hedin, L.O., Harms, K.E., Garcia, M.N., Corre, M.D., Reviewed, P., Wright, S.J., Joseph B. Yavitt, Wurzburger, N., Turner, B.L., Tanner, E.V.J., Sayer, E.J., Santiago, L.S., Kaspari, M., Hedin, L.O., Harms, K.E., Garcia, M.N., Corre, M.D., 2011. Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. Ecology 92, 1616–1625. doi:http://dx.doi.org/10.1890/10-1558.1

Xie, L., Guo, H., Gabler, C.A., Li, Q., Ma, C., 2015. Changes in spatial patterns of Caragana stenophylla along a climatic drought gradient on the Inner Mongolian Plateau. PLoS One 10, e0121234. doi:10.1371/journal.pone.0121234

Yamamoto, L.F., Kinoshita, L.S., Martins, F.R., 2007. Síndromes de polinização e de dispersão em fragmentos da Floresta Estacional Semidecídua Montana, SP, Brasil. Acta Bot. Brasilica 21, 553–573. doi:10.1590/S0102-33062007000300005

Zar, J.H., 2010. Biostatistical Analysis, Prentice Hall, New Jersey.

Zeng, N., Yoon, J.H., Marengo, J.A., Subramaniam, A., Nobre, C.A., Mariotti, A., Neelin, J.D., 2008. Causes and impacts of the 2005 Amazon drought. Environ. Res. Lett. 3, 014002. doi:10.1088/1748-9326/3/1/014002

Zhang, J., Song, B., Li, B.H., Ye, J., Wang, X.G., Hao, Z.Q., 2010. Spatial patterns and associations of six congeneric species in an old-growth temperate forest. Acta Oecologica 36, 29–38. doi:10.1016/j.actao.2009.09.005

Zhu, Y., Getzin, S., Wiegand, T., Ren, H., Ma, K., 2013. The relative importance of Janzen-Connell effects in influencing the spatial patterns at the Gutianshan subtropical forest. PLoS One 8, 1–8. doi:10.1371/journal.pone.0074560

Table 1. Comparison of mean annual mortality (M) and recruitment (R) rates of the diameter classes of the five most abundant species of trees evaluated among the periods 1996-2001, 2001-2004, 2004-2010, and 2010-2013, in a Brosimum rubescens Taub. monodominant forest in the transition zone Amazon rainforest-Cerrado. Acronyms: Amaioua guianensis (Ag); Brosimum rubescens (Br); Cheiloclinium cognatum (Cc); Protium pilosissimum (Pp), and Tetragastris altissima (Ta). The same uppercase and lowercase letters represent the same medians using the Wilcoxon and Friedman test (Dunn, post hoc). Uppercase letters= mortality x recruitment; lowercase letters= species.

	1996-2001		**2001-2004**		**2004-2010**		**2010-2013**	
Species	M	R	M	R	M	R	M	R
Ag	0.8Ab	1.5Aa	3.1ab	-	6.9Aab	0.0Ba	13.7Aa	2.8Ba
Br	1.6Aa	1.2Ab	3.2Aa	3.5Aab	3.9Aa	1.7Aab	5.4Aa	3.9Aa
Cc	2.2Aa	4.0Aa	4.1Aa	8.0Aa	5.5Aa	3.7Aa	10.1Aa	3.9Ba
Pp	7.1Aa	11.4Aa	12.6Aa	20.9Aa	10.1Aa	13.8Aa	12.6Aa	9.2Aa
Ta	1.5Aa	0.8Aa	0.9Aa	0.0Aa	2.2Aa	1.2Aa	6.4Aa	0.0Aa

Table 2. Spatial associations of species tree with edaphic properties over time (1996, 2001, 2004, 2010, and 2013) in a Brosimum rubescens Taub. monodominant forest in the transition zone Amazon rainforest-Cerrado, Brazil. The significance of the positive and negative (-) spatial associations is represented in bold (bimodal alpha = 0.05). Acronyms: Gravel (Gra); Amaioua guianensis (Ag); Brosimum rubescens (Br); Cheiloclinium cognatum (Cc); Protium pilosissimum (Pp), and Tetragastris altissima (Ta).

Species	Year	Ca/Mg	Ca	Mg	K	P	Fe	Mn	Cu	Zn	Al	pH	Gra
Ag	1996	**-0.50**	**-0.34**	**-0.32**	**-0.29**	-0.07	0.27	**-0.32**	-0.16	**-0.33**	-0.10	-0.13	**-0.29**
	2001	**-0.50**	**-0.39**	**-0.36**	**-0.28**	0.01	**0.29**	**-0.35**	-0.06	**-0.39**	0.06	-0.02	**-0.29**
	2004	**-0.49**	**-0.36**	-0.25	-0.22	0.02	**0.30**	-0.25	-0.07	**-0.36**	0.08	0.00	**-0.29**
	2010	**-0.25**	**-0.34**	**-0.34**	**-0.39**	-0.11	0.09	-0.23	-0.24	**-0.32**	0.04	-0.09	**-0.29**
	2013	0.06	-0.05	0.01	0.03	-0.23	-0.04	0.04	-0.11	-0.06	-0.05	0.17	-0.09
Br	1996	**0.40**	**0.31**	0.22	**0.40**	0.15	0.03	**0.34**	0.02	0.25	**0.29**	-0.15	0.19
	2001	**0.41**	**0.31**	0.24	**0.40**	0.12	-0.01	**0.35**	0.02	0.24	0.25	-0.10	0.13
	2004	**0.29**	0.23	0.19	**0.32**	0.11	0.08	**0.30**	0.01	0.13	0.24	-0.05	0.03
	2010	**0.33**	0.14	0.22	**0.35**	0.24	-0.01	0.23	-0.03	-0.01	**0.29**	-0.08	0.10
	2013	**0.32**	0.18	0.24	**0.39**	0.19	-0.00	**0.30**	-0.02	0.03	0.17	-0.00	0.24
Cc	1996	0.14	0.14	-0.06	-0.10	-0.17	-0.16	-0.06	-0.07	-0.27	-0.14	0.09	-0.03
	2001	0.17	-0.02	0.08	-0.02	-0.22	-0.27	0.05	-0.09	-0.08	-0.20	0.08	-0.08
	2004	0.16	-0.07	0.00	-0.03	-0.08	-0.16	-0.01	-0.14	-0.13	-0.12	0.01	-0.04
	2010	-0.15	-0.14	-0.08	-0.08	-0.27	-0.21	0.00	-0.17	-0.06	-0.10	0.05	-0.05
	2013	-0.20	**-0.36**	-0.21	-0.23	**-0.51**	-0.14	-0.20	0.02	-0.17	**-0.31**	**0.27**	-0.26
Pp	1996	**0.54**	**0.43**	**0.43**	**0.40**	0.11	-0.03	**0.45**	0.22	**0.29**	0.05	0.21	**0.34**
	2001	**0.48**	**0.53**	**0.54**	**0.47**	0.14	0.06	**0.57**	**0.30**	**0.41**	0.05	**0.28**	**0.44**
	2004	**0.62**	**0.54**	**0.50**	**0.45**	0.19	-0.07	**0.54**	0.17	**0.51**	0.13	0.11	**0.41**
	2010	**0.39**	**0.53**	**0.46**	**0.41**	0.09	0.00	**0.56**	0.23	**0.53**	0.12	0.20	**0.45**
	2013	**0.42**	**0.50**	**0.48**	**0.49**	0.06	0.18	**0.53**	0.22	**0.57**	0.12	0.17	**0.47**
Ta	1996	-0.04	0.04	0.10	0.05	-0.06	-0.27	0.03	0.20	0.26	-0.03	0.10	0.08
	2001	0.09	0.05	0.09	0.04	-0.11	-0.25	0.03	0.15	0.15	-0.10	0.08	0.04
	2004	0.10	0.01	0.02	-0.02	-0.17	-0.26	0.03	0.13	0.08	-0.13	0.20	0.07

2010	**0.26**	**0.32**	**0.35**	0.19	-0.08	-0.13	**0.37**	**0.29**	**0.33**	-0.11	**0.34**	0.23
2013	**0.31**	**0.55**	**0.56**	**0.45**	-0.02	-0.26	**0.54**	**0.26**	**0.51**	-0.04	**0.31**	**0.42**

Table 3. Interspecific spatial associations of the five most abundant species of trees over time (1996, 2001, 2004, 2010, and 2013) in a Brosimum rubescens Taub. monodominant forest in the transition zone Amazon rainforest-Cerrado, Brazil. Significant values of positive and negative (-) spatial associations are represented in bold (bimodal alpha = 0.05). Acronyms: Amaioua guianensis (Ag); Brosimum rubescens (Br); Cheiloclinium cognatum (Cc); Protium pilosissimum (Pp), and Tetragastris altissima (Ta).

	Inventories				
	1996	2001	2004	2010	2013
Ag-Br	-0.18	-0.20	-0.14	0.10	0.16
Ag-Cc	-0.02	-0.09	-0.12	0.22	0.21
Ag-Pp	**-0.59**	**-0.48**	**-0.55**	-0.19	-0.12
Ag-Ta	-0.20	-0.05	-0.00	**-0.31**	0.06
Br-Cc	-0.09	0.02	-0.02	-0.13	-0.02
Br-Pp	**0.26**	**0.31**	**0.35**	0.10	**0.26**
Br-Ta	-0.11	**-0.26**	**-0.35**	-0.12	-0.11
Cc-Pp	0.15	0.14	0.11	-0.24	-0.15
Cc-Ta	-0.14	0.13	0.11	0.02	-0.07
Pp-Ta	-0.23	-0.05	-0.09	0.17	0.15

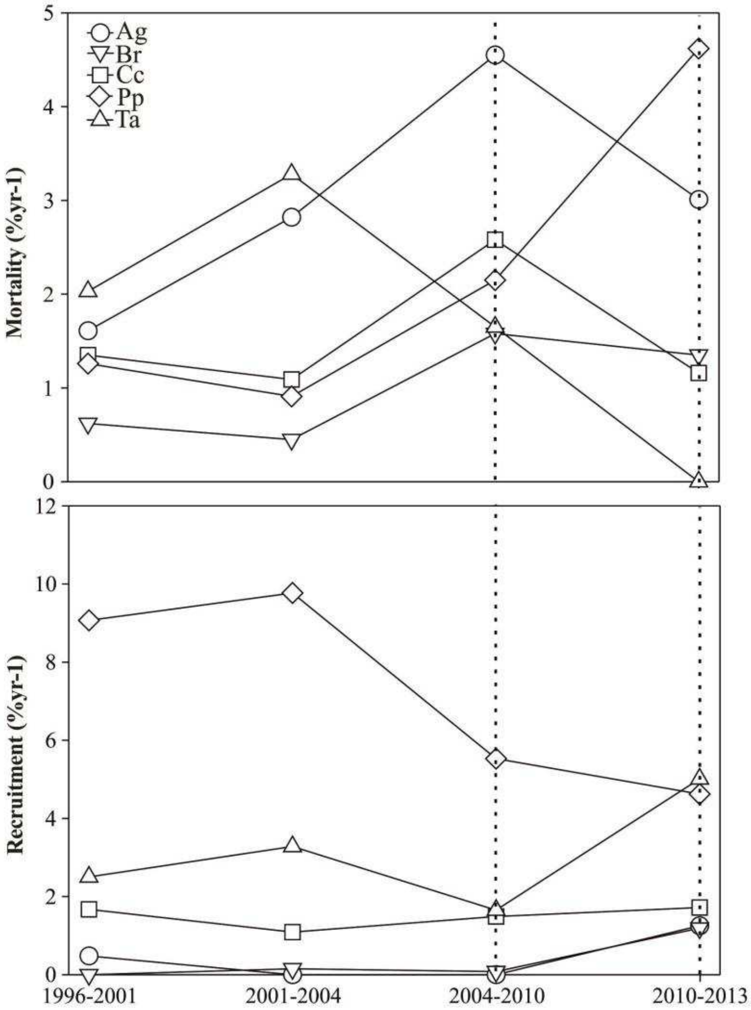

Figure 1. Mean annual rates of recruitment (lower panel) and mortality (top panel) of the five most abundant species of trees among the subplots in the periods 1996-2001, 2001-2004, 2004-2010, and 2010-2013, in a Brosimum rubescens Taub. monodominant forest in the transition zone Amazon rainforest-Cerrado, Brazil. No species varied significantly in mortality or recruitment rates among periods according to Repeated Measures ANOVA (p>0.05). Dashed lines indicate intense drought events. Acronyms: Amaioua guianensis (Ag); Brosimum rubescens (Br); Cheiloclinium cognatum (Cc); Protium pilosissimum (Pp), and Tetragastris altissima (Ta).

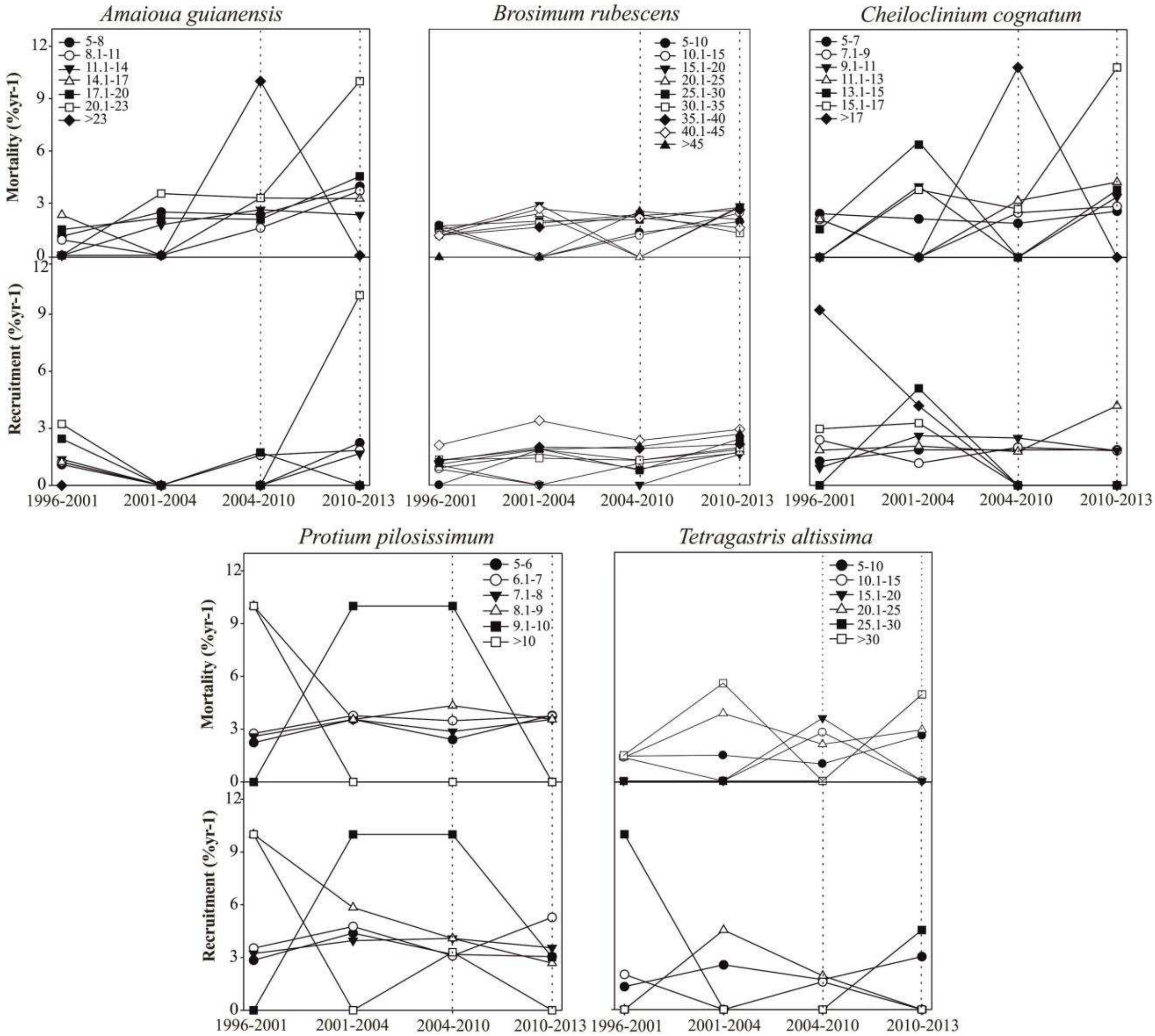

Figure 2. Mean annual mortality and recruitment rates of the five most abundant species of trees evaluated in different diameter classes (cm) in the periods 1996-2001, 2001-2004, 2004-2010, and 2010-2013, in a Brosimum rubescens Taub. monodominant forest in the transition zone Amazon rainforest-Cerrado. Dashed lines indicate intense drought events.

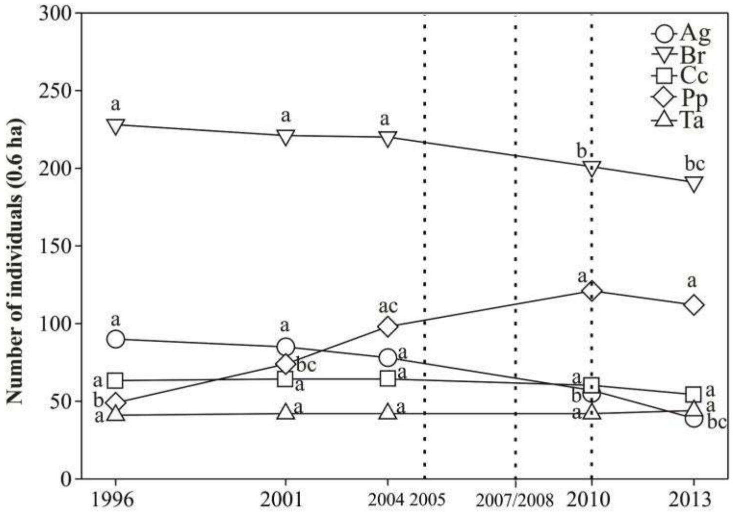

Figure 3. Number of individuals of the five most abundant species of trees over time (1996, 2001, 2004, 2010, and 2013) in a Brosimum rubescens Taub. monodominant forest in the transition zone Amazon rainforest-Cerrado, Brazil. Same letters represent significantly equal average density using ANOVA of repeated measures and Tukey's post hoc test. Dashed lines indicate intense drought events. Acronyms: Amaioua guianensis (Ag); Brosimum rubescens (Br); Cheiloclinium cognatum (Cc); Protium pilosissimum (Pp), and Tetragastris altissima (Ta).

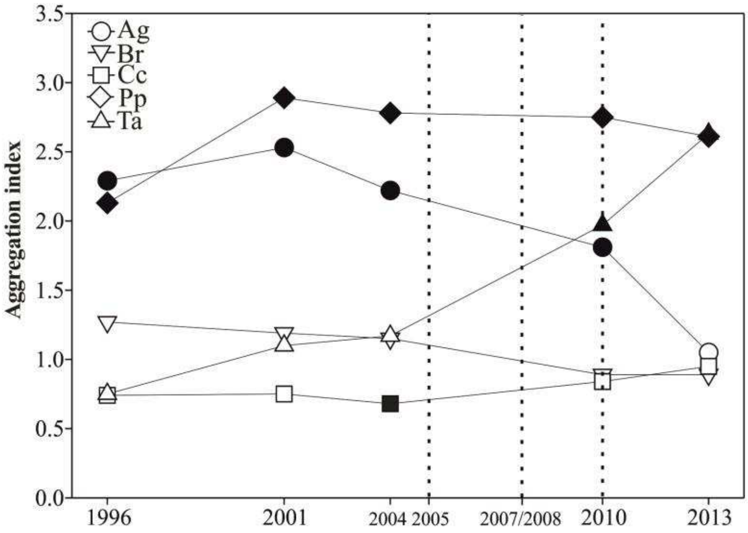

Figure 4. Spatial distribution of the five most abundant species of trees over time (1996, 2001, 2004, 2010, and 2013) in a Brosimum rubescens Taub. monodominant forest in the transition zone Amazon rainforest-Cerrado, Brazil. Significant Aggregation Index values (black) higher and lower than 1 indicates aggregation and regularity, respectively, whereas non-significant values (hollow) indicate randomness. Dashed lines indicate intense drought events. Acronyms: Amaioua guianensis (Ag); Brosimum rubescens (Br); Cheiloclinium cognatum (Cc); Protium pilosissimum (Pp), and Tetragastris altissima (Ta).

Supplementary material

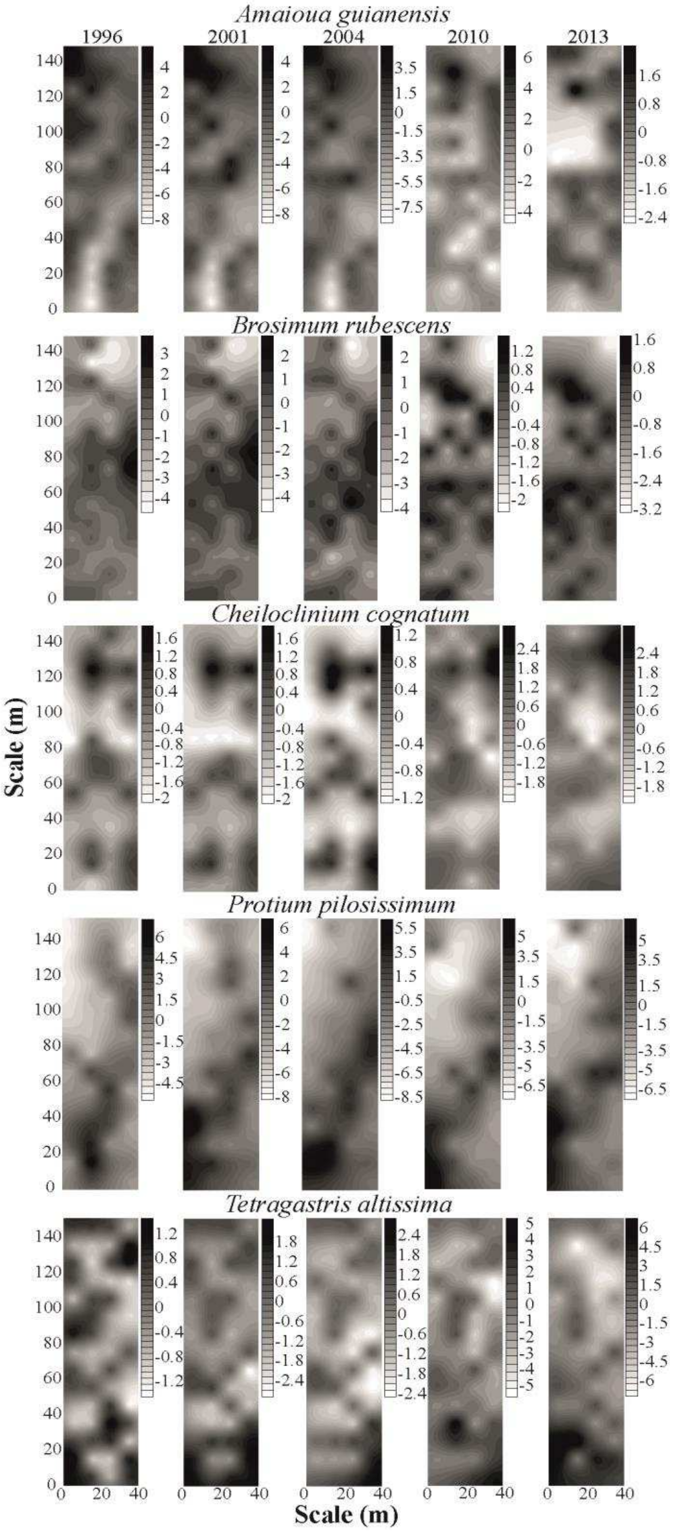

Figure A.1. Kriging maps of spatial distribution (aggregation index values) of the five most abundant species over time (1996, 2001, 2004, 2010, and 2013) in a Brosimum rubescens Taub. monodominant forest in the transition zone Amazon rainforest-Cerrado, Brazil.

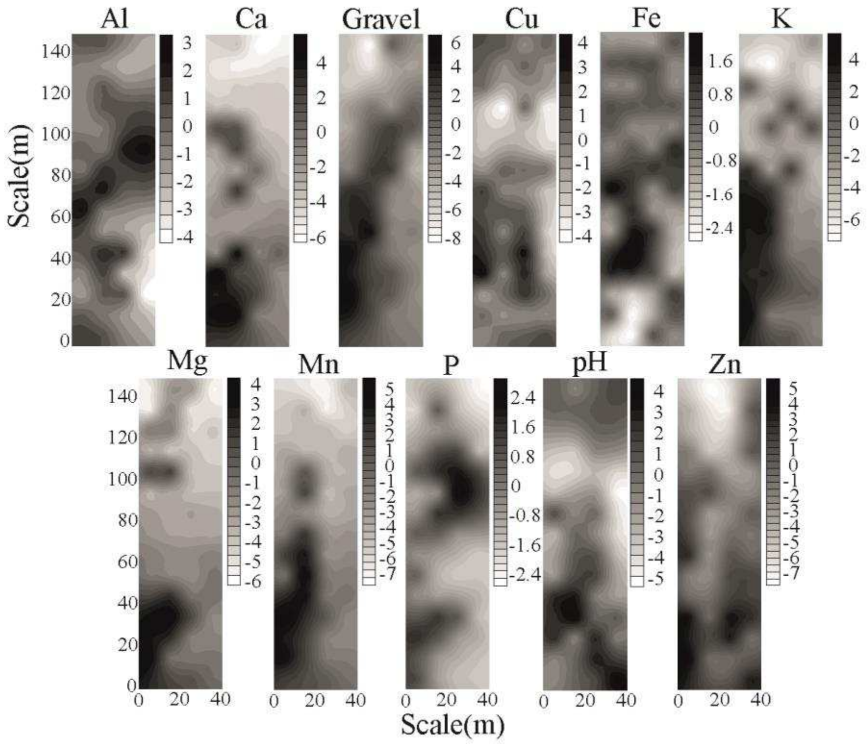

Figure A.2. Kriging maps of the spatial distribution (aggregation index values) of edaphic properties in a Brosimum rubescens Taub. monodominant forest in the transition zone Amazon rainforest-Cerrado, Brazil.

Table A.1. Predictions by linear mixed effects models (GLMM) for temporal variation (1996-2013) of mortality of the five species evaluated as a function of density, in a Brosimum rubescens Taub. monodominant forest in the transition zone Amazon rainforest-Cerrado, Brazil. The subplots represented the random effects.

	Estimate	**Std. Error**	**t**	**p-values**
(Intercept)	0.459	0.657	0.699	0.489
Amaioua guianensis	0.592	0.267	2.215	0.030
(Intercept)	-0.133	0.371	-0.36	0.719
Brosimum rubescens	0.232	0.088	2.631	0.009
(Intercept)	-0.466	0.394	-1.183	0.238
Cheiloclinium cognatum	0.904	0.238	3.793	0.000
(Intercept)	0.169	0.378	0.448	0.656
Protium pilosissimum	1.066	0.259	4.118	0.000
(Intercept)	-0.511	0.534	-0.957	0.340
Tetragastris altissima	0.907	0.388	2.337	0.020