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Drought generates large, long-term changes in tree and liana regeneration in a monodominant Amazon forest

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Abstract

The long-term dynamics of regeneration in tropical forests dominated by single tree species remains largely undocumented, yet is key to understanding the mechanisms by which one species can gain dominance and resist environmental change. We report here on the long-term regeneration dynamics in a monodominant stand of Brosimum rubescens Taub. (Moraceae) at the southern border of the Amazon forest. Here the climate has warmed and dried since the mid-1990's. Twenty-one years of tree and liana regeneration were evaluated in four censuses in 30 plots by assessing species abundance, dominance, and diversity in all regeneration classes up to 5 cm diameter. The density of B. rubescens seedlings declined markedly, from 85% in 1997 to 29% in 2018 after the most intense El Niño-driven drought. While the fraction contributed by other tree species changed little, the relative density of liana seedlings increased from just 1% to 54% and three-quarters of liana species underwent a ten-fold or greater increase in abundance. The regeneration community experienced a high rate of species turnover, with changes in the overall richness and species diversity determined principally by lianas, not trees. Long-term maintenance of monodominance in this tropical forest is threatened by a sharp decline in the regeneration of the monodominant species and the increase in liana density, suggesting that monodominance will prove to be a transitory condition. The close association of these rapid changes with drying indicates that monodominant B. rubescens forests are impacted by drought-driven changes in regeneration, and therefore are particularly sensitive to climatic change.

Keywords: drought • regeneration dynamics • saplings • seedlings • lianas.

Introduction

Tropical forests are renowned as being global centres of tree species richness and diversity (Connell et al. 1984; Gentry 1988). In general, tropical forests are also hyper-diverse at the local, community scale, with one hectare having as much as 30 times more tree species than an equivalent area in temperate forests (e.g., Gentry 1988; Condit et al. 1996; Torti et al. 2001). Such high alpha diversity typically pertains across the most extensive tropical forests of all in Amazonia (e.g., ter Steege et al. 2003), yet for some tropical forests the rule of high alpha-diversity does not hold. Across the tropics, several studies have reported 'monodominant' mature forests even on well-drained soils, in which one species may comprise from 50% to as much as 100% of the individuals and the total biomass (Connell and Lowman 1989; Marimon et al. 2001a; Peh et al. 2011b).

Several researchers have attempted to identify factors and mechanisms that enable a single species to reach and maintain monodominance in the tropics (e.g., Connell and Lowman 1989; Hart 1990; Torti et al. 2001; Marimon and Felfili 2006; Marimon et al. 2008, 2012, 2014; Peh et al. 2014; Nascimento et al. 2017; Elias et al. 2018). Peh et al. (2011b) discussed a total of eight hypotheses that have been proposed to explain the origin and maintenance of monodominance in tropical forests. They concluded that a variety of mechanisms likely interact to induce a species to attain monodominance locally, even when that species also grows in similar environmental conditions in adjacent mixed forests which have much greater tree diversity.

Meanwhile, it has long been appreciated that disturbance regimes can have a strong impact on tropical forest diversity; Connell's 'intermediate disturbance' hypothesis (Connell 1978), for example, suggests that there is an optimal level of disturbance frequency and intensity above and below which species diversity declines. Indeed disturbance regimes appear to be intimately associated with the phenomenon of monodominance (Tovar et al. 2019). Thus, while Ibanez and Birnbaum (2014) observed that monodominance can occasionally be a non-persistent state that occurs after severe disturbances ('early successional monodominance'), one of the factors most often hypothesised as responsible for favouring a species to reach monodominance is a long-term lack of large-scale disturbances (Connell and Lowman 1989; Hart 1990; Marimon et al. 2012). In this situation, species whose seedlings are able to grow under deep shade, and which also have high parental survivorship and potential to dominate canopies are expected to gain a long-term advantage. In all, multiple related biological traits and environmental characteristics are likely to be responsible for helping a species develop a monodominant state, including low gap formation frequency, strong interspecific competition, high parental survivorship and high survivorship under strong shading, litter characteristics, large seed size, and masting events (i.e., massive, infrequent seed production in regional synchrony with trees of the same species) (Connell and Lowman 1989; Hart 1990; Torti et al. 2001; Marimon and Felfili 2006; Peh et al. 2011b; Marimon et al. 2012; Hart 2012; Read et al. 2017; Henkel and Mayor 2019).

Evidently then most of the factors and mechanisms invoked in explanations of monodominance may be best evaluated through examining species regeneration (Connell and Lowman 1989; Read et al. 2017). For example, if diversity in tropical forests is normally maintained by compensatory mechanisms that benefit rare species (Connell et al. 1984), then monodominance may occur when regeneration mechanisms uncharacteristically instead favour common species and tree diversity remains low. More generally, evaluation of long-term regeneration dynamics should be able to determine whether changes in diversity occur in conjunction with changes in disturbance mechanisms, such as droughts, logging and anthropogenic climate change – all of which impact tree mortality, recruitment, carbon sequestration and species composition in Amazonia (Phillips et al. 2009; Costa et al. 2010; Brienen et al. 2015; Meir et al. 2015; Feldpausch et al. 2016; Esquivel-Muelbert et al. 2019). Yet studies of the stand dynamics of monodominant forest regeneration are difficult, extremely few, and so far have relied on single census inventories or short-term monitoring (c.f., Hart 1995; Marimon et al. 2012; Valverde-Berrantes and Rocha 2014).

As well as understanding species regeneration processes, exploring the ecological interactions between trees and lianas is also essential for understanding how tropical forests function (Caballé and Martin 2001; Comita et al. 2007). Lianas not only compete effectively with trees for water, light, space and nutrients (e.g., van der Heijden and Phillips 2009), but by contributing to gap formation they can accelerate processes of species substitution and forest dynamics (e.g., Phillips et al. 2005; van der Heijden and Phillips 2009; van der Heijden et al. 2013;

Magnago et al. 2017). Since lianas can grow almost ten times faster than trees during the dry season, they can also have a competitive advantage in forests subject to strongly seasonal environments (Schnitzer and Bongers 2011). If extreme events of drought and high temperature become more frequent (Fauset et al. 2012; Boisier et al. 2015) such climate changes could therefore drive large-scale increases in lianas. Indeed, the recent increases in Amazonian dry season intensity (e.g. Malhi et al. 2009; Gloor et al. 2013; Feldpausch et al. 2016; Esquivel-Muelbert et al. 2019) might help explain the increase in liana dominance that has been reported from many forests (e.g., Phillips et al. 2002; Nepstad et al. 2007; van der Heijden et al. 2013).

In Amazonia, one of the few species capable of attaining monodominant status is *Brosimum rubescens* Taub., a canopy tree in the Moraceae. *Brosimum* stands covered areas of up to 5,000 hectares, especially, until recently, in the transition zone between the two largest biomes in the continent, the Amazonian Forest and the Cerrado (savannah), in the Brazilian states of Mato Grosso, Pará and Tocantins (Marimon et al. 2001a, b, 2008, 2012, 2014). With large-scale regional deforestation for pasture and soya agriculture, and logging focussed on this species for use as fence-posts for pastures, today the *Brosimum*-dominated forests are few and small, restricted mostly to indigenous reserves and forest reserves on large farms. Typically the remaining patches of this unique habitat lack any management plan or any type of conservation action (Marimon et al. 2001a, b, 2008). Where *Brosimum* monodominant forests still occur they are situated in an area of particularly rapid recent climate change, and where future climates are expected to be warmer and drier (Costa et al. 2010, 2019). This climate change may already be inducing a regional acceleration of forest dynamics (Marimon et al. 2014; Elias et al. 2018), which could have the potential to radically alter the regeneration dynamics and liana dominance of the remaining intrinsically slow nutrient turnover monodominant systems (Torti et al. 2001; Peh et al. 2011a, b).

In the present study, we evaluated richness, species diversity and change of the regeneration in a monodominant *B. rubescens* forest over a 21-year period in the transition zone between the Cerrado and the Amazonian biomes. Because adult tree mortality in this patch has increased markedly over recent years, our main prediction was that the density of young individuals of *Brosimum* would have declined over time, while species diversity increased. We evaluated regeneration of woody plants over time and tested the hypotheses that after severe droughts density of the monodominant declines, and species composition changes. By including lianas as well as trees in our forest regeneration censuses we were able to investigate the role of lianas in forest regeneration. To our knowledge the present study represents by far the longest-running assessment of regeneration in monodominant forests to date anywhere in the tropics, and is the first attempt in such systems to explicitly account for the long-term regeneration of woody lianas as well as trees.

Materials and methods

Study site

The study was conducted in *Brosimum rubescens* monodominant forest located at 14º50’S and 52º10’W in a patch of about 1,000 ha inside an area bigger than 8,000 ha of the Vera Cruz Farm legal reserve. *Brosimum* dominates the forest biomass and comprises more than half of all individuals (Marimon 2005; Marimon et al. 2001a, 2014). This forest has been monitored since 1996 by the senior author using permanent plots. The climate is type Aw, according to Köppen’s classification, with a dry season from May to September and five to six months of rain (Alvares et al. 2013), leading to maximum cumulative water deficits (MCWD, Aragão et al. 2007) exceeding 400 mm in most years. Mean annual precipitation is 1432 mm and mean annual temperature 25°C. Severe droughts (here considered as total annual precipitation below 1,000 mm and with MCWD above 640 mm year^{-1}, were experienced in the study area in 2007-2008 and 2015-2016 (Feldpausch et al. 2016; Jiménez-Muñoz et al. 2016; Rifai et al. 2018), with a general trend of markedly increasing temperature and declining precipitation (more negative MCWD values) over the past 22 years (Fig. 1).

Data collection

In July 1997, within a permanent 1 ha plot, we established two parallel transects (10 m x 150 m) 10 m away from each other, each of which followed the gentle relief of the landscape so as to maintain the same altitude. Each transect was subdivided into 15 contiguous subplots of 10 m x 10 m each, where we counted and identified to species (or morphospecies) all individuals < 5 cm in dbh (diameter at breast height). Within these subplots we nested smaller plots to sample vegetation in different size classes, totaling 30 per class: 1 m × 1 m (seedlings: height $\leq$ 30 cm), 2 m × 2 m (saplings: > 30 cm to $\leq$ 60 cm), 5 m × 5 m (poles or young stems: > 60 cm to $\leq$ 200 cm) and 10 m × 10 m (treelets: height > 200 cm and diameter < 5 cm). To evaluate temporal regeneration dynamics the forest was resampled in July 2002, December 2010 and August 2018, using the same procedures, and the data from the two transects were grouped for each class. The same botanist and field leader (BSM) participated in all four inventories to ensure standardized identification of the species. We consider in the different size classes all species whose stems can reach diameters $\geq$ 5 cm, including woody lianas and palms.

Data analysis

To characterize the change in moisture stress, we calculated temporal trends in MCWD (Aragão et al. 2007). MCWD is an annual water deficit metric based only on climatic variables and for which the starting point each year is defined as the wettest month, when the soil is completely saturated. Climate data were obtained from the INMET (National Institute of Meteorology) meteorological station (World Weather Station 83319; inmet.gov.br), located in Nova Xavantina, Mato Grosso state, 25 km from the study area. Evapotranspiration data were based on Malhi et al. (2009).

We calculate Pielou’s evenness and Shannon diversity (H’) indices for each regeneration class (seedlings, saplings, poles and treelets) for each census using the `veganR` package (Oksanen et al. 2018), both when including (All= all species) and excluding lianas (WL= without lianas) from the analyses. In order to compare the species richness of all regeneration classes among the censuses, we used sample-based rarefaction curves (Gotelli and Colwell 2001) performed in the `BiodiversityR` package (Kindt and Coe 2005), and based on 9999 Monte Carlo permutations.

To evaluate changes in the species composition of the regeneration classes among censuses, we performed a permutation-based test of multivariate homogeneity of group dispersions (PERMDISP) on each distance matrix using ‘permutest.betadisper’ function in the `vegan` package (Oksanen et al. 2018). If one of the groups (here surveys) has a significantly higher mean distance, then this group has more dissimilar assemblages on average and greater beta diversity (Anderson et al. 2006). Euclidean distance among the groups was estimated in a Principal Coordinates Analysis (PCoA). The significance and pairwise comparisons of Betadisper’s groups were tested by a permutational multivariate analyses of variance – PERMANOVA (Anderson 2001; Anderson and Walsh 2013) based on 9999 permutations.

We tested the spatial autocorrelation on the abundance and richness in plots and subplots using Mantel Correlogram (Borcard and Legendre 2012) performed in the `ncf` package (Bjornstad 2018). To evaluate patterns in density of individuals in all regeneration classes between censuses we used repeated-measured ANOVA based in the `stats` package (`R` Core Team 2018). All statistical analyses and graphs were performed in software `R` 3.5.1 at 5% alpha-level (`R` Core Team 2018).

Results

For most size-classes rarefaction curves rapidly saturated (Supplementary Fig. S.1), indicating that the local woody regeneration community was effectively sampled. No spatial autocorrelation was detected for any regeneration class in any census. There were notable differences in diversity between censuses however. In particular, when we consider all species together, for both the seedling and treelet size-classes, species richness had significantly increased by 2018. Yet once lianas were removed from the analysis, in all four regeneration size classes tree species richness was maximal in 2002, and had declined substantially by the time of the inventories conducted after the 2007-2008 drought (2010) and the 2015-2016 drought (2018) (Supp. Fig. S.1).

When all regeneration size classes are treated together there was no obvious trend in species richness (Table 1). However, when we analyzed the data by each size class, we detected a marked increase in the species richness of seedlings and saplings between 1997 and 2018. Furthermore, in all regeneration size classes the proportion of liana species and liana abundance increased (Table 1). The increases in both absolute and relative abundance of lianas were particularly marked among the seedling and sapling classes, and particularly so in the latter censuses, with lianas contributing less than 1% of woody plant seedlings in 1997 but more than 50% of all woody plant seedlings by 2018.

Overall, the abundance of seedlings and saplings declined over the monitoring period, especially after the drought events. This was true whether analyses were conducted with or without lianas (Fig. 2). Nevertheless, the species richness of treelets (F= 49.67, *P*= 0.001), and the Shannon's diversity of treelets (F= 28.52, P= 0.001) and seedlings (F= 7.07, *P*= 0.006) were all higher after the 2015-2016 extreme drought event, but only significantly so when lianas are included (Fig. 2). Evenness varied between the regeneration classes, being lower in 2018 for poles (All: F= 12.56, *P*= 0.001; WL: F= 11.99, *P*= 0.002), higher in 2018 for seedlings (All: F= 12.01, *P*= 0.002; WL: F= 22.47, *P*= 0.001) and saplings (All: F= 6.61, *P*= 0.009; WL: F= 13.01, *P*= 0.001), while for treelets it did not change over the censuses (Fig. 2).

While total species richness varied little (Table 1), except for the treelet size class when lianas were included (cf Fig. 2), there was substantial species turnover through time for all regeneration classes (Supp. Fig. S.2). For instance we observed: (1) 13 species in the first survey that were not observed in the second; (2) 15 in the second that were not observed in the first; (3) 18 in the second not observed in the third; (4) 14 in the third not observed in the second; (5) eight in the third not observed in the fourth; and (6) 18 species in the fourth survey that were not observed in the third. This resulted in an average rate of change in species composition of nearly three species per year. Thus, while we find that overall species diversity was remarkably stable, species composition changed substantially, and this holds whether or not lianas are included in the analysis (Supp. Fig. S.2).

The most abundant species sampled in all regeneration classes in all four surveys were *Brosimum rubescens* Taub. (Moraceae), *Protium pilosissimum* Engl. (Burseraceae), *Ephedranthus parviflorus* S.Moore (Annonaceae), *Inga heterophylla* Willd. (Fabaceae), and *Myrciaria floribunda* (H.West ex Willd.) O.Berg (Myrtaceae). Other species, such as *Cheiloclinium cognatum* (Miers) A.C.Sm. (Celastraceae), *Protium altissimum* (Aubl.) Marchand (Burseraceae), and the liana, *Anthodon decussatus* Ruiz & Pav. (Celastraceae), were also well represented, but in some surveys did not appear in all regeneration classes. Among the most abundant species, the only one that increased in number of individuals in all regeneration classes and in all surveys was the liana *Anthodon decussatus.* We registered a total of 19 species of lianas in all regeneration classes and all surveys. Of these 16 increased by between 1 to 2,324 individuals/100 m^2 from the first (1997) to the last (2018) survey. Three-quarters of all liana species underwent a ten-fold or greater increase in the number of individuals.

Most of the changes observed for tree seedlings was due to a sharp decrease in the *Brosimum rubescens* population over time (Fig. 3). There were significantly more *B. rubescens* seedlings in the first census than in any other, with particularly low densities of seedlings and saplings by the time of the final two surveys (Fig. 3). Over the 21 year period, the proportion of *B. rubescens* seedlings as a fraction of the total population declined from 82% to 45%. In addition, *B. rubescens* seedlings as a fraction of the whole community declined from 85% in 1997 to just 29% in 2018. Part of this relative decline in *B. rubescens* seedlings was due to increase in the regeneration of ten liana species, which had only one seedling species and almost no seedling individuals in the first census, but represented 53.3% of the community’s total seedlings by 2018 (Table 1; Fig. 3). Between 1997 and 2018, the proportion of lianas of the combined regeneration in the forest increased from 1 to 37% (Table 1), with a significant increase in all regeneration classes (Fig. 3). The remarkable gains in liana seedling and sapling relative abundance is thus not only because lianas increased greatly, but also because there was in numerical terms an even bigger reduction of *B. rubescens* and other tree species in these classes (Fig. 3).

Discussion

Here we report the first long-term analyses of trends in the recruitment of a monodominant tropical forest. We found unexpectedly large changes, including a dramatic decline in dominance of the smaller size classes of *Brosimum rubescens*, and a compensatory shift towards dominance of the seedling community by lianas. The nature and the timing of the shifts and the length of the observation window is consistent with drought events inducing long-term shifts in the structure and floristic composition of the forest regeneration (seedlings, saplings, poles and treelets), particularly via increases in liana richness and abundance.

Differences in beta diversity over the years indicate that the regeneration component of the monodominant forest has been undergoing a shift in floristic composition, again with lianas playing a key and growing role. Thus the community richness and diversity of the regeneration classes in the forest changed significantly throughout time, especially comparing the first (1997) and last surveys (2018), and this occurred because nine species of lianas entered the community. Regardless of mortality patterns among larger trees (Meir et al. 2015; Elias et al. 2018), these changes in the regenerating cohorts could eventually drive the disappearance of species from the community as the floristic composition of juveniles will shape the woody community that reaches the canopy in coming years (Hart 1995; Schnitzer et al. 2000; Marimon et al. 2012, 2014).

We also find a sharp decline in the density of *Brosimum rubescens* among regenerating taxa. Such declines in principle might be attributable to several internal and external factors, including increases in drought frequency and intensity, air temperature, interspecific competition for resources, and human-induced disturbances among others (Feldpausch et al. 2016; Elias et al. 2018; Esquivel-Muelbert et al. 2019). While our study forest showed no signs of recent human-induced disturbance nor herbivory or disease outbreaks, it did experience substantial increases in temperature and declines in precipitation (more negative MCWD) especially between 2007 and 2017. Thus, we infer that the observed temporal change in regeneration of *B. rubescens* is associated with the recent, strong and repeated drought events (c.f. Marengo et al. 2011; Boisier et al. 2015; Brienen et al. 2015; Feldpausch et al. 2016; Esquivel-Muelbert et al. 2019) that in turn have long-term cumulative effects in diversity and richness of the whole community. Elsewhere, in north-eastern Amazonia, some species studied by Costa et al. (2010) during a seven year experimental drought showed similar rates of mature tree mortality as we reported here for *B. rubescens* regeneration. Observations from our site and elsewhere suggest that drought (1) negatively affects production and survivorship of monodominant species seeds, whose dispersion usually occurs at the dry-season peak, and (2) limits their germination, which occurs in the beginning of the rainy season, as persistent water deficits inhibit germination and so act as a regeneration filter in low rainfall years (Marimon and Felfili 2006). However, it is also possible that numbers at the initial survey (1996) were boosted partly by higher than normal rainfall in years prior to the first sampling (Marimon et al. 2012), or other factors such as interspecific competition may also affect recruitment. However even if *Brosimum* seedlings were boosted by earlier higher rainfall, we can be sure that this didn't happen again over the subsequent 21 years. Moreover, while reliable weather records locally only date to the 1990s, we know from other records in the oldest weather station of Mato Grosso, dating back to 1911 (Bombled 1976; Silva 2015; INMET 2019) that our monitoring period was climatically exceptional. The precipitation registered in Nova Xavantina in both the 2007 and 2015-16 droughts were unprecedented in terms of low rainfall in the recorded history of the region.

Some studies suggested that intense reproductive investment, mast-fruiting and exceptional seedling survival all tend to characterise monodominant species (Torti et al. 2001; Peh et al. 2011b; Henkel and Mayor 2019). Marimon and Felfili (2006) observed these same characteristics in *Brosimum rubescens*, and also suggested that this species has an episodic recruitment. These authors also observed that in 1997 there was a large seedling bank in the forest, probably originated from prior mast-fruiting events, thus is possible that drought mortality can have disproportionate impacts on the recruitment capacity of this species particularly if the drought occurs in the same year as the episodic recruitment. Elsewhere, in a Mediterranean environment, Pérez-Ramos et al. (2010) observed from a long-term data set and a rainfall exclusion experiment that mast-fruiting of *Quercus ilex* itself declined significantly under drier conditions, leading to negative consequences for recruitment.

Regardless of the cause, the decline in *B. rubescens* sapling density between the second (2002) and third survey (2010), and between the third and fourth surveys (2018) resulted from a lack of seedlings to replace individuals in this category, indicating that this species' size structure is unstable and that the population is declining. Notably, other, earlier studies of Neotropical monodominant forests found no such evidence for decline of the dominant. Both in a monodominant forest of *Peltogyne gracilipes* Ducke in northern Amazonia (Nascimento and Proctor 1997; Nascimento et al. 2014) and a gallery forest in central Brazil (Felfili 1997), the dominant taxon appeared to have a stable population, with large numbers of individuals in each class, a high density of seedlings, and a constant proportion among classes through time.

In contrast to the performance of our dominant, the density of seedlings of some other species increased through time. These winners included especially the liana species, which may be benefiting from the openness of the forest (Schnitzer et al. 2000) recorded in recent years after increased mortality of adult trees (Elias et al. 2018), but also the tree species *Protium altissimum*, whose seed production occurs in the middle of the rainy season (Marimon and Felfili 2006) when the forest is fully hydrated so that even in low rainfall periods seed production is less likely to be affected. Ultimately though, these species' populations may be controlled by competition from the monodominant for space and light, since the seedlings of *B. rubescens* are able to establish and survive under closed canopy. This enables this species to occupy the available understory sites and grow quickly when a canopy gap forms, suppressing the other competitors by limiting their space and available light (Marimon and Felfili 2006; Hirzel and Lay 2008). The competitive advantage of some liana species in drier conditions (Cai et al. 2009; Campanello et al. 2016) may lead to the replacement of *B. rubescens* (as clearly recorded for 2010 and 2018) by other species. Indeed elsewhere in the tropics, studies clearly show more liana infestation of trees in more seasonal climates and less rain, and potential for liana growth to be several times more rapid than trees in the dry season (De Walt et al. 2010; Toledo et al. 2011; Schnitzer and Bongers 2011). In addition to *B. rubescens*, the group of more abundant tree species also declined in number of individuals over the 21 years of study, indicating instability in their regeneration and suggesting that they too may be in decline as an oligarchy. Consistent with our findings and interpretation that this forest is undergoing drought-induced shifts in tree species composition, a recent Amazon-wide analysis of trees >10 cm diameter found that dry-affiliated genera have become more abundant and that small-statured non-pioneer taxa have decreased in abundance in the last 30 years (Esquivel-Muelbert et al. 2019). While drought is clearly capable of shifting Amazon tree communities (Costa et al. 2010; Meir et al. 2015), our analysis suggests that some monodominant forests may be particularly vulnerable to drought-induced shifts in the long-term.

The large increase in the proportion of liana seedlings in our forest may also be at least in part a consequence of changes in regional climate. In particular, the increase in temperatures and the highly variable precipitation experienced over the last two decades has already impacted Amazon tree biomass and mortality rates (Phillips et al. 2009; Brienen et al. 2015; Feldpausch et al. 2016; Esquivel-Muelbert et al. 2019). This mortality increase may be changing the illumination and moisture conditions experienced by young plants in the understory sufficiently to favour lianas. The strong competitive capacity of lianas (Putz 1980; Phillips et al. 2005) contributes to their abundance in tropical forests, and their ability especially to compete below-ground for scarce water resources (e.g., Schnitzer 2005) may help to explain a tendency within Amazonia for lianas to be particularly dominant in some forests with long dry seasons (e.g., Pérez-Salicrup et al. 2001).

In our study, by the time of the final survey the proportion of lianas in the total community of regenerating plants (37%) was greater than expected in mixed tropical forests where lianas usually account for between 15 and 25% of stems and woody species (Gentry 1991; Condit et al. 1996; Torti et al. 2001; Oliveira et al. 2014). The proportion of lianas in our forest is also higher than reported from Barro Colorado Island in Panama, where lianas composed 17% of the individuals $\geq$ 20 cm in height and < 1 cm dbh (Comita et al. 2007). However, in three surveys carried out by Marimon (2005) in our forest, adult lianas (dbh ≥ 5 cm) accounted for less than 10% of the woody individuals, while Nascimento et al. (2007) likewise observed a low density of adult lianas in a monodominant forest of *Peltogyne gracilipes* in Amazonia. This suggests that the proportion of lianas in low turnover monodominant forests, like other late successional communities (Ladwig and Meiners 2010), is generally low. This strengthens the interpretation that the general increase of liana regeneration observed in our study is related to changes in the frequency of disturbance caused by drought-induced tree mortality and tree-fall (Marimon et al. 2014; Elias et al. 2018).

Elsewhere in Neotropical forests, gains in lianas have also been noted but these reports all come for mixed forests with higher initial populations of lianas than in the monodominant forests. A general increase in Amazon liana dominance and density was first reported almost two decades ago (Phillips et al. 2002), and was linked to the long-term increase in forest dynamics already being experienced in mature old-growth forests across Amazonia (Phillips et al. 2004). More recent work has tended to confirm that many neotropical forests have been experiencing a prolonged increase in liana density and dominance (e.g., Schnitzer and Bongers 2011), but the mechanism(s) responsible remain unclear. Our study strengthens the case for drought as a driver of long-term increases in neotropical liana populations.

The observed increase in the proportion of lianas may therefore represent an additional threat to the stability of this forest and to the maintenance of *Brosimum rubescens* monodominance. This is because lianas alter interspecific competitive relationships by impacting the growth of some tree species more than others (van der Heijden and Phillips 2009). Further, by increasing the rate of tree fall (Phillips et al. 2005), lianas may create conditions suitable for further expansion and affect the regeneration and dynamics of woody seedlings (Schnitzer et al. 2000; Restom and Nepstad 2004).

In conclusion, we found that changes in the richness and diversity of the forest regeneration were determined by the liana species. The greatest increase in density was also observed for lianas, such that during the 21-year study period this guild went from being initially almost inconsequential, to attaining levels higher than those found in tropical forests with high diversity, and well above levels reported for monodominant forests elsewhere. This recent increase in lianas is in line with observations from across Amazonia and beyond but is considerably more marked here. This may be because our forest is situated at the climatic margins of Amazonia, where recent droughts and a long-term increase in temperatures may be especially favourable to lianas. In parallel, there has been a sharp decline in the smallest size-classes of the monodominant tree species, *Brosimum rubescens.* If these trends (increase in lianas, hotter and more variable climate, and decline in *B. rubescens* regeneration) continue, we anticipate that the structure and the floristic composition of this tropical monodominant forest will experience large changes, potentially becoming transformed into a mixed forest. Since ongoing land-use change, climatic changes, and increases in lianas appear to be almost ubiquitous among tropical forests of the Americas, our results suggest a high level of threat to the survival and maintenance of remaining *Brosimum rubescens* monodominant forests.

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Table 1 Total species richness (Sp), proportion of liana species (%L_{sp}) and liana abundance (%L_{ab}) in relation to total community, by year and regeneration size classes in a monodominant forest in Southern Amazonia, Brazil. Note the rapid increase in liana diversity and especially in liana dominance in all regeneration classes. Seedlings: height $\leq$ 30 cm; saplings: > 30 cm to $\leq$ 60 cm; poles or young stems: > 60 cm to $\leq$ 200 cm; treelets: height > 200 cm and diameter < 5 cm.

Regeneration class	1997			2002			2010			2018		
	Sp	%L_{sp}	%L_{ab}	Sp	%L_{sp}	%L_{ab}	Sp	%L_{sp}	%L_{ab}	Sp	%L_{sp}	%L_{ab}
Seedlings	10	10	0.8	15	20	1.7	14	28	23.1	19	53	53.3
Saplings	13	15	0.9	28	18	3.1	18	22	3.2	22	32	16.9
Poles	50	16	6.0	53	9	3.9	43	21	4.4	49	27	10.3
Treelets	52	11	2.7	56	4	0.3	53	21	6.3	62	24	14.7
All	64	11	1.0	63	10	2.3	60	23	13.3	71	24	36.8

Figure captions

Fig. 1 A) MCWD (maximum climatological water deficit, mm year^{-1}) and B) average air temperature (ºC) from 1996 to 2018, with the first month of the dry season (May) representing the beginning of each year's climatic calendar. Precipitation and temperature data were collected at the Meteorological Station (World Weather Station 83319) in Nova Xavantina, Mato Grosso state, 25 km from the study area. Dashed lines indicate the year of each census (1997, 2002, 2010 and 2018).

Fig. 2 Average (and confidence intervals) values of the density (100 m^{-2}), species richness, evenness and Shannon's diversity (H ') in four regeneration classes (seedlings: height $\leq$ 30 cm; saplings: > 30 cm to $\leq$ 60 cm; poles or young stems: > 60 cm to $\leq$ 200 cm; and treelets: height > 200 cm and diameter < 5 cm; N= 30 plots per class) in a monodominant forest in Southern Amazonia. Different letters denote significant differences between surveys in each regeneration class (Repeated-Measures PERMANOVA). Note that lianas form a small fraction of woody regeneration early on but become increasingly more important especially in the smallest size-classes.

Fig. 3 Average number of individuals and confidence interval of *Brosimum rubescens*, other woody species, and liana-only regeneration in four classes (seedlings: height $\leq$ 30 cm; saplings: > 30 cm to $\leq$ 60 cm; poles or young stems: > 60 cm to $\leq$ 200 cm; and treelets: height > 200 cm and diameter < 5 cm; N= 30 plots per class) and four surveys in the monodominant forest in Southern Amazonia, Brazil. Density = average number of individuals per 100 m^2 plots. Different letters mean significant differences between surveys in each regeneration class (Repeated-Measures PERMANOVA).

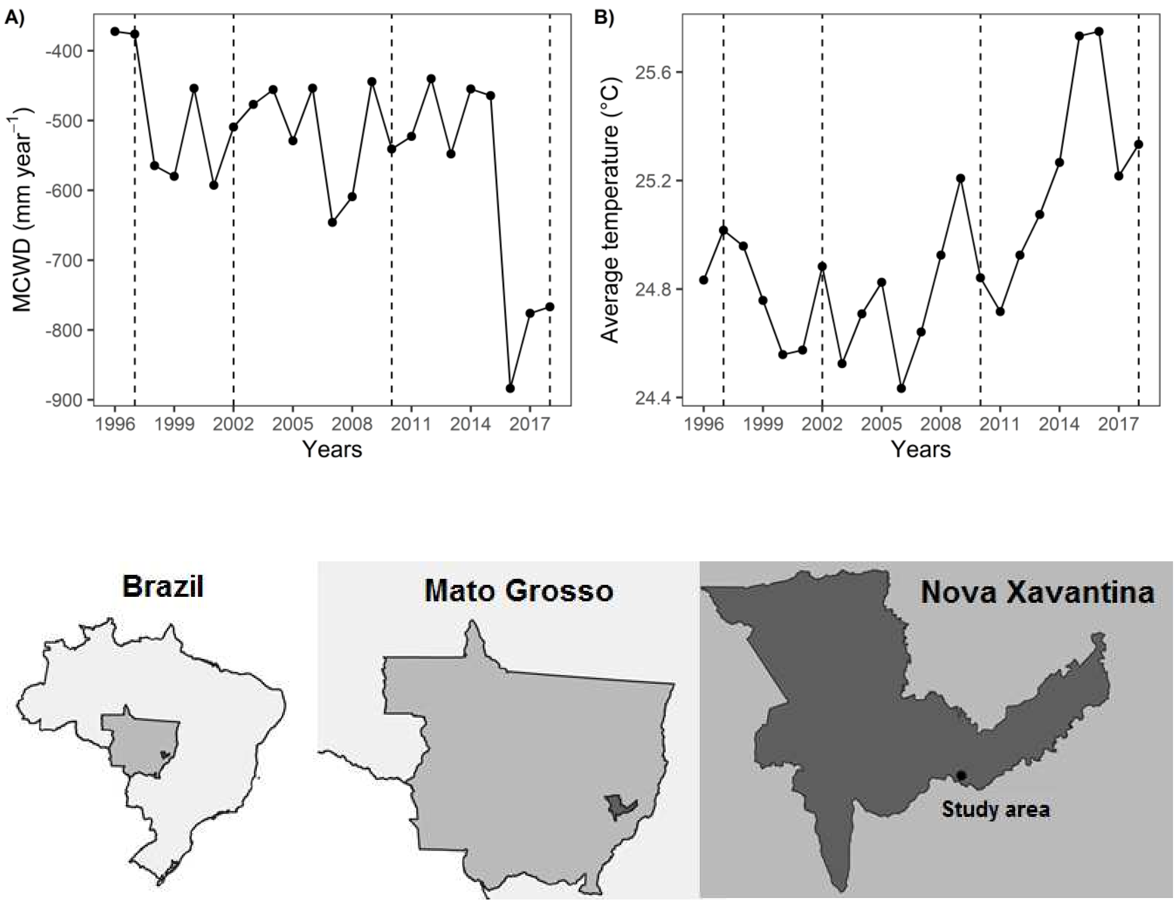

A)
MCWD (mm year^{-1})
-400
-500
-600
-700
-800
-900
Years
1996
1999
2002
2005
2008
2011
2014
2017
B)
Average temperature (°C)
25.6
25.2
24.8
24.4
Years
Brazil
Mato Grosso
Nova Xavantina
Study area

Figure 1

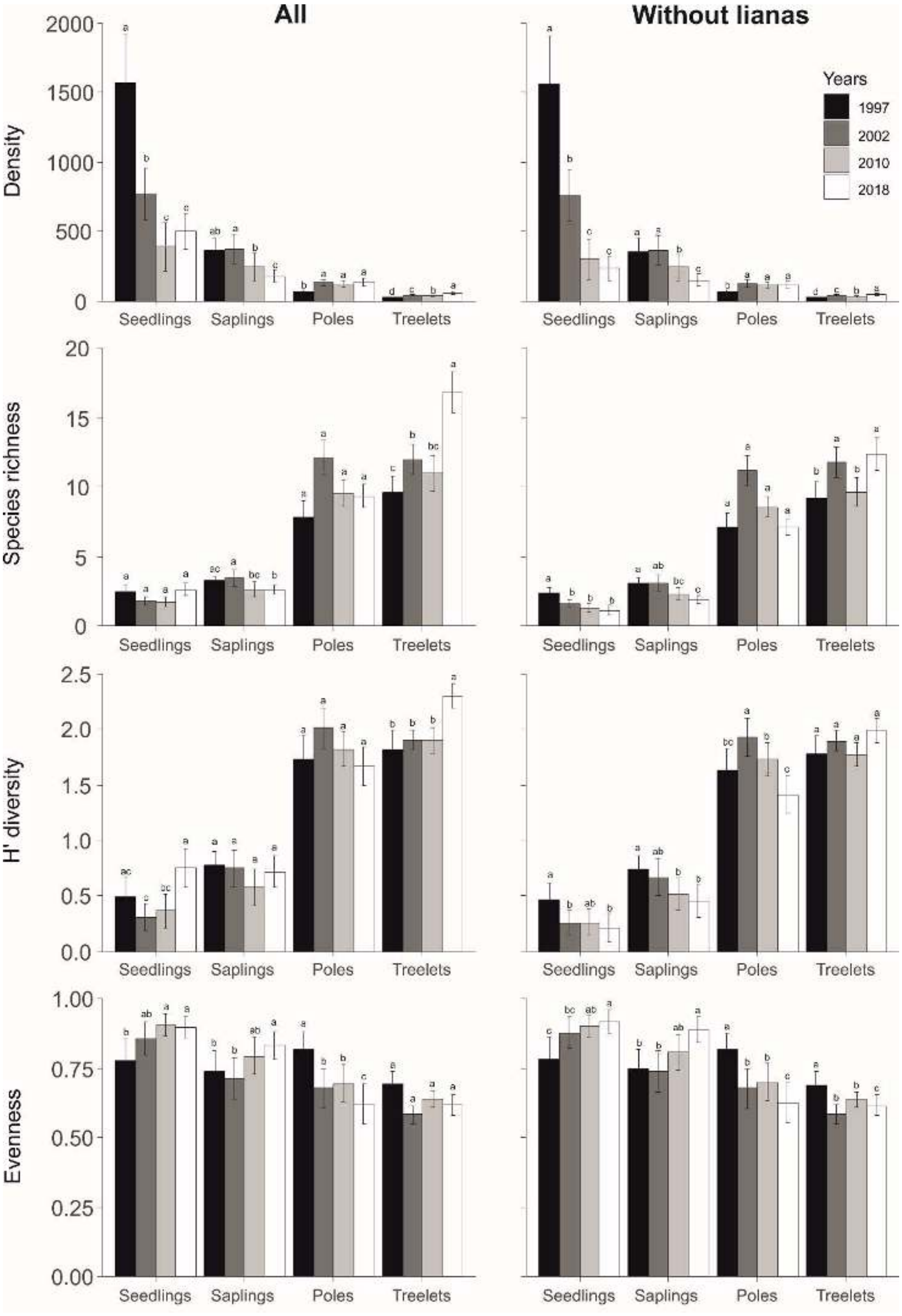

All
Without lianas
Years
1997
2002
2010
2018
Density
2000
1500
1000
500
0
Species richness
20
15
10
5
0
H' diversity
2.5
2.0
1.5
1.0
0.5
0.0
Evenness
1.00
0.75
0.50
0.25
0.00
Seedlings
Saplings
Poles
Treelets

Figure 2

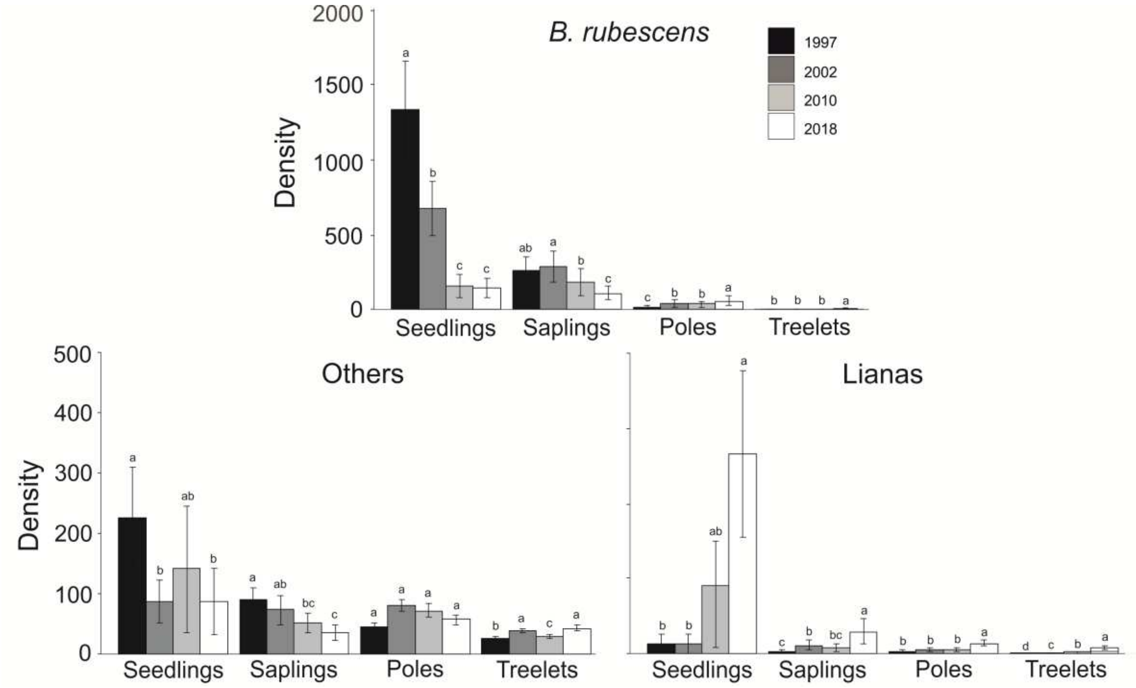
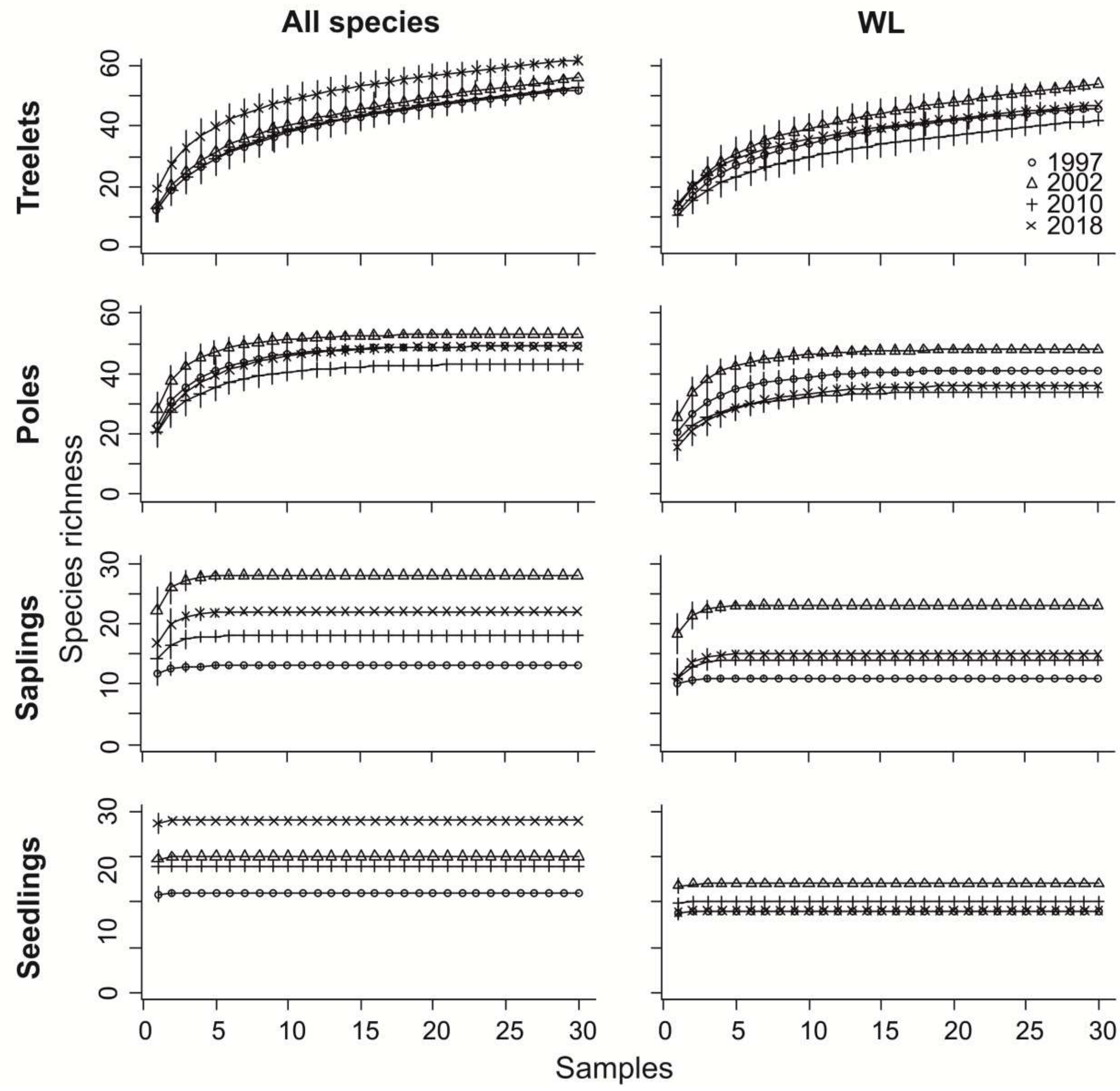

B. rubescens
1997
2002
2010
2018
Density
2000
1500
1000
500
0
a
b
c
c
ab
a
b
c
c
b
b
a
b
b
b
a
Seedlings
Saplings
Poles
Treelets
Others
Lianas
500
400
300
200
100
0
a
b
ab
b
a
ab
bc
c
a
a
a
a
b
a
c
a
b
b
ab
a
c
b
bc
a
b
b
b
a
d
c
b
a

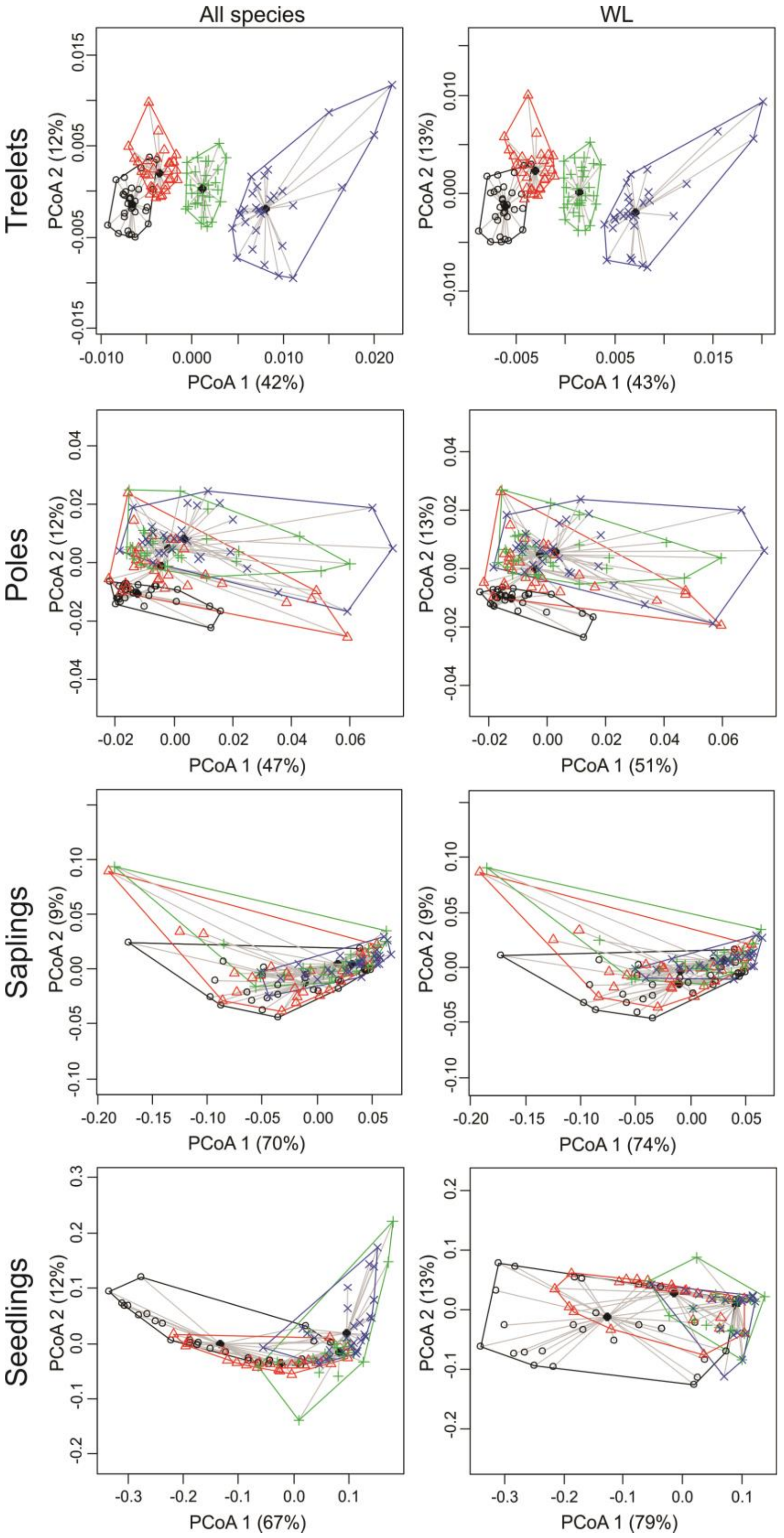
Figure 3

Supplementary file 1 related to "Drought induces large, long-term changes in the regeneration of a monodominant Amazon forest" (B. S. Marimon, C. Oliveira-Santos, B. H. Marimon-Junior, F. Elias, E. A. de Oliveira, P. S. Morandi, N. C. C. dos S. Prestes, L. H. Mariano, O. R. Pereira, T. R. Feldpausch and O. L. Phillips)



Supplementary Fig. S.1 Sample-based rarefaction curves for species richness for each census (1997, 2002, 2010 and 2018) and for each regeneration size class (seedlings: height ≤ 30 cm; saplings: > 30 cm to ≤ 60 cm; poles or young stems: > 60 cm to ≤ 200 cm; and treelets: height > 200 cm and diameter < 5 cm) in a monodominant forest in Southern Amazonia, Brazil. The level of probability of the confidence intervals is 95%. WL= without lianas.

Supplementary file 2 related to “Drought induces large, long-term changes in the regeneration of a monodominant Amazon forest” (B. S. Marimon, C. Oliveira-Santos, B. H. Marimon-Junior, F. Elias, E. A. de Oliveira, P. S. Morandi, N. C. C. dos S. Prestes, L. H. Mariano, O. R. Pereira, T. R. Feldpausch and O. L. Phillips)



Supplementary Fig. S.2 Beta diversity of treelets, poles, saplings and seedlings over 21 years in a monodominant forest in Southern Amazonia. Principal coordinates (PCoA) biplots show the Euclidean distance between floristic composition assemblages within each survey. The black circles indicate group centroids, and lines, symbols and colors represented the minimum convex hulls around each group. Black: 1997, Red: 2002, Green: 2010 and Blue: 2018. WL= without lianas.