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

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5,298 words

31 **Abstract**

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

50

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

52

53 **Introduction**

54 Tropical forests are renowned as being global centres of tree species richness and diversity
55 (Connell et al. 1984; Gentry 1988). In general, tropical forests are also hyper-diverse at the local,
56 community scale, with one hectare having as much as 30 times more tree species than an equivalent

57 area in temperate forests (e.g., Gentry 1988; Condit et al. 1996; Torti et al. 2001). Such high alpha
58 diversity typically pertains across the most extensive tropical forests of all in Amazonia (e.g., ter
59 Steege et al. 2003), yet for some tropical forests the rule of high alpha-diversity does not hold.
60 Across the tropics, several studies have reported ‘monodominant’ mature forests even on well-
61 drained soils, in which one species may comprise from 50% to as much as 100% of the individuals
62 and the total biomass (Connell and Lowman 1989; Marimon et al. 2001a; Peh et al. 2011b).

63 Several researchers have attempted to identify factors and mechanisms that enable a single
64 species to reach and maintain monodominance in the tropics (e.g., Connell and Lowman 1989; Hart
65 1990; Torti et al. 2001; Marimon and Felfili 2006; Marimon et al. 2008, 2012, 2014; Peh et al.
66 2014; Nascimento et al. 2017; Elias et al. 2018). Peh et al. (2011b) discussed a total of eight
67 hypotheses that have been proposed to explain the origin and maintenance of monodominance in
68 tropical forests. They concluded that a variety of mechanisms likely interact to induce a species to
69 attain monodominance locally, even when that species also grows in similar environmental
70 conditions in adjacent mixed forests which have much greater tree diversity.

71 Meanwhile, it has long been appreciated that disturbance regimes can have a strong impact
72 on tropical forest diversity; Connell’s ‘intermediate disturbance’ hypothesis (Connell 1978), for
73 example, suggests that there is an optimal level of disturbance frequency and intensity above and
74 below which species diversity declines. Indeed disturbance regimes appear to be intimately
75 associated with the phenomenon of monodominance (Tovar et al. 2019). Thus, while Ibanez and
76 Birnbaum (2014) observed that monodominance can occasionally be a non-persistent state that
77 occurs after severe disturbances (‘early successional monodominance’), one of the factors most
78 often hypothesised as responsible for favouring a species to reach monodominance is a long-term
79 lack of large-scale disturbances (Connell and Lowman 1989; Hart 1990; Marimon et al. 2012). In
80 this situation, species whose seedlings are able to grow under deep shade, and which also have high
81 parental survivorship and potential to dominate canopies are expected to gain a long-term
82 advantage. In all, multiple related biological traits and environmental characteristics are likely to be

83 responsible for helping a species develop a monodominant state, including low gap formation
84 frequency, strong interspecific competition, high parental survivorship and high survivorship under
85 strong shading, litter characteristics, large seed size, and masting events (i.e., massive, infrequent
86 seed production in regional synchrony with trees of the same species) (Connell and Lowman 1989;
87 Hart 1990; Torti et al. 2001; Marimon and Felfili 2006; Peh et al. 2011b; Marimon et al. 2012; Hart
88 2012; Read et al. 2017; Henkel and Mayor 2019).

89 Evidently then most of the factors and mechanisms invoked in explanations of
90 monodominance may be best evaluated through examining species regeneration (Connell and
91 Lowman 1989; Read et al. 2017). For example, if diversity in tropical forests is normally
92 maintained by compensatory mechanisms that benefit rare species (Connell et al. 1984), then
93 monodominance may occur when regeneration mechanisms uncharacteristically instead favour
94 common species and tree diversity remains low. More generally, evaluation of long-term
95 regeneration dynamics should be able to determine whether changes in diversity occur in
96 conjunction with changes in disturbance mechanisms, such as droughts, logging and anthropogenic
97 climate change – all of which impact tree mortality, recruitment, carbon sequestration and species
98 composition in Amazonia (Phillips et al. 2009; Costa et al. 2010; Brienen et al. 2015; Meir et al.
99 2015; Feldpausch et al. 2016; Esquivel-Muelbert et al. 2019). Yet studies of the stand dynamics of
100 monodominant forest regeneration are difficult, extremely few, and so far have relied on single
101 census inventories or short-term monitoring (c.f., Hart 1995; Marimon et al. 2012; Valverde-
102 Berrantes and Rocha 2014).

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

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

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

132 In the present study, we evaluated richness, species diversity and change of the regeneration
133 in a monodominant *B. rubescens* forest over a 21-year period in the transition zone between the
134 Cerrado and the Amazonian biomes. Because adult tree mortality in this patch has increased

135 markedly over recent years, our main prediction was that the density of young individuals of
136 *Brosimum* would have declined over time, while species diversity increased. We evaluated
137 regeneration of woody plants over time and tested the hypotheses that after severe droughts density
138 of the monodominant declines, and species composition changes. By including lianas as well as
139 trees in our forest regeneration censuses we were able to investigate the role of lianas in forest
140 regeneration. To our knowledge the present study represents by far the longest-running assessment
141 of regeneration in monodominant forests to date anywhere in the tropics, and is the first attempt in
142 such systems to explicitly account for the long-term regeneration of woody lianas as well as trees.

143

144 **Materials and methods**

145

146 Study site

147 The study was conducted in *Brosimum rubescens* monodominant forest located at 14°50'S
148 and 52°10'W in a patch of about 1,000 ha inside an area bigger than 8,000 ha of the Vera Cruz
149 Farm legal reserve. *Brosimum* dominates the forest biomass and comprises more than half of all
150 individuals (Marimon 2005; Marimon et al. 2001a, 2014). This forest has been monitored since
151 1996 by the senior author using permanent plots. The climate is type Aw, according to Köppen's
152 classification, with a dry season from May to September and five to six months of rain (Alvares et
153 al. 2013), leading to maximum cumulative water deficits (MCWD, Aragão et al. 2007) exceeding
154 400 mm in most years. Mean annual precipitation is 1432 mm and mean annual temperature 25°C.
155 Severe droughts (here considered as total annual precipitation below 1,000 mm and with MCWD
156 above 640 mm year⁻¹, were experienced in the study area in 2007-2008 and 2015-2016 (Feldpausch
157 et al. 2016; Jiménez-Muñoz et al. 2016; Rifai et al. 2018), with a general trend of markedly
158 increasing temperature and declining precipitation (more negative MCWD values) over the past 22
159 years (Fig. 1).

160

161 Data collection

162 In July 1997, within a permanent 1 ha plot, we established two parallel transects (10 m x 150 m) 10
163 m away from each other, each of which followed the gentle relief of the landscape so as to maintain
164 the same altitude. Each transect was subdivided into 15 contiguous subplots of 10 m x 10 m each,
165 where we counted and identified to species (or morphospecies) all individuals < 5 cm in dbh
166 (diameter at breast height). Within these subplots we nested smaller plots to sample vegetation in
167 different size classes, totaling 30 per class: 1 m x 1 m (seedlings: height \leq 30 cm), 2 m x 2 m
168 (saplings: > 30 cm to \leq 60 cm), 5 m x 5 m (poles or young stems: > 60 cm to \leq 200 cm) and 10 m x
169 10 m (treelets: height > 200 cm and diameter < 5 cm). To evaluate temporal regeneration dynamics
170 the forest was resampled in July 2002, December 2010 and August 2018, using the same
171 procedures, and the data from the two transects were grouped for each class. The same botanist and
172 field leader (BSM) participated in all four inventories to ensure standardized identification of the
173 species. We consider in the different size classes all species whose stems can reach diameters \geq 5
174 cm, including woody lianas and palms.

175

176 Data analysis

177 To characterize the change in moisture stress, we calculated temporal trends in MCWD
178 (Aragão et al. 2007). MCWD is an annual water deficit metric based only on climatic variables and
179 for which the starting point each year is defined as the wettest month, when the soil is completely
180 saturated. Climate data were obtained from the INMET (National Institute of Meteorology)
181 meteorological station (World Weather Station 83319; inmet.gov.br), located in Nova Xavantina,
182 Mato Grosso state, 25 km from the study area. Evapotranspiration data were based on Malhi et al.
183 (2009).

184 We calculate Pielou's evenness and Shannon diversity (H') indices for each regeneration
185 class (seedlings, saplings, poles and treelets) for each census using the `veganR` package (Oksanen
186 et al. 2018), both when including (All= all species) and excluding lianas (WL= without lianas) from

187 the analyses. In order to compare the species richness of all regeneration classes among the
188 censuses, we used sample-based rarefaction curves (Gotelli and Colwell 2001) performed in the
189 `BiodiversityR` package (Kindt and Coe 2005), and based on 9999 Monte Carlo permutations.

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

199 We tested the spatial autocorrelation on the abundance and richness in plots and subplots
200 using Mantel Correlogram (Borcard and Legendre 2012) performed in the `ncf` package (Bjornstad
201 2018). To evaluate patterns in density of individuals in all regeneration classes between censuses
202 we used repeated-measured ANOVA based in the `stats` package (R Core Team 2018). All
203 statistical analyses and graphs were performed in software R 3.5.1 at 5% alpha-level (R Core Team
204 2018).

205

206 **Results**

207 For most size-classes rarefaction curves rapidly saturated (Supplementary Fig. S.1),
208 indicating that the local woody regeneration community was effectively sampled. No spatial
209 autocorrelation was detected for any regeneration class in any census. There were notable
210 differences in diversity between censuses however. In particular, when we consider all species
211 together, for both the seedling and treelet size-classes, species richness had significantly increased
212 by 2018. Yet once lianas were removed from the analysis, in all four regeneration size classes tree

213 species richness was maximal in 2002, and had declined substantially by the time of the inventories
214 conducted after the 2007-2008 drought (2010) and the 2015-2016 drought (2018) (Supp. Fig. S.1).

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

222 Overall, the abundance of seedlings and saplings declined over the monitoring period,
223 especially after the drought events. This was true whether analyses were conducted with or without
224 lianas (Fig. 2). Nevertheless, the species richness of treelets ($F= 49.67$, $P= 0.001$), and the
225 Shannon's diversity of treelets ($F= 28.52$, $P= 0.001$) and seedlings ($F= 7.07$, $P= 0.006$) were all
226 higher after the 2015-2016 extreme drought event, but only significantly so when lianas are
227 included (Fig. 2). Evenness varied between the regeneration classes, being lower in 2018 for poles
228 (All: $F= 12.56$, $P= 0.001$; WL: $F= 11.99$, $P= 0.002$), higher in 2018 for seedlings (All: $F= 12.01$, $P=$
229 0.002 ; WL: $F= 22.47$, $P= 0.001$) and saplings (All: $F= 6.61$, $P= 0.009$; WL: $F= 13.01$, $P= 0.001$),
230 while for treelets it did not change over the censuses (Fig. 2).

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

239 composition changed substantially, and this holds whether or not lianas are included in the analysis
240 (Supp. Fig. S.2).

241 The most abundant species sampled in all regeneration classes in all four surveys were
242 *Brosimum rubescens* Taub. (Moraceae), *Protium pilosissimum* Engl. (Burseraceae), *Ephedranthus*
243 *parviflorus* S.Moore (Annonaceae), *Inga heterophylla* Willd. (Fabaceae), and *Myrciaria floribunda*
244 (H.West ex Willd.) O.Berg (Myrtaceae). Other species, such as *Cheiloclinium cognatum* (Miers)
245 A.C.Sm. (Celastraceae), *Protium altissimum* (Aubl.) Marchand (Burseraceae), and the liana,
246 *Anthodon decussatus* Ruiz & Pav. (Celastraceae), were also well represented, but in some surveys
247 did not appear in all regeneration classes. Among the most abundant species, the only one that
248 increased in number of individuals in all regeneration classes and in all surveys was the liana
249 *Anthodon decussatus*. We registered a total of 19 species of lianas in all regeneration classes and all
250 surveys. Of these 16 increased by between 1 to 2,324 individuals/100 m² from the first (1997) to the
251 last (2018) survey. Three-quarters of all liana species underwent a ten-fold or greater increase in the
252 number of individuals.

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

265 because lianas increased greatly, but also because there was in numerical terms an even bigger
266 reduction of *B. rubescens* and other tree species in these classes (Fig. 3).

267

268 **Discussion**

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

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

285 We also find a sharp decline in the density of *Brosimum rubescens* among regenerating taxa.
286 Such declines in principle might be attributable to several internal and external factors, including
287 increases in drought frequency and intensity, air temperature, interspecific competition for
288 resources, and human-induced disturbances among others (Feldpausch et al. 2016; Elias et al. 2018;
289 Esquivel-Muelbert et al. 2019). While our study forest showed no signs of recent human-induced
290 disturbance nor herbivory or disease outbreaks, it did experience substantial increases in

291 temperature and declines in precipitation (more negative MCWD) especially between 2007 and
292 2017. Thus, we infer that the observed temporal change in regeneration of *B. rubescens* is
293 associated with the recent, strong and repeated drought events (c.f. Marengo et al. 2011; Boisier et
294 al. 2015; Brienen et al. 2015; Feldpausch et al. 2016; Esquivel-Muelbert et al. 2019) that in turn
295 have long-term cumulative effects in diversity and richness of the whole community. Elsewhere, in
296 north-eastern Amazonia, some species studied by Costa et al. (2010) during a seven year
297 experimental drought showed similar rates of mature tree mortality as we reported here for *B.*
298 *rubescens* regeneration. Observations from our site and elsewhere suggest that drought (1)
299 negatively affects production and survivorship of monodominant species seeds, whose dispersion
300 usually occurs at the dry-season peak, and (2) limits their germination, which occurs in the
301 beginning of the rainy season, as persistent water deficits inhibit germination and so act as a
302 regeneration filter in low rainfall years (Marimon and Felfili 2006). However, it is also possible that
303 numbers at the initial survey (1996) were boosted partly by higher than normal rainfall in years
304 prior to the first sampling (Marimon et al. 2012), or other factors such as interspecific competition
305 may also affect recruitment. However even if *Brosimum* seedlings were boosted by earlier higher
306 rainfall, we can be sure that this didn't happen again over the subsequent 21 years. Moreover, while
307 reliable weather records locally only date to the 1990s, we know from other records in the oldest
308 weather station of Mato Grosso, dating back to 1911 (Bombléd 1976; Silva 2015; INMET 2019)
309 that our monitoring period was climatically exceptional. The precipitation registered in Nova
310 Xavantina in both the 2007 and 2015-16 droughts were unprecedented in terms of low rainfall in the
311 recorded history of the region.

312 Some studies suggested that intense reproductive investment, mast-fruiting and exceptional
313 seedling survival all tend to characterise monodominant species (Torti et al. 2001; Peh et al. 2011b;
314 Henkel and Mayor 2019). Marimon and Felfili (2006) observed these same characteristics in
315 *Brosimum rubescens*, and also suggested that this species has an episodic recruitment. These
316 authors also observed that in 1997 there was a large seedling bank in the forest, probably originated

317 from prior mast-fruiting events, thus is possible that drought mortality can have disproportionate
318 impacts on the recruitment capacity of this species particularly if the drought occurs in the same
319 year as the episodic recruitment. Elsewhere, in a Mediterranean environment, Pérez-Ramos et al.
320 (2010) observed from a long-term data set and a rainfall exclusion experiment that mast-fruiting of
321 *Quercus ilex* itself declined significantly under drier conditions, leading to negative consequences
322 for recruitment.

323 Regardless of the cause, the decline in *B. rubescens* sapling density between the second
324 (2002) and third survey (2010), and between the third and fourth surveys (2018) resulted from a
325 lack of seedlings to replace individuals in this category, indicating that this species' size structure is
326 unstable and that the population is declining. Notably, other, earlier studies of Neotropical
327 monodominant forests found no such evidence for decline of the dominant. Both in a
328 monodominant forest of *Peltogyne gracilipes* Ducke in northern Amazonia (Nascimento and
329 Proctor 1997; Nascimento et al. 2014) and a gallery forest in central Brazil (Felfili 1997), the
330 dominant taxon appeared to have a stable population, with large numbers of individuals in each
331 class, a high density of seedlings, and a constant proportion among classes through time.

332 In contrast to the performance of our dominant, the density of seedlings of some other
333 species increased through time. These winners included especially the liana species, which may be
334 benefiting from the openness of the forest (Schnitzer et al. 2000) recorded in recent years after
335 increased mortality of adult trees (Elias et al. 2018), but also the tree species *Protium altissimum*,
336 whose seed production occurs in the middle of the rainy season (Marimon and Felfili 2006) when
337 the forest is fully hydrated so that even in low rainfall periods seed production is less likely to be
338 affected. Ultimately though, these species' populations may be controlled by competition from the
339 monodominant for space and light, since the seedlings of *B. rubescens* are able to establish and
340 survive under closed canopy. This enables this species to occupy the available understory sites and
341 grow quickly when a canopy gap forms, suppressing the other competitors by limiting their space
342 and available light (Marimon and Felfili 2006; Hirzel and Lay 2008). The competitive advantage of

343 some liana species in drier conditions (Cai et al. 2009; Campanello et al. 2016) may lead to the
344 replacement of *B. rubescens* (as clearly recorded for 2010 and 2018) by other species. Indeed
345 elsewhere in the tropics, studies clearly show more liana infestation of trees in more seasonal
346 climates and less rain, and potential for liana growth to be several times more rapid than trees in the
347 dry season (De Walt et al. 2010; Toledo et al. 2011; Schnitzer and Bongers 2011). In addition to *B.*
348 *rubescens*, the group of more abundant tree species also declined in number of individuals over the
349 21 years of study, indicating instability in their regeneration and suggesting that they too may be in
350 decline as an oligarchy. Consistent with our findings and interpretation that this forest is undergoing
351 drought-induced shifts in tree species composition, a recent Amazon-wide analysis of trees >10 cm
352 diameter found that dry-affiliated genera have become more abundant and that small-statured non-
353 pioneer taxa have decreased in abundance in the last 30 years (Esquivel-Muelbert et al. 2019).
354 While drought is clearly capable of shifting Amazon tree communities (Costa et al. 2010; Meir et al.
355 2015), our analysis suggests that some monodominant forests may be particularly vulnerable to
356 drought-induced shifts in the long-term.

357 The large increase in the proportion of liana seedlings in our forest may also be at least in
358 part a consequence of changes in regional climate. In particular, the increase in temperatures and
359 the highly variable precipitation experienced over the last two decades has already impacted
360 Amazon tree biomass and mortality rates (Phillips et al. 2009; Brien et al. 2015; Feldpausch et al.
361 2016; Esquivel-Muelbert et al. 2019). This mortality increase may be changing the illumination and
362 moisture conditions experienced by young plants in the understory sufficiently to favour lianas. The
363 strong competitive capacity of lianas (Putz 1980; Phillips et al. 2005) contributes to their abundance
364 in tropical forests, and their ability especially to compete below-ground for scarce water resources
365 (e.g., Schnitzer 2005) may help to explain a tendency within Amazonia for lianas to be particularly
366 dominant in some forests with long dry seasons (e.g., Pérez-Salicrup et al. 2001).

367 In our study, by the time of the final survey the proportion of lianas in the total community
368 of regenerating plants (37%) was greater than expected in mixed tropical forests where lianas

369 usually account for between 15 and 25% of stems and woody species (Gentry 1991; Condit et al.
370 1996; Torti et al. 2001; Oliveira et al. 2014). The proportion of lianas in our forest is also higher
371 than reported from Barro Colorado Island in Panama, where lianas composed 17% of the
372 individuals ≥ 20 cm in height and < 1 cm dbh (Comita et al. 2007). However, in three surveys
373 carried out by Marimon (2005) in our forest, adult lianas (dbh ≥ 5 cm) accounted for less than 10%
374 of the woody individuals, while Nascimento et al. (2007) likewise observed a low density of adult
375 lianas in a monodominant forest of *Peltogyne gracilipes* in Amazonia. This suggests that the
376 proportion of lianas in low turnover monodominant forests, like other late successional
377 communities (Ladwig and Meiners 2010), is generally low. This strengthens the interpretation that
378 the general increase of liana regeneration observed in our study is related to changes in the
379 frequency of disturbance caused by drought-induced tree mortality and tree-fall (Marimon et al.
380 2014; Elias et al. 2018).

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

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

395 the regeneration and dynamics of woody seedlings (Schnitzer et al. 2000; Restom and Nepstad
396 2004).

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

413

414 **References**

- 415 Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM, Sparovek G (2013) Köppen's climate
416 classification map for Brazil. Meteorol Z 22:711–728. [https://doi.org/10.1127/0941-](https://doi.org/10.1127/0941-2948/2013/0507)
417 [2948/2013/0507](https://doi.org/10.1127/0941-2948/2013/0507)
- 418 Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral
419 Ecol 26:32–46. [https:// doi.org/10.1111/j.1442-9993.2001.01070.pp.x](https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x)

- 420 Anderson MJ, Ellingsen KE, McArdle BH (2006) Multivariate dispersion as a measure of beta
421 diversity. *Ecol Lett* 9:683–693. <https://doi.org/10.1111/j.1461-0248.2006.00926.x>
- 422 Anderson MJ, Walsh DCI (2013) PERMANOVA, ANOSIM, and the Mantel test in the face of
423 heterogeneous dispersions: What null hypothesis are you testing? *Ecol Monogr* 83:557–574.
424 <https://doi.org/10.1890/12-2010.1>
- 425 Aragão LEOC, Malhi Y, Roman- Cuesta RM, Saatchi S, Anderson LO, Shimabukuro YE (2007)
426 Spatial patterns and fire response of recent Amazonian droughts. *Geophys Res Lett*
427 34(7):L07701. <https://doi.org/10.1029/2006GL028946>
- 428 Bjornstad ON (2018) `ncf`: Spatial Covariance Functions. Retrieved from CRAN. R-
429 project.org/package=ncf
- 430 Boisier JP, Ciais P, Ducharne A, Guimberteau M (2015) Projected strengthening of Amazonian dry
431 season by constrained climate model simulations. *Nat Clim Change* 5:656–660.
432 <https://doi.org/10.1038/nclimate2658>
- 433 Bombled J (1976) *Meio século de meteorologia*. EdUFMT, Universidade Federal de Mato Grosso,
434 Cuiabá
- 435 Borcard D, Legendre P (2012) Is the Mantel Correlogram powerful enough to be useful in
436 ecological analysis? A simulation study. *Ecology* 93(6):1473–1481. [https://doi.org/10.1890/11-](https://doi.org/10.1890/11-1737.1)
437 [1737.1](https://doi.org/10.1890/11-1737.1)
- 438 Brienen RJW, Phillips OL, Feldpausch TR, Gloor E, Baker TR, Lloyd J, Lopez-Gonzalez G,
439 Monteagudo-Mendoza A, Malhi Y, Lewis SL, Vásquez Martinez R, Alexiades M, Álvarez
440 Dávila E, Alvarez-Loayza P, Andrade A, Aragão LEOC, Araujo-Murakami A, Arets EJMM,
441 Arroyo L, Aymard CGA, Bánki OS, Baraloto C, Barroso J, Bonal D, Boot RGA, Camargo
442 JLC, Castilho CV, Chama V, Chao KJ, Chave J, Comiskey JA, Cornejo Valverde F, da Costa
443 L, de Oliveira EA, Di Fiore A, Erwin TL, Fauset S, Forsthofer M, Galbraith DR, Grahame ES,
444 Groot N, Hérault B, Higuchi N, Honorio Coronado EN, Keeling H, Killeen TJ, Laurance WF,
445 Laurance S, Licona J, Magnussen WE, Marimon BS, Marimon-Junior BH, Mendoza C, Neill

- 446 DA, Nogueira EM, Núñez P, Pallqui Camacho NC, Parada A, Pardo-Molina G, Peacock J,
447 Peña-Claros M, Pickavance GC, Pitman NCA, Poorter L, Prieto A, Quesada CA, Ramírez F,
448 Ramírez-Angulo H, Restrepo Z, Roopsind A, Rudas A, Salomão RP, Schwarz M, Silva N,
449 Silva-Espejo JE, Silveira M, Stropp J, Talbot J, ter Steege H, Teran-Aguilar J, Terborgh J,
450 Thomas-Caesar R, Toledo M, Torello-Raventos M, Umetsu RK, van der Heijden GMF, van der
451 Hout P, Guimarães Vieira IC, Vieira SA, Vilanova E, Vos VA, Zagt RJ (2015) Long-term
452 decline of the Amazon carbon sink. *Nature* 519:344–8. <https://doi.org/10.1038/nature14283>
- 453 Caballé G, Martin A (2001) Thirteen years of change in trees and lianas in a Gabonese rainforest.
454 *Plant Ecol.* 152(2):167–173. <https://doi.org/10.1023/A:1011497027749>
- 455 Cai ZQ, Schnitzer SA, Bongers F (2009) Seasonal differences in leaf-level physiology give lianas a
456 competitive advantage over trees in a tropical seasonal forest. *Oecologia* 161:25–33.
457 <https://doi.org/10.1007/s00442-009-1355-4>
- 458 Campanello PI, Manzané E, Villagra M, Zhang YJ, Panizza AM, di Francescantonio D, Rodrigues
459 SA, Chen YJ, Santiago LS, Goldstein G (2016) Carbon allocation and water relations of lianas
460 versus trees. In: Goldstein G, Santiago L (eds) *Tropical Tree Physiology*. Springer, New York
461 pp 103–124. https://doi.org/10.1007/978-3-319-27422-5_5
- 462 Comita LS, Aguilar S, Perez R, Lao S, Hubbell SP (2007) Patterns of woody plant species
463 abundance and diversity in the seedling layer of a tropical forest. *J Veg Sci* 18:163–174.
464 www.jstor.org/stable/4499212
- 465 Condit R, Hubbell SP, Lafrankie JV, Sukumar R, Manokaran N, Foster RB, Ashton PS (1996)
466 Species-area and species-individual relationships for tropical trees: a comparison of three 50-ha
467 plots. *J. Ecol.* 84:549–562. <https://doi.org/10.2307/2261477>
- 468 Connell JH (1978) Diversity in tropical rainforests and coral reefs. *Science* 199:1302–1310.
469 <https://doi.org/10.1126/science.199.4335.1302>

- 470 Connell JH, Tracey JG, Webb LJ (1984) Compensatory recruitment, growth, and mortality as
471 factors maintaining rain forest tree diversity. *Ecol Monogr* 54:141–164.
472 <https://doi.org/10.2307/1942659>
- 473 Connell JH, Lowman MD (1989) Low-diversity tropical rain forests: some possible mechanisms for
474 their existence. *Am Nat* 134:88–119. <https://doi.org/10.1086/284967>
- 475 Costa ACL, Galbraith D, Almeida S, Portela BTT, Costa M, Silva-Junior JA, Braga AP, Gonçalves
476 PHL, Oliveira ARR, Fisher R, Phillips OL, Metcalfe DB, Levy P, Meir P (2010) Effect of 7 yr
477 of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian
478 rainforest. *New Phytologist* 187:579–591. <https://doi.org/10.1111/j.1469-8137.2010.03309.x>
- 479 Costa MH, Fleck LC, Cohn AS, Abrahão GM, Brando PM, Coe MT, Fu R, Lawrence D, Pires GF,
480 Pousa R, Soares-Filho BS (2019) Climate risks to Amazon agriculture suggest a rationale to
481 conserve local ecosystems. *Front Ecol Environ* 17(10):584–590.
482 <https://doi.org/10.1002/fee.2124>
- 483 De Walt SJ, Schnitzer SA, Chave J, Bongers F, Burnham RJ, Cai ZQ, Chuyong G, Clark DB,
484 Ewango CEN, Gerwing JJ, Gortaire E, Hart T, Ibarra-Manríquez G, Ickes K, Kenfack D, Macía
485 MJ, Makana JR, Martinez-Ramos M, Mascaro J, Moses S, Muller-Landau H, Parren MPE,
486 Parthasarathy N, Pérez-Salicrup DR, Putz FE, Romero-Saltos H, Duncan T (2010) Annual
487 rainfall and seasonality predict pan-tropical patterns of liana density and basal area. *Biotropica*
488 42:309–317. <https://doi.org/10.1111/j.1744-7429.2009.00589.x>
- 489 Elias F, Marimon BS, Marimon-Junior BH, Budke JC, Esquivel-Muelbert A, Morandi PS, Reis SM,
490 Phillips OL (2018) Idiosyncratic soil-tree species associations and their relationships with
491 drought in a monodominant Amazon forest. *Acta Oecol* 91:127–136.
492 <https://doi.org/10.1016/j.actao.2018.07.004>
- 493 Esquivel-Muelbert A, Baker TR, Dexter KG, Lewis SL, Brienens RJW, Feldpausch TR, Lloyd J,
494 Monteagudo-Mendoza A, Arroyo L, Álvarez-Dávila E, Higuchi N, Marimon BS, Marimon-
495 Junior BH, Silveira M, Vilanova E, Gloor E, Malhi Y, Chave J, Barlow J, Bonal D, Cardozo

496 ND, Erwin T, Fauset S, Hérault B, Laurance S, Porter L, Qie L, Stahl C, Sullivan MJP, ter
497 Steege H, Vos VA, Zuidema PA, Almeida E, Oliveira EA, Andrade A, Aragão L, Araújo-
498 Murakami A, Arets E, Aymard GA, Baraloto C, Camargo PB, Barroso JG, Bongers F, Boot R,
499 Camargo JL, Castro W, Moscoso VC, Comiskey J, Valverde FC, Costa ACL, Pasquel TA, Di
500 Fiore A, Duque LF, Elias F, Engel J, Llampazo GF, Galbraith D, Fernández RH, Coronado EH,
501 Hubau W, Jimenez-Rojas E, Lima AJN, Umetsu RK, Laurance W, Lopez-Gonzalez G, Lovejoy
502 T, Cruz OAM, Morandi PS, Neill D, Vargas PN, Camacho NCP, Gutierrez AP, Pardo G,
503 Peacock J, Peña-Claros M, Peñuela-Mora MC, Petronelli P, Pickavance GC, Pitman N, Prieto
504 A, Quesada C, Ramírez-Angulo H, Réjou-Méchain M, Correa ZR, Roopsind A, Rudas A,
505 Salomão R, Silva N, Silva-Espejo J, Singh J, Stropp J, Terborgh J, Thomas R, Toledo M,
506 Torres-Lezama A, Gamarra LV, van der Meerd PJ, van der Heijden G, van der Hout P,
507 Martinez RV, Vela C, Vieira ICG, Phillips OL (2019) Compositional response of Amazon
508 forests to climate change. *Global Change Biol* 25:39–56. <https://doi.org/10.1111/gcb.14413>

509 Fauset S, Baker TR, Lewis SL, Feldpausch TR, Affum-Baffoe K, Foli EG, Hamer KC, Swaine MD
510 (2012) Drought-induced shifts in the floristic and functional composition of tropical forests in
511 Ghana. *Ecol Lett* 15(10):1120–1129. <https://doi.org/10.1111/j.1461-0248.2012.01834.x>

512 Feldpausch TR, Phillips OL, Brienen RJW, Gloor E, Lloyd J, Lopez-Gonzalez G, Monteagudo-
513 Mendoza A, Malhi Y, Alarcón A, Álvarez Dávila E, Alvarez-Loayza P, Andrade A, Aragão
514 LEOC, Arroyo L, Aymard CGA, Baker TR, Baraloto C, Barroso J, Bonal D, Castro W, Chama
515 V, Chave J, Domingues TF, Fauset S, Groot N, Honorio Coronado E, Laurance S, Laurance
516 WF, Lewis SL, Licona JC, Marimon BS, Marimon-Junior BH, Bautista CM, Neill DA,
517 Oliveira EA, Santos CO, Camacho NCP, Pardo-Molina G, Prieto A, Quesada CA, Ramírez F,
518 Ramírez-Angulo H, Réjou-Méchain M, Rudas A, Saiz G, Salomão RP, Silva-Espejo JE,
519 Silveira M, ter Steege H, Stropp J, Terborgh J, Thomas-Caesar R, van der Heijden GMF,
520 Vásquez-Martinez R, Vilanova E, Vos VA (2016) Amazon forest response to repeated
521 droughts. *Global Biogeochem Cyc* 30:964–982. <https://doi.org/10.1002/2015GB005133>

- 522 Felfili JM (1997) Dynamics of the natural regeneration in the Gama gallery forest in central Brazil.
523 Forest Ecol Manag 91:235–245. [https://doi.org/10.1016/S0378-1127\(96\)03862-5](https://doi.org/10.1016/S0378-1127(96)03862-5)
- 524 Gentry AH (1988) Tree species richness of upper Amazonian forests. P Natl Acad Sci. 85:156–159.
525 <https://doi.org/10.1073/pnas.85.1.156>
- 526 Gentry AH (1991) The distribution and evolution of climbing plants. In: Putz FE, Mooney HA (eds)
527 The Biology of Vines. Cambridge University Press, Cambridge, pp 3–53.
528 <https://doi.org/10.1017/CBO9780511897658.003>
- 529 Gloor MRJW, Brienen RJ, Galbraith D, Feldpausch TR, Schöngart J, Guyot JL, Espinoza JC, Lloyd
530 J, Phillips OL (2013) Intensification of the Amazon hydrological cycle over the last two
531 decades. Geophys Res Lett 40(9):1729–1733. <https://doi:10.1002/grl.50377>
- 532 Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the
533 measurement and comparison of species richness. Ecol Lett 4:379–391.
534 <https://doi.org/10.1046/j.1461-0248.2001.00230.x>
- 535 Hart PJ (2012) Patterns of tree mortality in a monodominant tropical forest. In: Sudarshana P,
536 Nageswara-Rao M, Soneji JR (eds) Tropical forests. InTech, Shanghai, pp 349–358.
537 <https://doi.org/10.5772/29762>
- 538 Hart TB (1990) Monospecific dominance in tropical rain forests. Trends Ecol Evol 5:6–11.
539 [https://doi.org/10.1016/0169-5347\(90\)90005-X](https://doi.org/10.1016/0169-5347(90)90005-X)
- 540 Hart TB (1995) Seed, seedling and sub-canopy survival in monodominant and mixed forests of the
541 Ituri Forest, Africa. J Trop Ecol 11:443–459. <https://doi.org/10.1017/S0266467400008919>
- 542 Henkel TW, Mayor JR (2019) Implications of a long-term mast seeding cycle for climatic
543 entrainment, seedling establishment and persistent monodominance in a Neotropical,
544 ectomycorrhizal canopy tree. Ecol Res 34(4):472–484. <https://doi.org/10.1111/1440-1703.12014>
- 545
546 Hirzel AH, Lay GL (2008) Habitat suitability modelling and niche theory. J Appl Ecol 45:1372–
547 1381. <https://doi.org/10.1111/j.1365-2664.2008.01524.x>

- 548 Ibanez T, Birnbaum P (2014) Monodominance at the rainforest edge: case study of *Codia*
549 *mackeeana* (Cunoniaceae) in New Caledonia. *Aust J Bot* 62:312–321.
550 <https://doi.org/10.1071/BT14062>
- 551 INMET – Instituto Nacional de Meteorologia (2019) Historical meteorological data. Available in
552 <http://www.inmet.gov.br/portal/index.php?r=bdmep/bdmep>; accessed in 02 Jan 2019
- 553 Jiménez-Muñoz JC, Mattar C, Barichivich J, Santamaría-Artigas A, Takahashi K, Malhi Y, Sobrino
554 JA, van der Schrier G (2016) Record-breaking warming and extreme drought in the Amazon
555 rainforest during the course of El Niño 2015–2016. *Sci Rep-UK* 6:33130.
556 <https://doi.org/10.1038/srep33130>
- 557 Kindt R, Coe R (2005) Tree diversity analysis: A manual and software for common statistical
558 methods for ecological and biodiversity studies. World Agroforestry Centre (ICRAF), Nairobi.
559 <https://www.worldagroforestry.org/downloads/Publications/PDFS/b13695.pdf>
- 560 Ladwig LM, Meiners SJ (2010) Spatiotemporal dynamics of lianas during 50 years of succession to
561 temperate forest. *Ecology* 91:671–680. <https://doi.org/10.1890/08-1738.1>
- 562 Magnago LFS, Magrach A, Barlow J, Schaefer CEGR, Laurance WF, Martins SV, Edwards DP
563 (2017) Do fragment size and edge effects predict carbon stocks in trees and lianas in tropical
564 forests? *Funct Ecol* 31:542–552. <https://doi.org/10.1111/1365-2435.12752>
- 565 Malhi Y, Aragão LEOC, Galbraith D, Huntingford C, Fisher R, Zelazowski P, Sitch S, McSweeney
566 C, Meir P (2009) Exploring the likelihood and mechanism of a climate-change-induced dieback
567 of the Amazon rainforest. *PNAS* 106(49):20610–20615.
568 <https://doi.org/10.1073/pnas.0804619106>
- 569 Marengo JA, Tomasella J, Alves LM, Soares WR, Rodriguez DA (2011) The drought of 2010 in
570 the context of historical droughts in the Amazon region. *Geophys Res Lett* 38:L12703.
571 <https://doi.org/10.1029/2011gl047436>

- 572 Marimon BS (2005) Dinâmica de uma floresta monodominante de *Brosimum rubescens* Taub. e
573 comparação com uma floresta mista em Nova Xavantina-MT. Ph.D. Thesis, Universidade de
574 Brasília, Brasília, Brazil
- 575 Marimon BS, Felfili JM (2006) Chuva de sementes em uma floresta monodominante de *Brosimum*
576 *rubescens* Taub. e em uma floresta mista adjacente no Vale do Araguaia, MT, Brasil. Acta Bot
577 Bras 20:423–432. <http://dx.doi.org/10.1590/S0102-33062006000200017>
- 578 Marimon BS, Felfili JM, Haridasan M (2001a) Studies in monodominant forests in eastern Mato
579 Grosso, Brazil: I. A forest of *Brosimum rubescens* Taub. Edinb J Bot 58:123–137.
580 <http://dx.doi.org/10.1017/S096042860100049X>
- 581 Marimon BS, Felfili JM, Haridasan M (2001b) Studies in monodominant forests in eastern Mato
582 Grosso, Brazil: II. a forest in the Areões Xavante Indian Reserve. Edinb J Bot 58:483–497.
583 <https://doi.org/10.1017/S0960428601000798>
- 584 Marimon BS, Felfili JM, Marimon-Junior BH, Franco AC, Fagg CW (2008) Desenvolvimento
585 inicial e partição de biomassa de *Brosimum rubescens* Taub. (Moraceae) sob diferentes níveis
586 de sombreamento. Acta Bot Bras 22:941–953. [http://dx.doi.org/10.1590/S0102-](http://dx.doi.org/10.1590/S0102-33062008000400005)
587 [33062008000400005](http://dx.doi.org/10.1590/S0102-33062008000400005)
- 588 Marimon BS, Felfili JM, Fagg CW, Marimon-Junior BH, Umetsu RK, Oliveira-Santos C, Morandi
589 P, Lima HS, Nascimento ART (2012) Monodominance in a *Brosimum rubescens* Taub. forest:
590 structure and dynamics of natural regeneration. Acta Oecol 43:134–139.
591 <https://doi.org/10.1016/j.actao.2012.07.001>
- 592 Marimon BS, Marimon-Junior BH, Feldpausch TR, Oliveira-Santos C, Mews HA, Lopez-Gonzalez
593 G, Franczak DD, Oliveira EA, Maracahipes L, Miguel A, Lenza E, Phillips OL (2014)
594 Disequilibrium and hyperdynamic tree turnover at the forest-cerrado transition zone in southern
595 Amazonia. Plant Ecol Divers 7:281–292. <https://doi.org/10.1080/17550874.2013.818072>

- 596 Meir P, Wood TE, Galbraith DR, Brando PM, Costa ACL, Rowland L, Ferreira LV (2015)
597 Threshold responses to soil moisture deficit by trees and soil in tropical rain forests: insights
598 from field experiments. *Bioscience* 65(9):882–892. <https://doi.org/10.1093/biosci/biv107>
- 599 Nascimento MT, Carvalho LCS, Barbosa RI, Villela DM (2014) Variation in floristic composition,
600 demography and above-ground biomass over a 20-year period in an Amazonian monodominant
601 forest. *Plant Ecol Divers* 7(1-2):293–303. <https://doi.org/10.1080/17550874.2013.772673>
- 602 Nascimento MT, Barbosa MI, Dexter KG, Castilho CV, Carvalho LCS, Villela DM (2017) Is the
603 *Peltogyne gracilipes* monodominant forest characterised by distinct soils? *Acta Oecol* 85:104–
604 107. <http://dx.doi.org/10.1016/j.actao.2017.10.001>
- 605 Nascimento MT, Barbosa RI, Villela DM, Proctor J (2007) Above-ground biomass changes over an
606 11-year period in Amazon monodominant forest and two other lowland forests. *Plant Ecol*
607 192:181–192. <https://doi.org/10.1007/s11258-007-9303-z>
- 608 Nascimento MT, Proctor J (1997) Population dynamics of five tree species in a monodominant
609 *Peltogyne* forest and two other forest types on Maracá Island, Roraima, Brazil. *Forest Ecol*
610 *Manag* 94:115–128. [https://doi.org/10.1016/S0378-1127\(96\)03968-0](https://doi.org/10.1016/S0378-1127(96)03968-0)
- 611 Nepstad DC, Tohver IM, Ray D, Moutinho P, Cardinot G (2007) Mortality of large trees and lianas
612 following experimental drought in an Amazon forest. *Ecology* 88(9):2259–2269.
613 <https://doi.org/10.1890/06-1046.1>
- 614 Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O’Hara RB,
615 Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2018) *vegan*: Community
616 Ecology Package. v.2.5-3. <https://cran.r-project.org>, <https://github.com/vegandevs/vegan>
- 617 Oliveira EA, Marimon BS, Feldspach T, Colli GR, Marimon-Junior BH, Lloyd J, Lenza E,
618 Maracahipes L, Santos CO, Phillips OL (2014) Diversity, abundance and distribution of lianas
619 of the Cerrado-Amazonian forest transition, Brazil. *Plant Ecol Divers* 7:231–240.
620 <https://doi.org/10.1080/17550874.2013.816799>

- 621 Peh KSH, Bonaventure S, Lloyd J, Quesada CA, Lewis SL, (2011a) Soil does not explain
622 monodominance in a Central African tropical forest. *Plos One* 6(2):e16996.
623 <https://doi.org/10.1371/journal.pone.0016996>
- 624 Peh KSH, Lewis SL, Lloyd J (2011b) Mechanisms of monodominance in diverse tropical tree-
625 dominated systems. *J Ecol* 99:891–898. <https://doi.org/10.1111/j.1365-2745.2011.01827.x>
- 626 Peh KSH, Sonké B, Séné O, Djuikouo M-NK, Nguembou CK, Taedoumg H, Begne SK, Lewis SL
627 (2014) Mixed-forest species establishment in a monodominant forest in Central Africa:
628 implications for tropical forest invasibility. *PLoS One* 9(5):e97585.
629 <https://doi.org/10.1371/journal.pone.0097585>
- 630 Pérez-Ramos IM, Ourcival JM, Limousin JM, Rambal S (2010) Mast fruiting under increasing
631 drought: results from a long-term data set and from a rainfall exclusion experiment. *Ecology*
632 91(10):3057–3068. <https://doi.org/10.1890/09-2313.1>
- 633 Pérez-Salicrup DR, Sork VL, Putz FE (2001) Lianas and trees in a liana forest of Amazonian
634 Bolivia. *Biotropica* 33:34–47. <https://doi.org/10.1111/j.1744-7429.2001.tb00155.x>
- 635 Phillips OL, Aragão L, Lewis SL, Fisher JB, Lloyd J, Lopez-Gonzalez G, Malhi Y, Monteagudo A,
636 Peacock J, Quesada CA, van der Heijden G, Almeida S, Amaral I, Arroyo L, Aymard G, Baker
637 TR, Banki O, Blanc L, Bonal D, Brando P, Chave J, de Oliveira ACA, Cardozo ND, Czimczik
638 CI, Feldpausch TR, Freitas MA, Gloor E, Higuchi N, Jimenez E, Lloyd G, Meir P, Mendoza C,
639 Morel A, Neill DA, Nepstad D, Patino S, Penuela MC, Prieto A, Ramirez F, Schwarz M, Silva
640 J, Silveira M, Thomas AS, ter Steege H, Stropp J, Vasquez R, Zelazowski P, Davila EA,
641 Andelman S, Andrade A, Chao KJ, Erwin T, Di Fiore A, Honorio E, Keeling H, Killeen TJ,
642 Laurance WF, Cruz AP, Pitman NCA, Vargas PN, Ramirez-Angulo H, Rudas A, Salamão, R,
643 Silva N, Terborgh J, Torres-Lezama A (2009) Drought sensitivity of the Amazon rainforest.
644 *Science* 323:1344–1347. <https://doi.org/10.1126/science.1164033>
- 645 Phillips OL, Baker TR, Arroyo L, Higuchi N, Killeen T, Laurance WF, Lewis SL, Lloyd J, Malhi
646 Y, Monteagudo A, Neill D, Núñez Vargas P, Silva N, Terborgh J, Vásquez Martínez R,

- 647 Alexiades M, Almeida S, Brown S, Chave J, Comiskey JA, Czimczik CI, Di Fiore A, Erwin T,
648 Kuebler C, Laurance SG, Nascimento HEM, Olivier J, Palacios W, Patiño S, Pitman N,
649 Quesada CA, Saldias M, Torres Lezama A, Vinceti B (2004) Pattern and process in Amazon
650 forest dynamics, 1976-2001. *Philos T R Soc B* 359:381–407.
651 <https://doi.org/10.1098/rstb.2003.1438>
- 652 Phillips OL, Martínez RV, Arroyo L, Baker TR, Killeen T, Lewis SL, Malhi Y, Mendoza AM,
653 Neill D, Vargas PN, Alexiades M, Cerón C, Fiore A, Erwin T, Jardim A, Palacios W, Saldias
654 M, Vinceti B (2002) Increasing dominance of large lianas in Amazonian forests. *Nature*
655 418:770–774. <https://doi.org/10.1038/nature00926>
- 656 Phillips OL, Martinez RV, Mendoza AM, Baker TR, Vargas PN (2005) Large lianas as
657 hyperdynamic elements of the tropical forest canopy. *Ecology* 86:1250–1258.
658 <https://doi.org/10.1890/04-1446>
- 659 Putz FE (1980) Lianas vs trees. *Biotropica* 12:224–225. <https://doi.org/10.2307/2387978>
- 660 R Core Team (2018) R: A language and environment for statistical computing. R Found. Stat.
661 Comput. <https://www.r-project.org/>
- 662 Read J, McCoy S, Jaffré T, Sanson G, Logan M (2017) Growth and biomass allocation in seedlings
663 of rain-forest trees in New Caledonia: monodominants vs. subordinates and episodic vs.
664 continuous regenerators. *J Trop Ecol* 33(2):128–142.
665 <https://doi.org/10.1017/S0266467416000638>
- 666 Restom TG, Nepstad DC (2004) Seedling growth dynamics of a deeply rooting liana in a secondary
667 forest in eastern Amazonia. *Forest Ecol Manag* 190:109–118.
668 <https://doi.org/10.1016/j.foreco.2003.10.010>
- 669 Rifai SW, Girardin CAJ, Berenguer E, Del Aguila-Pasquel J, Dahlsjö CAL, Doughty CE, Jeffery
670 KJ, Moore S, Oliveras I, Riutta T, Rowland LM, Murakami AA, Addo-Danso SD, Brando
671 P, Burton C, Ondo FE, Duah-Gyamfi A, Amézquita FF, Freitag R, Pacha FH, Huasco
672 WH, Ibrahim F, Mbou AT, Mihindou VM, Peixoto KS, Rocha W, Rossi LC, Seixas M, Silva-

- 673 Espejo JE, Abernethy KA, Adu-Bredu S, Barlow J, da Costa ACL, Marimon BS, Marimon-
674 Junior BH, Meir P, Metcalfe DB, Phillips OL, White LJT, Malhi Y (2018) ENSO Drives
675 interannual variation of forest woody growth across the tropics. *Philos Trans R Soc Lond B*
676 *Biol Sci* 373: 20170410. <http://dx.doi.org/10.1098/rstb.2017.0410>
- 677 Schnitzer SA (2005) A mechanistic explanation for global patterns of liana abundance and
678 distribution. *Am Nat* 166:262–276. <https://doi.org/10.1086/431250>
- 679 Schnitzer SA, Bongers F (2011) Increasing liana abundance and biomass in tropical forests:
680 emerging patterns and putative mechanisms. *Ecol Lett* 14:397–406.
681 <https://doi.org/10.1111/j.1461-0248.2011.01590.x>
- 682 Schnitzer SA, Dalling JW, Carson WP (2000) The impact of lianas on tree regeneration in tropical
683 forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. *J Ecol*
684 88:655–666. <https://doi.org/10.1046/j.1365-2745.2000.00489.x>
- 685 Silva MP (2015) Ritmos e ciclos no clima local de Cuiabá/Várzea Grande-MT: uma análise secular
686 (1912-2012). Master Thesis, Universidade Federal de Mato Grosso, Cuiabá, Brazil
- 687 ter Steege H, Pitman N, Sabatier D, Castellanos H, van Der Hout P, Daly DC, Silveira M, Phillips
688 O, Vasquez R, van Andel T, Duivenvoorden J (2003) A spatial model of tree α -diversity and
689 tree density for the Amazon. *Biodivers Conserv* 12(11):2255–2277.
690 <https://doi.org/10.1023/A:1024593414624>
- 691 Toledo M, Poorter L, Peña-Claros M, Alarcón A, Balcázar J, Leño C, Licona JC, Bongers F
692 (2011) Climate and soil drive forest structure in Bolivian lowland forests. *J Trop Ecol* 27:333–
693 345. <https://doi.org/10.1017/S0266467411000034>
- 694 Torti SD, Coley PD, Kursar TA (2001) Causes and consequences of monodominance in tropical
695 lowland forests. *Am Nat* 157:141–153. <https://doi.org/10.1086/318629>
- 696 Tovar C, Harris DJ, Breman E, Brncic T, Willis KJ (2019) Tropical monodominant forest resilience
697 to climate change in Central Africa: A *Gilbertiodendron dewevrei* forest pollen record over the
698 past 2,700 years. *J Veg Sci* 30(3):575–586. <https://doi.org/10.1111/jvs.12746>

- 699 Valverde-Barrantes OJ, Rocha O (2014) Logging impacts on forest structure and seedling dynamics
700 in a *Prioria copaifera* (Fabaceae) dominated tropical rain forest (Talamanca, Costa Rica). Rev
701 Biol Trop 62(1):347–357
- 702 van der Heijden G, Phillips OL (2009) Liana infestation impacts tree growth in a lowland tropical
703 moist forest. Biogeosciences 6:2217–2226. <https://doi.org/10.5194/bg-6-2217-2009>
- 704 van der Heijden GM, Schnitzer SA, Powers JS, Phillips OL (2013) Liana impacts on carbon
705 cycling, storage and sequestration in tropical forests. Biotropica 45(6):682–692.
706 <https://doi.org/10.1111/btp.12060>
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720 **Table 1** Total species richness (Sp), proportion of liana species (%L_{sp}) and liana abundance (%L_{ab})
 721 in relation to total community, by year and regeneration size classes in a monodominant forest in
 722 Southern Amazonia, Brazil. Note the rapid increase in liana diversity and especially in liana
 723 dominance in all regeneration classes. Seedlings: height \leq 30 cm; saplings: $>$ 30 cm to \leq 60 cm;
 724 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

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738 **Figure captions**

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

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746 **Fig. 2** Average (and confidence intervals) values of the density (100 m⁻²), species richness,
 747 evenness and Shannon's diversity (H') in four regeneration classes (seedlings: height ≤ 30 cm;
 748 saplings: > 30 cm to ≤ 60 cm; poles or young stems: > 60 cm to ≤ 200 cm; and treelets: height >
 749 200 cm and diameter < 5 cm; N= 30 plots per class) in a monodominant forest in Southern
 750 Amazonia. Different letters denote significant differences between surveys in each regeneration
 751 class (Repeated-Measures PERMANOVA). Note that lianas form a small fraction of woody
 752 regeneration early on but become increasingly more important especially in the smallest size-
 753 classes.

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755 **Fig. 3** Average number of individuals and confidence interval of *Brosimum rubescens*, other woody
 756 species, and liana-only regeneration in four classes (seedlings: height ≤ 30 cm; saplings: > 30 cm to
 757 ≤ 60 cm; poles or young stems: > 60 cm to ≤ 200 cm; and treelets: height > 200 cm and diameter <
 758 5 cm; N= 30 plots per class) and four surveys in the monodominant forest in Southern Amazonia,
 759 Brazil. Density = average number of individuals per 100 m² plots. Different letters mean significant
 760 differences between surveys in each regeneration class (Repeated-Measures PERMANOVA).

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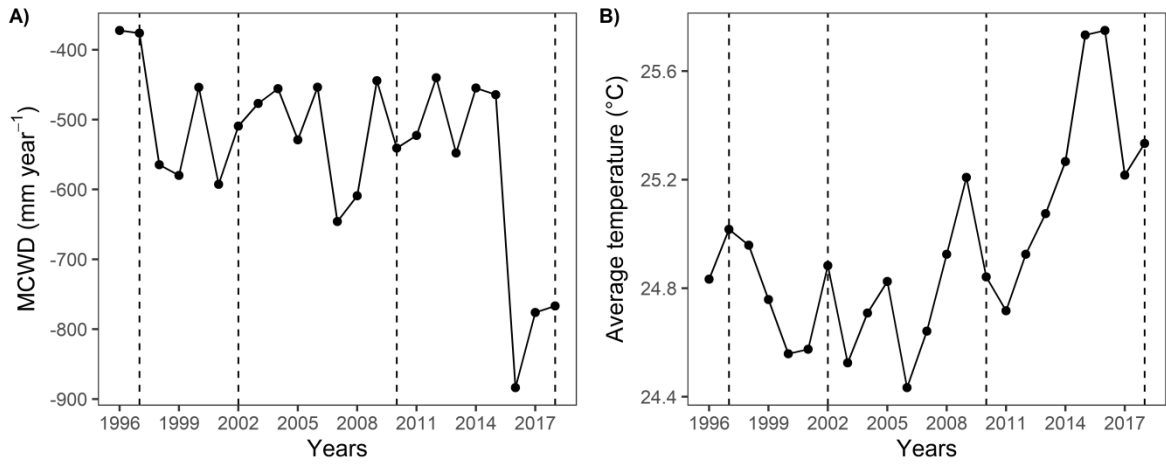
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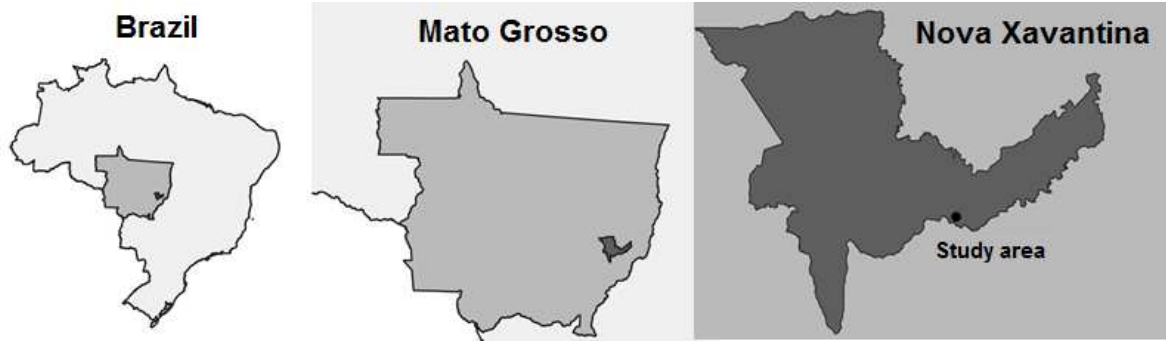
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778 **Figure 1**

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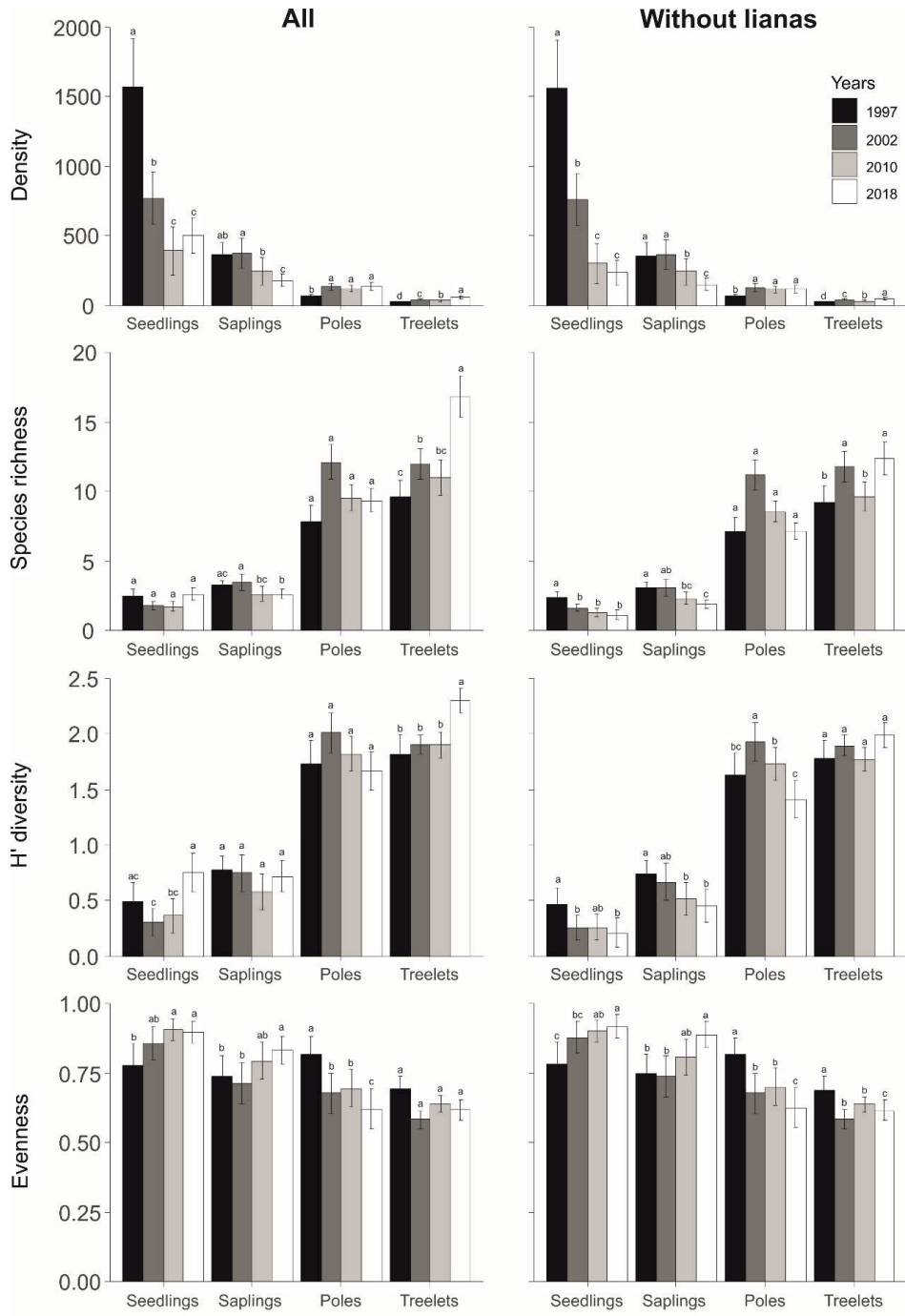
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792 **Figure 2**

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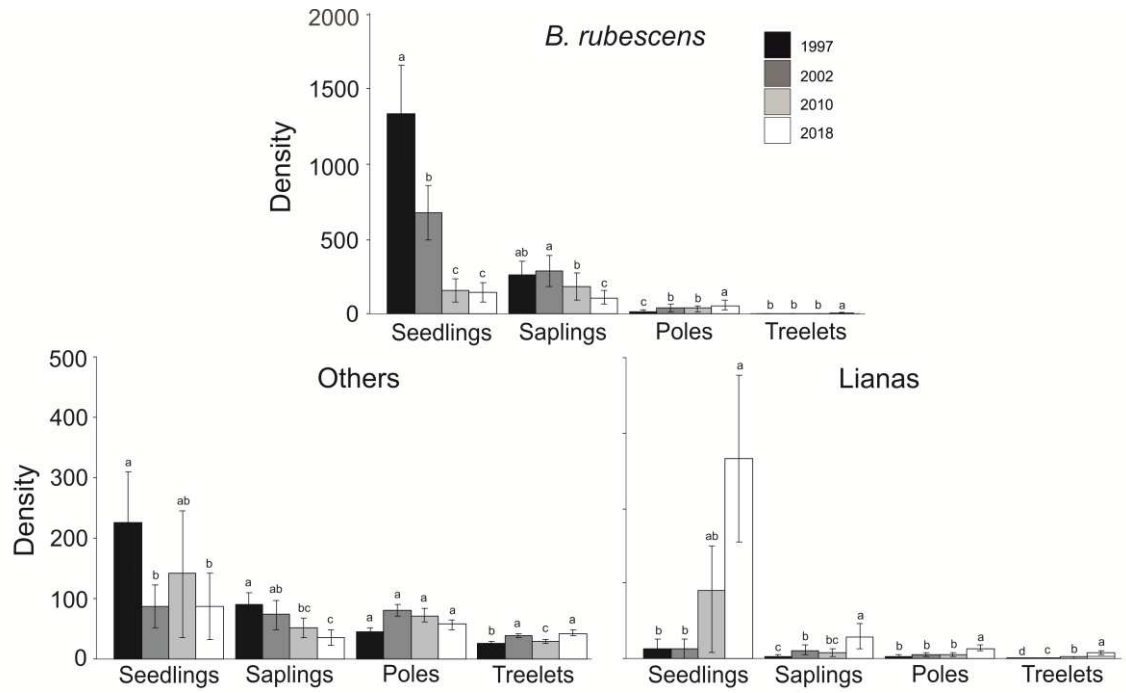
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800 **Figure 3**

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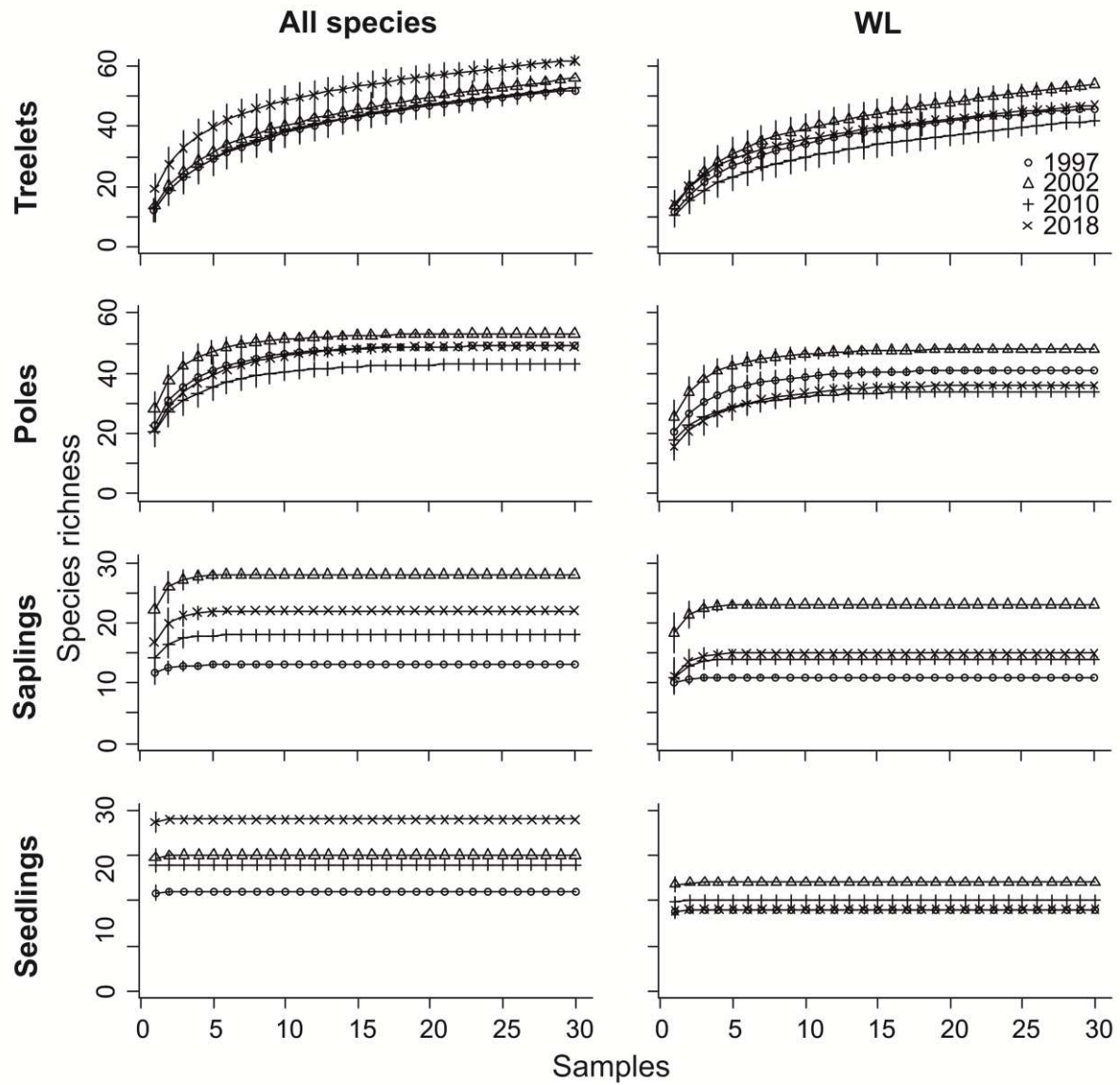
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816 **Supplementary file 1** related to “Drought induces large, long-term changes in the regeneration of a monodominant
 817 Amazon forest” (B. S. Marimon, C. Oliveira-Santos, B. H. Marimon-Junior, F. Elias, E. A. de Oliveira, P. S. Morandi,
 818 N. C. C. dos S. Prestes, L. H. Mariano, O. R. Pereira, T. R. Feldpausch and O. L. Phillips)
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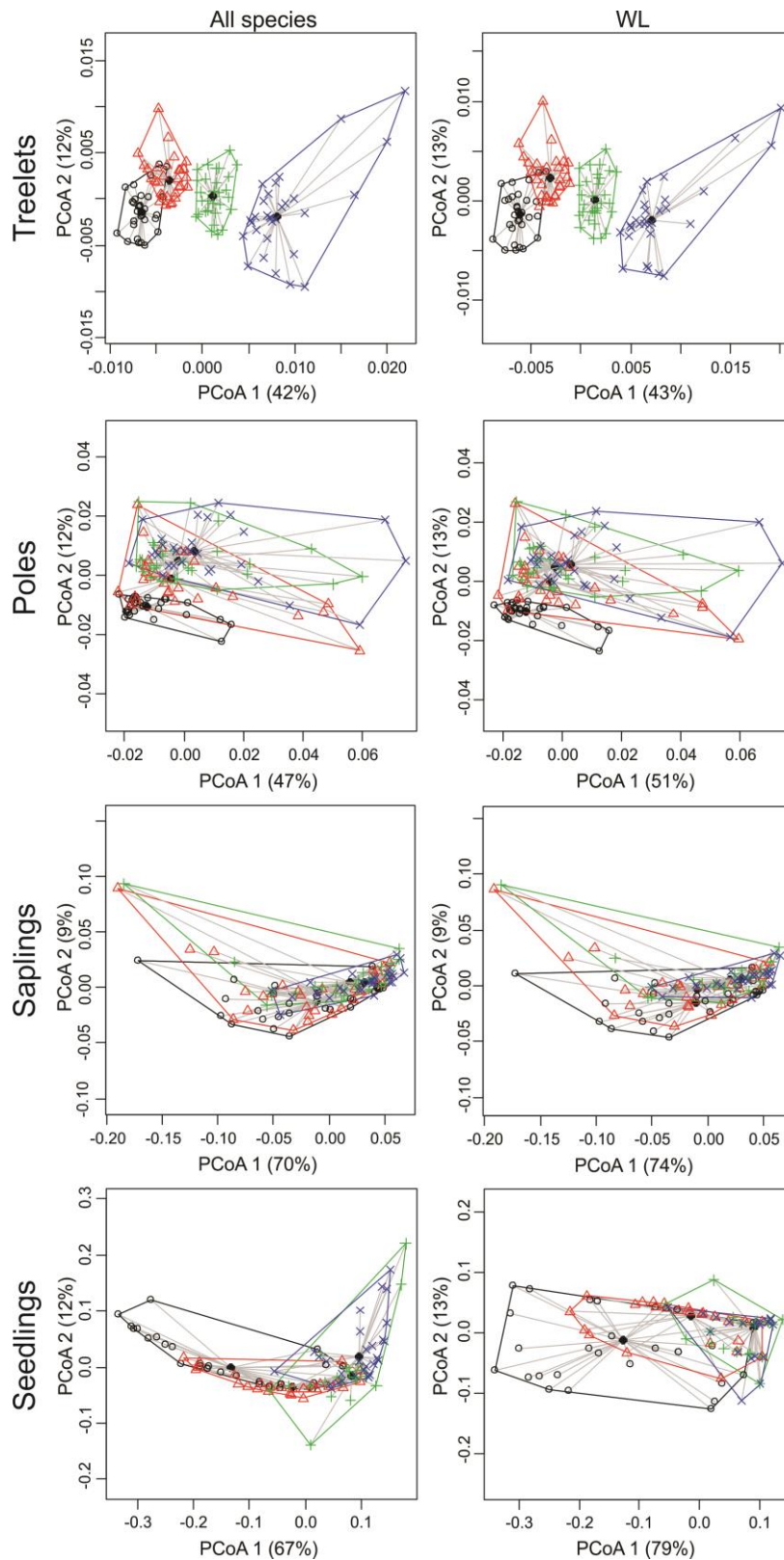
823 **Supplementary Fig. S.1** Sample-based rarefaction curves for species richness for each census (1997, 2002, 2010 and
 824 2018) and for each regeneration size class (seedlings: height ≤ 30 cm; saplings: > 30 cm to ≤ 60 cm; poles or young
 825 stems: > 60 cm to ≤ 200 cm; and treelets: height > 200 cm and diameter < 5 cm) in a monodominant forest in Southern
 826 Amazonia, Brazil. The level of probability of the confidence intervals is 95%. WL= without lianas.
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831 **Supplementary file 2** related to “Drought induces large, long-term changes in the regeneration of a monodominant
 832 Amazon forest” (B. S. Marimon, C. Oliveira-Santos, B. H. Marimon-Junior, F. Elias, E. A. de Oliveira, P. S. Morandi,
 833 N. C. C. dos S. Prestes, L. H. Mariano, O. R. Pereira, T. R. Feldpausch and O. L. Phillips)
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857 **Supplementary Fig. S.2** Beta diversity of treelets, poles, saplings and seedlings over 21 years in a monodominant
 858 forest in Southern Amazonia. Principal coordinates (PCoA) biplots show the Euclidean distance between floristic
 859 composition assemblages within each survey. The black circles indicate group centroids, and lines, symbols and colors
 860 represented the minimum convex hulls around each group. Black: 1997, Red: 2002, Green: 2010 and Blue: 2018. WL=
 861 without lianas.