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# 1 **Drought generates large, long-term changes in tree and liana regeneration in a** 2 **monodominant Amazon forest**

3  
 4 Beatriz S. Marimon<sup>a,b,\*</sup>, Claudinei Oliveira-Santos<sup>c</sup>, Ben Hur Marimon-Junior<sup>a,b</sup>, Fernando Elias<sup>d</sup>,  
 5 Edmar A. de Oliveira<sup>a</sup>, Paulo S. Morandi<sup>a</sup>, Nayane C. C. dos Santos Prestes<sup>b</sup>, Lucas H. Mariano<sup>b</sup>,  
 6 Oriales R. Pereira<sup>a</sup>, Ted R. Feldpausch<sup>e</sup> and Oliver L. Phillips<sup>f</sup>

7  
 8 <sup>a</sup>*Universidade do Estado de Mato Grosso (UNEMAT), Departamento de Ciências Biológicas,*  
 9 *Laboratório de Ecologia Vegetal, Caixa Postal 08, CEP 78.690-000, Nova Xavantina, MT, Brazil;*

10 <sup>b</sup>*Universidade do Estado de Mato Grosso (UNEMAT), Programa de Pós-graduação em Ecologia e*  
 11 *Conservação, Caixa Postal 08, CEP 78.690-000, Nova Xavantina, MT, Brazil;*

12 <sup>c</sup>*Universidade Federal de Goiás (UFG), Programa de Pós-Graduação em Ciências Ambientais,*  
 13 *CEP 74.690-900, Goiânia, GO, Brazil;*

14 <sup>d</sup>*Universidade Federal do Pará (UFPA)/Embrapa Amazônia Oriental, Programa de Pós-*  
 15 *graduação em Ecologia, CEP 66.075-110, Belém, PA, Brazil;*

16 <sup>e</sup>*College of Life and Environmental Sciences, University of Exeter, Exeter, EX4 4RJ, UK;*

17 <sup>f</sup>*School of Geography, University of Leeds, LS2 9JT, Leeds, UK.*

18 \*Corresponding author. E-mail: biamarimon@unemat.br (Faxphone: +55 6634381224)

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30 **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<sup>-1</sup>, 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 m<sup>2</sup> 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  $\geq 20$  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  $\geq 5$  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

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720 **Table 1** Total species richness (Sp), proportion of liana species (%L<sub>sp</sub>) and liana abundance (%L<sub>ab</sub>)  
 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 <sub>sp</sub>	%L <sub>ab</sub>	Sp	%L <sub>sp</sub>	%L <sub>ab</sub>	Sp	%L <sub>sp</sub>	%L <sub>ab</sub>	Sp	%L <sub>sp</sub>	%L <sub>ab</sub>
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<sup>-1</sup>) 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<sup>-2</sup>), 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 m<sup>2</sup> plots. Different letters mean significant  
760 differences between surveys in each regeneration class (Repeated-Measures PERMANOVA).

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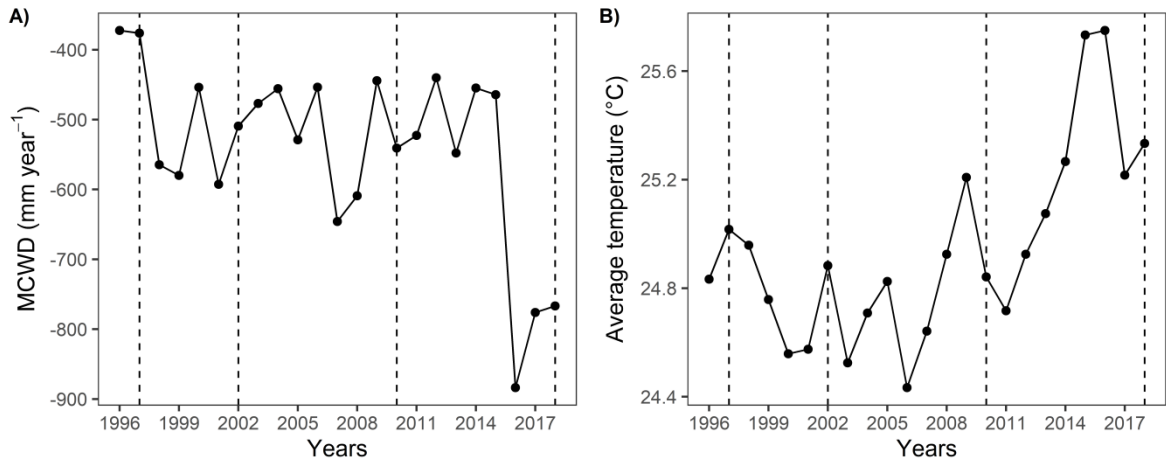
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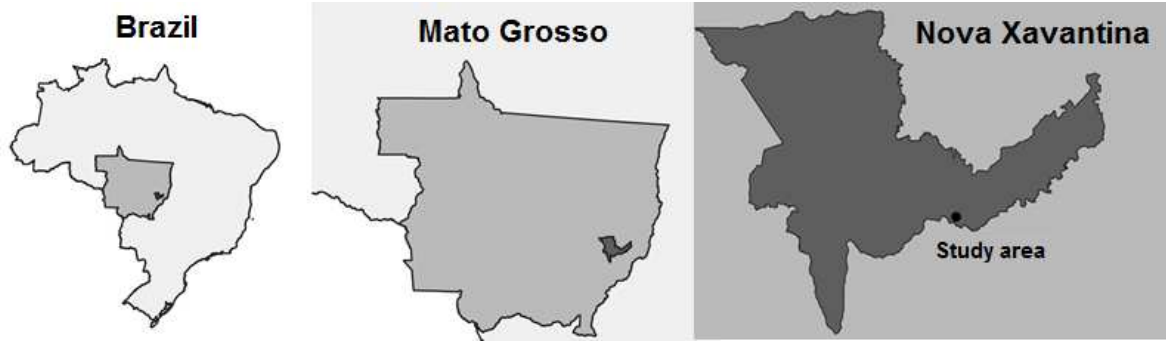
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778 **Figure 1**

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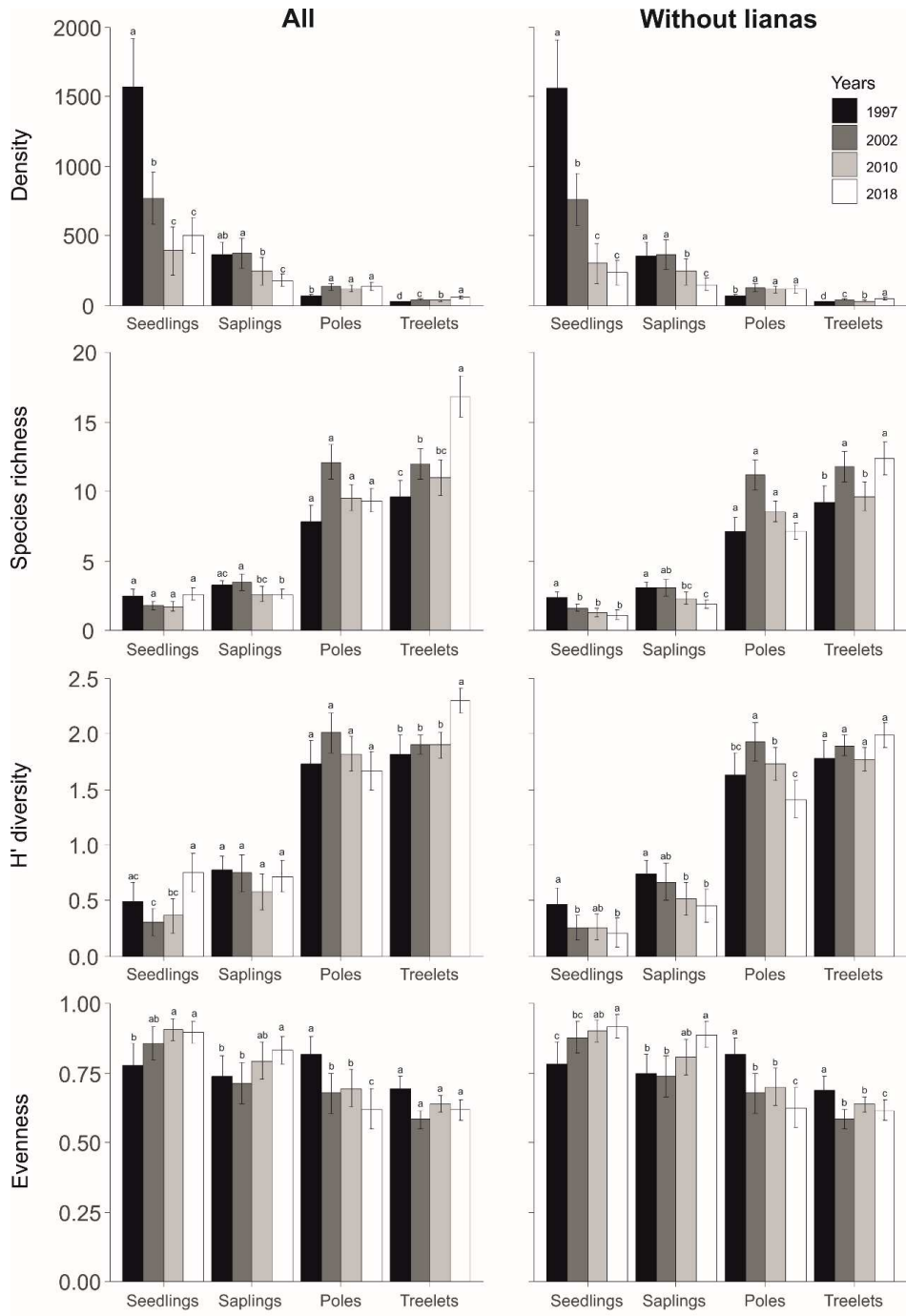
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792 **Figure 2**

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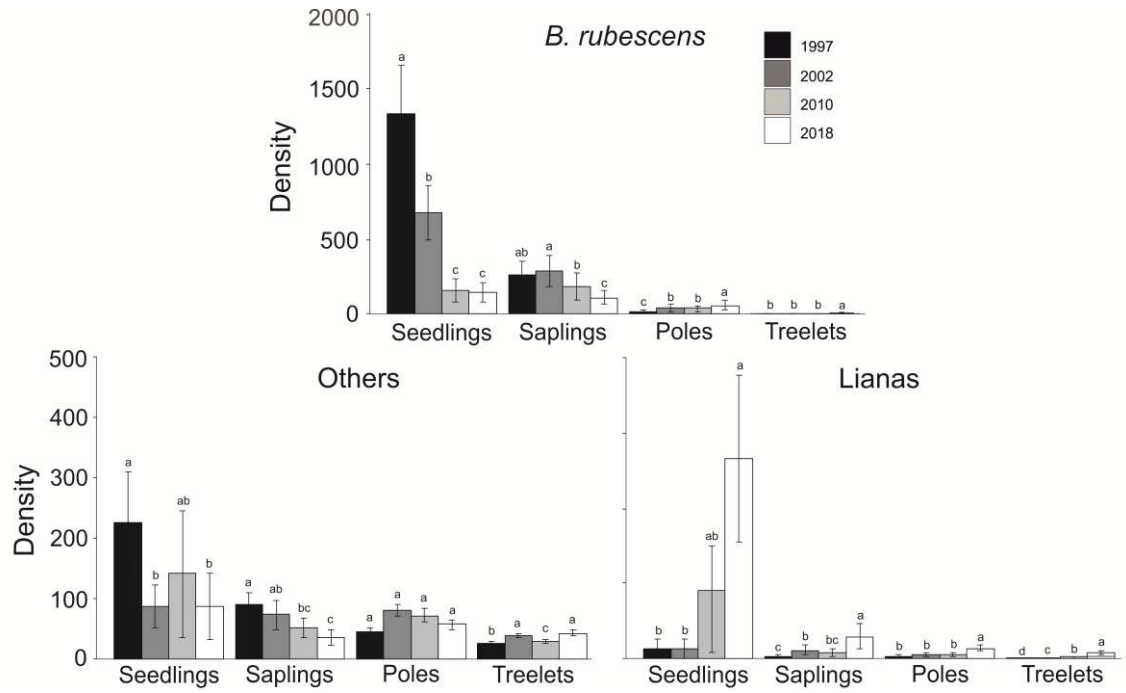
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800 **Figure 3**

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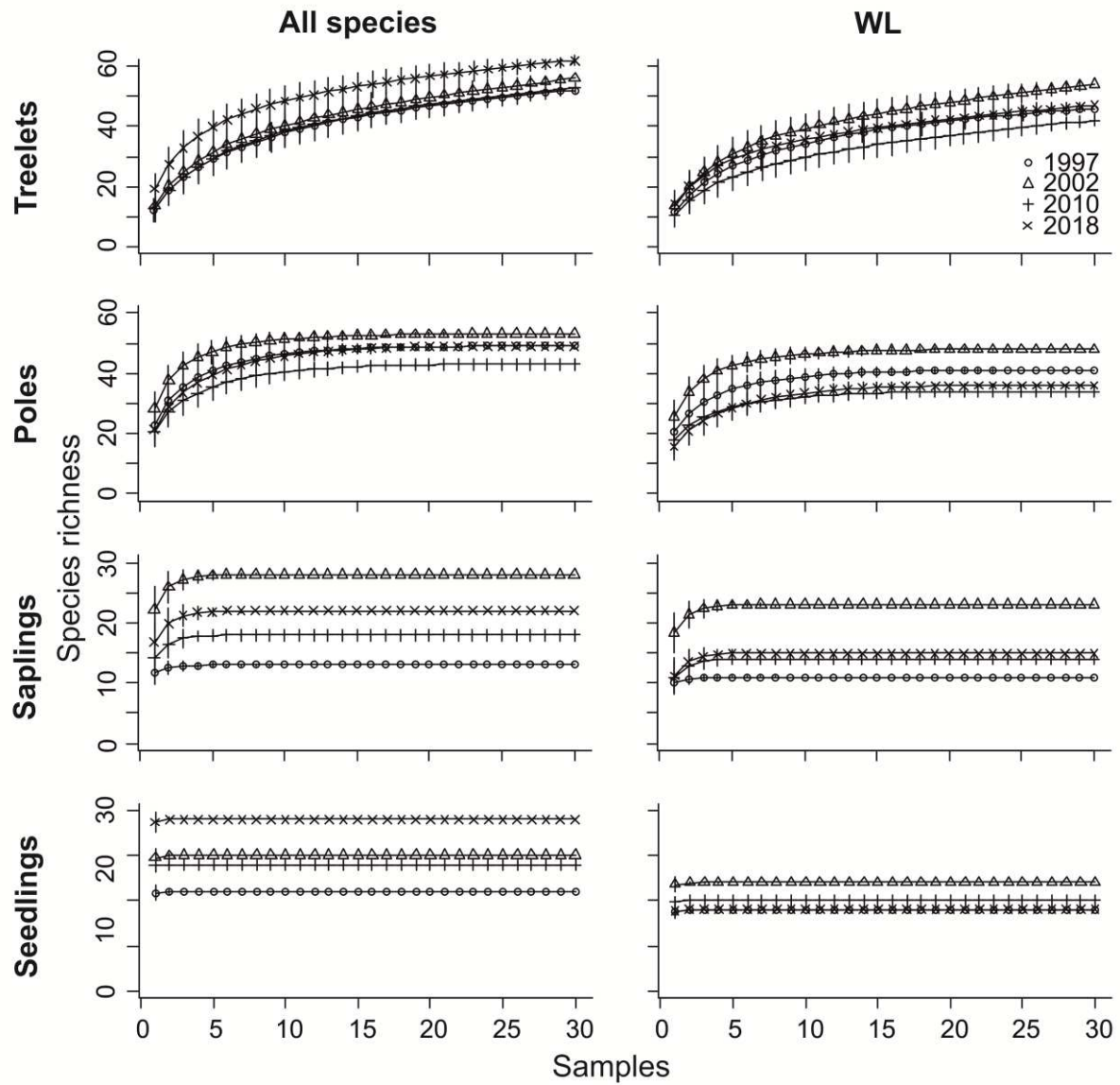
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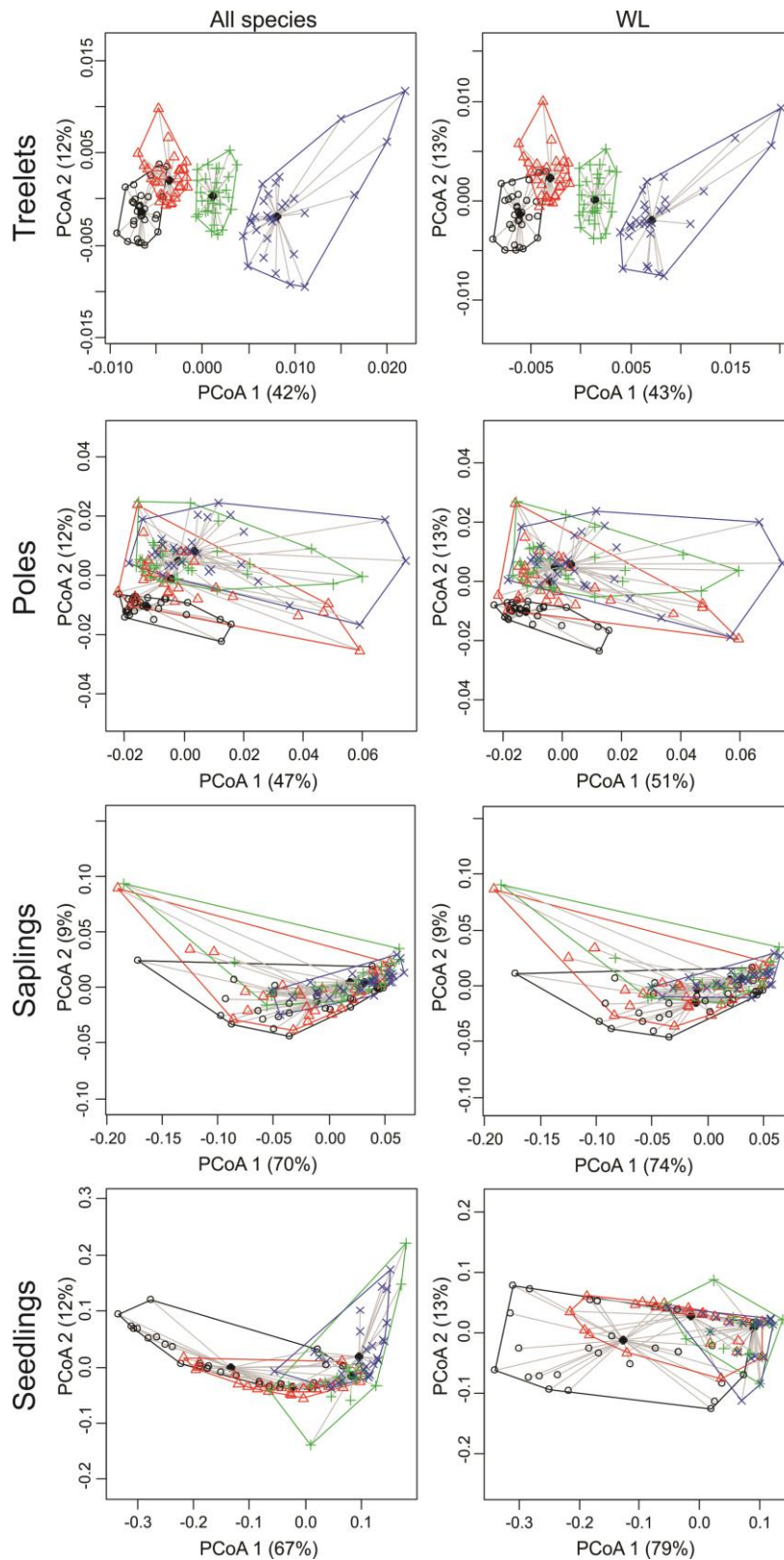
816 **Supplementary file 1** related to “Drought induces large, long-term changes in the regeneration of a monodominant  
 817 Amazon forest” (B. S. Marimon, C. Oliveira-Santos, B. H. Marimon-Junior, F. Elias, E. A. de Oliveira, P. S. Morandi,  
 818 N. C. C. dos S. Prestes, L. H. Mariano, O. R. Pereira, 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  $\leq 30$  cm; saplings:  $> 30$  cm to  $\leq 60$  cm; poles or young  
 825 stems:  $> 60$  cm to  $\leq 200$  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.