1　**Idiosyncratic soil-tree species associations and their relationships with drought in a**

2　**monodominant Amazon forest**

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28 **Abstract**

29 Monodominant forests are characterized by the strong influence of a single species on the

30 structure and diversity of the community. In the tropics, monodominant forests are rare

31 exceptions within the generally highly diverse tropical forest biome. Some studies have shown

32 that tree monodominance may be a transient state caused by successional and demographic

33 variation among species over time. Working in a Brosimum rubescens Taub. (Moraceae)

34 monodominant forest at the southern edge of Amazonia, we tested the hypotheses that local-

35 scale variation in intra- and interspecific spatial patterns of dominant tree species is affected by i)

36 demographic rates of recruitment and mortality following severe droughts, ii) local variation in

37 edaphic properties, and iii) occupation of species in the vertical layer of the forest. We quantified

38 intra- and interspecific spatial patterns and edaphic associations of the five most abundant

39 species using aggregation and association distance indices, and examined changes over time. We

40 found some support for all hypotheses. Thus, intra- and interspecific spatial patterns of most

41 species varied over time, principally after severe drought, emphasizing species-level variability

42 and their interactions in sensitivity to this disturbance, even as B. rubescens monodominance was

43 maintained. While positive and negative spatial associations with edaphic properties provide

44 evidence of habitat specialization, the absence of negative spatial associations of B. rubescens

45 with edaphic properties indicates that this species experiences little environmental restriction,

46 and this may be one of the factors that explain its monodominance. Spatial repulsion and

47 attraction between species in the same and in different vertical layers, respectively, indicates

48 niche overlap and differentiation, while changes over time indicate that the relationships between

49 species are dynamic and affected by drought disturbance.

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

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1. Introduction

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

The exact causes of tropical monodominance remain elusive, in spite of considerable effort (Torti et al., 2001; Peh et al., 2011a, 2011b; Marimon et al., 2016). Nevertheless, a potentially key finding may be that monodominance emerges when normal processes of ecological succession and recovery of alpha diversity are greatly slowed (Peh et al., 2011a; Newberry et al., 2013). In this case, the monodominance can persist for a long period of time even in periods of marked disturbances (Ibanez and Birnbaum, 2014), although why this may be is unclear. Within Amazonia and potentially throughout the tropics, drought is a major disturbance driver, with important consequences for forest structure and dynamics (Phillips et al., 2009; Bennett et al., 2015; Brienen et al., 2015; Doughty et al., 2015; Feldpausch et al., 2016) - and potentially also for species diversity as most moist forest species do not tolerate long dry

78   seasons (Clinebell et al., 1995; Esquivel-Muelbert et al., 2016, 2017). Most notably over the past

79   decade at least two major droughts have affected southern Amazonia (in 2005 and 2010, cf.

80   Phillips et al., 2009; Lewis et al., 2011; Marengo et al., 2011), with additional unusual drying in

81   Mato Grosso during 2007/2008 (Brando et al., 2008). These droughts have driven increases in

82   mortality in Amazonia and elsewhere (e.g., Phillips et al., 2009, 2010; Brienen et al., 2015), and

83   periodic drying may also be partly responsible for the 'hyperdynamic' nature of forests at the

84   southern Amazon margin (Marimon et al., 2014). However, very little is known on how intra-

85   and interspecific spatial patterns of species in monodominant forests respond over time to

86   tropical drought. Here, evaluation of the spatial patterns of tree species might help to understand

87   intrinsic demographic processes in these communities, as spatial patterns reflect different factors

88   that act upon the survival of individuals (Getzin et al., 2014; Luo and Chen, 2015; Xie et al.,

89   2015). For example, if monodominance is promoted by moisture stress (because relatively few

90   tropical moist species thrive in more seasonal forests), then we would expect the dominants in

91   these forests to respond positively to drought - or at least to be less adversely affected than their

92   neighbours.

93   Drought is not the only factor capable of strongly impacting tropical tree distributions.

94   For instance, the traditional Janzen-Connell (J-C) model proposes that after the initial

95   establishment of species, density-dependent biotic processes reduce survival and intraspecific

96   aggregation, thus tending towards spatial regularity of individuals and enhancing overall

97   community diversity (Janzen, 1970; Connell, 1971). However, in tropical communities, these "J-

98   C processes" might be disguised by the effect of environmental conditions and niche separation

99   among life stages (Soliveres et al., 2010; Zhu et al., 2013; Xie et al., 2015), as habitat

100   specialization and tolerance limits means that intraspecific aggregations of tree species are also

101   determined by the spatial structuring of resources (Arieira et al., 2016). Notably, edaphic

102   conditions comprise one of the most variable axes of the spatial niche, and are among the best

103   predictors of distribution patterns of tree species (e.g., Harms et al., 2001; Phillips et al., 2003;

104   Getzin et al., 2008). For instance, the ability to accumulate toxic elements such as aluminum and

105   manganese in leaves can provide a localized competitive advantage for some species at sites with

106   higher abundance of these elements (Haridasan, 2000), while species intolerant to those elements

107   are likely to have distributions anti-correlated with the distribution of toxic metals and of metal-

108   tolerators (Malavolta et al., 1997).

109   Naturally, as well as showing differing tolerances of stress factors, plant species compete

110   with each other for essential resources needed for plant establishment, development, and

111   reproduction, notably water, light, nutrients, and space (Barot and Gignoux, 2004). Therefore,

112   for prolonged coexistence to occur there must be differentiation in some niche dimensions

113   (Amarasekare, 2003), because niche similarity intensifies interspecific competition and

114   consequently reinforces negative interactions among species (Zhang et al., 2010; Sühs and

115   Budke, 2011). The separation of the species among vertical layers in forests indicates niche

116   differentiation, since occupation of each layer is related to the functional characteristics of

117   species, such as photosynthetic capacity (Ellsworth and Reich, 1993), leaf traits (Bündchen et al.,

118   2015), growth (Enquist et al., 2011) and pollinator vectors (Yamamoto et al., 2007). Thus,

119   species that occupy the same layer are more likely to compete with one-another and hence may

120   be more likely to separate spatially in the horizontal dimension (Sühs and Budke, 2011).

121   Conversely, if stochastic community processes such as extinction, speciation and limitation of

122   dispersion then species patterns of spatial distribution are more likely to be stochastic in time and

123   space (Chave and Leigh Jr., 2002; Hubbell, 2005).

124   Thus, assessing these multiple factors and their interactions over time is essential for

125   understanding better the ecological patterns that regulate the distribution of species at different

126   spatial scales in tropical forests. This study evaluates the effects of severe drought and of edaphic

127   properties on intra- and interspecific spatial patterns of tree species over time in a monodominant

128 forest in southern Amazonia. We tested the hypotheses that i) demographic rates (recruitment

129 and mortality) after severe droughts, ii) spatial structure of edaphic properties, and iii)

130 occupation of species in the vertical layer of the forest may each account for variation in intra-

131 and interspecific spatial patterns of dominant tree species at the local scale.

132

133 **2. Material and Methods**

134 2.1. Study Area

135   This study was conducted in a semideciduous seasonal forest located at $14^{\circ}50'47''$ S and

136 $52^{\circ}08'37''$ W, in the locality of Fazenda Veracruz, close to Nova Xavantina, in the eastern region

137 of the state of Mato Grosso. This forest has been monitored using permanent plots since 1996,

138 and is characterized by the monodominance of Brosimum rubescens Taub. (Moraceae), which

139 locally dominates the forest biomass (Marimon et al., 2001a). The monodominant patch is found

140 within the wider transition zone between the Amazon rainforest and Cerrado biomes (Marimon

141 et al., 2001a, 2014).

142   The climate of the region is tropical with dry winter (Aw in the Köppen classification),

143 with strong precipitation seasonality and two well-defined periods, rainy from October to March

144 and dry from April to September (Alvares et al., 2013). Mean annual rainfall and temperature are

145 ~1,500 mm and 24.7º C, respectively, and altitude ranges from 190 to 280 m (Marimon et al.,

146 2001a). Severe droughts were experienced in the study area in 1998, 2005, 2007 and 2010 (Zeng

147 et al., 2008; Lewis et al., 2011; Feldpausch et al., 2016).

148   The soil in the forest is a plintosol, being dystrophic, acidic, shallow, and with low

149 cation-exchange capacity, base saturation, and Ca/Mg ratio (1:3). Gravel fraction is around 28%

150 down to 10-cm depth, with intermediate K levels, and high proportion of Fe (Marimon et al.,

151 2001a).

152

153   2.2. Data collection

154   In 1996, Marimon et al. (2001a) established 60 contiguous subplots of 10 x 10 m (0.6 ha)

155   in the Brosimum rubescens patch, where all individuals with diameter at breast height ≥ 5 cm

156   were measured and identified. In 2001, 2004, 2010, and 2013, all individuals were remeasured

157   and those that reached the minimum limits (DBH ≥ 5 cm) were included in the sampling.

158   Identification was performed in the field and by comparing samples to herbarium vouchers from

159   Herbarium NX (UNEMAT-Nova Xavantina), UB (Universidade de Brasília), and from virtual

160   herbaria (The New York Botanic Garden, Kew Garden, and CRIA). Nomenclature of taxa was

161   reviewed according to the List of Flora Species of Brazil (BFG, 2015), and botanical

162   classification followed the APG IV (2016). Data used in this study are stored in 'ForestPlots.net'

163   digital platform (Lopez-Gonzalez et al., 2011).

164   Detailed information on the chemical and physical properties of the soil are found in

165   Marimon et al. (2001a), who collected random samples of surface soil (0–10 cm depth) in each

166   10 x 10 m subplot. Percentage gravel was determined by sieving particles through a sieve with 2

167   mm mesh, and pH was determined by soil-water suspension (ratio soil: water 1:2.5; Anderson

168   and Ingram, 1993). Exchangeable Ca, Mg, and Al concentrations were determined in 1 mol L^{-1}

169   KCl (Sumner and Miller, 1996) and P, K, Fe, Mn, Cu, and Zn contents in Mehlich-I solution

170   (0.0125 mol L^{-1} + HCl 0.05 mol L^{-1}; Nelson et al., 1953).

171

172   2.3. Data analysis

173   We selected the five tree species with the highest absolute density in the first inventory

174   (1996) distributed between the overstory (Brosimum rubescens Taub. – Moraceae and

175   Tetragastris altissima (Aubl.) Swart – Burseraceae) and understory strata (Amaioua guianensis

176   Aubl. – Rubiaceae, Cheiloclinium cognatum (Miers) A.C.Sm. – Celastraceae, and Protium

177   pilosissimum Engl. – Burseraceae). We compared the density of these species among inventories

178   (1996, 2001, 2004, 2010, and 2013) using ANOVA of repeated measures and using Tukey's

179   multiple comparison as a post hoc (Zar, 2010) in the R program using the 'stats' package (R

180   Development Core Team, 2016). Assumptions of residual normality and variance homogeneity

181   were checked using the Shapiro-Wilk's and Bartlett's tests, respectively (Zar, 2010).

182   To assess variation in demographic rates in each species among inventories, we

183   calculated mean annual mortality and recruitment rates - hereafter mortality and recruitment -

184   based on the abundance of species for different diameter classes (Sheil et al., 1995). We

185   standardize the best interval between the diameter classes by the formula IC = A/K (A=

186   amplitude of values; K= Sturges' constant) (Spiegel, 1976). Here, the formula guarantees

187   proportionality in the distribution of individuals among diameter classes. We square-root

188   transformed mortality and recruitment values among diameter classes and subsequently plotted

189   them in frequency histograms. We compared mean annual mortality and recruitment rates of

190   diameter classes for each species (1996-2001, 2001-2004, 2004-2010, and 2010-2013) using the

191   Wilcoxon test, and between periods using Friedman's and Dunn's as post hoc tests (Zar, 2010) in

192   the R program using package 'stats' (R Development Core Team, 2016). To evaluate the

193   influence of density (fixed effect) of each species on the mortality rate over time, we use linear

194   mixed effect models (GLMM) (Zuur et al., 2009) in the R program using 'lme4' package (Bates

195   et al., 2013). Outliers that exceeded the maximum limit of 3 SD (standard deviation) were

196   excluded from the model using 'outliers' package (Komsta, 2015). Because they are measures

197   repeated in space and time, we use the subplots as a random effect in the GLMM models. The

198   assumptions of the GLMM were verified by graphical analysis (Zuur et al., 2009).

199   We described the intraspecific spatial patterns of species and edaphic properties among

200   inventories using the Aggregation Index - Spatial Analysis by Distance Indices – SADIE (Perry,

201   1995, 1998). In order to define aggregation, the index estimates distance from regularity (D), i.e.,

202   the distance individuals from a population must travel between sampling units (subplots) so that

203   both units have the same density. In this case, sampling units with higher D values have higher

204   aggregation and those with lower D values have lower aggregation, and it is possible to evaluate

205   the partial contribution of gaps and aggregates to the overall spatial pattern of the population. We

206   performed kriging of the species spatial distribution in each inventory with the Surfer program

207   (Golden Software, 1999). Aggregation Index values higher or lower than 1, when significant,

208   indicate aggregation and regularity, respectively, whereas non-significant values indicate

209   randomness (Perry, 1995, 1998).

210   We described interspecific spatial patterns of species (i.e., the spatial associations of each

211   species to each other, and to edaphic properties) using the SADIE Association Index (Perry,

212   1997; Perry et al., 1999). Based on Pearson's correlations, this index calculates pair overlap of

213   two datasets and varies from +1 (positive association, $p < 0.025$) to -1 (negative association, $p >$

214   0.975). Thus, when there is spatial association (two-tailed p-values), high values of the

215   association index indicate a high relation between the spatial distribution of the species (or with

216   the characteristics of the soil). Positive associations are characterized by the spatial overlap

217   between two species, in other words, occurs when there is spatial coincidence between the

218   aggregates and the gaps of both species. In contrast, negative associations are observed when

219   clusters and gaps are not coincident in space and, therefore, generate negative association index

220   values (cf. Perry et al., 1999). The significance of Aggregation and Association Indexes values

221   was evaluated using Monte Carlo permutations (Perry, 1998). Calculations of Aggregation and

222   Association Indices were performed using the software SADIEShell 1.2 (Perry et al., 1996;

223   Perry, 1998). For all analyses, we used an alpha level of 5%.

224

225   **3. Results**

226   3.1. Intraspecific spatial patterns and population demography

227   The mortality and recruitment rates of the species in the subplots did not show significant

228   variation over time (Figure 1). However, within diameter classes, density, mortality and

229   recruitment rates did vary by years, mainly after the severe 2005, 2007 and 2010 droughts (Figs.

230   2, 3; Table 1). Thus, both Amaioua guianensis and Brosimum rubescens had significantly

231   reduced total densities in the final two inventories (Fig. 3). Notably, the mortality rate among the

232   diameter classes of A. guianensis exceeded recruitment in 2004-2010 and 2010-2013, excluding

233   all individuals with diameter larger than 20.1 cm (Fig. 2). Brosimum rubescens also lost

234   individuals over time but remained strongly dominant. The relative density of A. guianensis, B.

235   rubescens, C. cognatum, P. pilosissimum and T. altissima in the final inventory was 6.9, 39.9,

236   10.3, 24.8 and 9.7%, respectively. Brosimum rubescens also had strong recruitment among

237   almost all diameter classes in the final period (Fig. 2; Table 1). The species T. altissima and C.

238   cognatum did not vary significantly in density between inventories (Fig. 3). However, from 2010

239   to 2013, mortality of C. cognatum, mainly in larger size classes, outnumbered recruitment (Fig.

240   2; Table 1). Mortality and recruitment rates among diameter classes of P. pilosissimum and T.

241   altissima did not show significant variation among the periods analyzed (Fig. 2; Table 1). Yet, P.

242   pilosissimum had the greatest proportional variation in density among inventories, with net gains

243   of 51, 32, and 23% in the censuses of 2001, 2004, and 2010, respectively compared to the first

244   inventory (Figs. 2, 3; Table 1). In the final inventory, after the 2010 drought, this species

245   accumulated losses of 13% in number of individuals, mainly those of larger diameter classes

246   (Figs. 2, 3; Table 1). In addition, mortality of all species evaluated was positively related with

247   density in the subplots (Table A.1).

248   The five most abundant species varied in how their individuals are distributed locally.

249   Brosimum rubescens and Protium pilosissimum maintained random and aggregated spatial

250   patterns among inventories, respectively, in spite of experiencing variations in density (Figs. 3,

251   4, A.1). The other three species showed variations in intraspecific spatial patterns among

252 inventories, mainly after the severe drought in 2010 (Figs. 4, A.1). Amaioua guianensis had

253 aggregated distribution in the first four inventories, and random distribution in 2013, while

254 Tetragastris altissima showed spatial randomness in the first three inventories and aggregation in

255 2010 and 2013 (Figs. 4, A.1). On the other hand, spatial distribution of Cheiloclinium cognatum

256 was random in 1996 and 2001, and regular in 2004. After the 2005-2007 droughts, the

257 intraspecific distribution of C. cognatum returned to the random pattern of the two first

258 inventories (Figs. 4, A.1).

259

260 3.2. Spatial relationships of species vs. edaphic properties

261   We observed significant spatial associations between the dominant tree species and

262 edaphic properties, as well as changes in these relationships over time (Table 2; Figs. A.1, A.2).

263 The two most abundant species in the study area, Brosimum rubescens and Protium

264 pilosissimum, were positively associated with Ca, K, Mn and Ca/Mg, and showed no negative

265 spatial relationships with any edaphic properties. B. rubescens was exclusively associated with

266 Al, and P. pilosissimum was associated with Mg, Cu, pH, and gravel (Table 2; Figs. A1, A.2).

267 Amaioua guianensis showed negative association with Ca, Mg, K, Zn, Ca/Mg, and gravel, and

268 positive association with Fe (Table 2). However, in the last inventory, after the 2010 drought,

269 these spatial associations were not observed. Conversely, spatial associations of Cheiloclinium

270 cognatum and Tetragastris altissima only started to occur in the last two inventories; C.

271 cognatum showed negative associations with Ca, P, and Al, and positive associations with pH. In

272 turn, T. altissima was positively associated with Ca, Mg, K, Mn, Cu, Zn, pH, and gravel (Table

273 2; Fig. A1).

274

275 3.3. Interspecific spatial patterns of species

276   Differences in interspecific spatial associations are related to the position of the species in

277   the vertical layers of the forest (Table 3; Fig. A.1). For example, two typical understory species,

278   Amaioua guianensis and Protium pilosissimum, were negatively associated in space in the first

279   three inventories (1996, 2001, and 2004) prior to the droughts of 2005, 2007 and 2010 (Table 3;

280   Fig. A.1). These species show distinct associations with overstory species: A. guianensis was

281   negatively associated with Tetragastris altissima in 2010, and P. pilosissimum was positively

282   associated with Brosimum rubescens in nearly all inventories (Table 3; Fig. A.1). Likewise, the

283   overstory species, B. rubescens and T. altissima, were negatively associated between 2001 and

284   2004 (Table 3; Fig. A.1).

285

286   **4. Discussion**

287   Our results show that spatial patterns of dominant species are subject to changes

288   according to changes in demography after intense drought events, and partly reflect spatial

289   structure of soil properties in the habitat and the position of the species in the forest strata,

290   providing support to each of our initial hypotheses. Nevertheless, the monodominance and

291   spatial pattern of Brosimum rubescens were maintained over time, even with variations in

292   density after the intense drought events of 2005 and 2010, demonstrating the strong resistance

293   and resilience of the species. The absence of negative spatial associations of B. rubescens with

294   edaphic characteristics indicates lack of environmental restriction here, and this may help to

295   explain the maintenance of its monodominance in the study area.

296

297   4.1. Intraspecific spatial patterns and demography

298   The dominant tree species show variation in intraspecific spatial patterns over time,

299   consistent with demographic oscillations related to severe droughts, corroborating our initial

300   hypothesis. This result shows the heterogeneity and spatial dynamics of forest communities, as

301   well as the different strategies used by species to occupy space, may vary over time. For

302   instance, the decrease in aggregation towards spatial randomness of Amaioua guianensis might

303   be related to variations in density over time and to the initial proportions of individuals among

304   life stages. In this case, the self-thinning process which recruits experience as their life stages

305   advance may have been intensified by severe droughts, as observed by Johnson et al. (2014) and

306   Clyatt et al. (2016) in temperate forests. On the other hand, the fact that intraspecific spatial

307   patterns of Brosimum rubescens and Protium pilosissimum were maintained among inventories,

308   even while there were variations in density and demography, shows the robustness of the

309   intraspecific distributions of these species, remaining unchanged even in the face of significant

310   drought disturbance. Thus, the events that occurred in the study area may not have been

311   sufficient to cause changes in the spatial distribution of these species, as observed by Elias et al.

312   (2013) in a cerradão (savanna woodland).

313   The predominantly random spatial pattern of B. rubescens and the slightly decrease in

314   total density over time is an indication that density-dependent mortality is the major determining

315   factor of the spatial distribution of this species, and that this process has intensified over time.

316   The unimodal height distribution of this species and its dominance in the canopy of the study

317   area (Marimon et al., 2001a), suggest that most individuals are in the intermediate or advanced

318   life stages, which are generally distributed randomly or regularly according to the Janzen-

319   Connell model (Stoll and Bergius, 2005; Getzin et al., 2011; Clyatt et al., 2016). The J-C model

320   also explains the spatial history of Cheiloclinium cognatum in the first three inventories, prior to

321   the 2005 drought, when the species showed decrease in spatial randomness towards regularity.

322   However, the fact that it returned to spatial randomness after the 2005 drought and that it

323   maintained this pattern until the last inventory emphasizes the sensitivity of this species to this

324   disturbance, as well as its recurrence over time. Similarly, the high mortality rates of C.

325   cognatum, which exceeded recruitment over the latest periods, appear responsible for the

326   changes and maintenance of random spatial patterns after droughts. Meanwhile, the increased

327   recruitment of B. rubescens in the final inventories reveals a clear difference in the resilience

328   capacity of this species and C. cognatum in the face of severe droughts. Considering the

329   demographic dynamics of the main species and the resilience of B. rubescens after the drought

330   events, we expect that the monodominance will be maintained in the long term even in the face

331   of occasional disturbances.

332   The changes in Tetragastris altissima from random to aggregate spatial patterns after

333   drought is an indication that this disturbance concentrated mortality at sites with higher water

334   stress (Luo and Chen, 2015; Challis et al., 2016; Panayotov et al., 2016). This might have led to

335   the aggregation of the surviving individuals, even under density-dependent effects, considering

336   this pattern is more influenced by habitat than intraspecific associations (Luo et al., 2012; Arieira

337   et al., 2016). Similar results were found by Elias et al. (2013) in a 'savanna woodland' in the

338   transition zone between Amazon rainforest and Cerrado. These authors reported that droughts

339   determine tree species aggregation over time, confirming the sensitivity of intraspecific spatial

340   patterns to predict these disturbances, as suggested by Flugge et al. (2012).

341

342   4.2. Spatial relationships of species vs. edaphic properties

343   Positive spatial associations between tree species and the edaphic properties analyzed

344   indicate the influence of habitat on spatial distribution patterns, and show that there is niche

345   specialization among species. Positive spatial associations of Brosimum rubescens and Protium

346   pilosissimum with Ca/Mg, Ca, K, and Mn demonstrate the wide niche range of these species and

347   might justify their dominance in the study area. This is due to the fact that Ca and K are shown to

348   be important modulators of tree species structure in tropical forests (Wright et al., 2011; Santiago

349   et al., 2012; Lloyd et al., 2015), acting together with Mn in growth, carbohydrate transport,

350   photosynthesis, gas exchanges, hormone control, and mainly, resistance to diseases (Malavolta et

351 al., 1997). Therefore, the positive associations of species with these elements, mostly K, might

352 favor reproductive success and high abundance in the study area. This corroborates the findings

353 of Marimon et al. (2001b), who recorded high K and Mn concentrations in leaves of B.

354 rubescens, which are generally consistent with concentrations at the soil level (Brady and Weil,

355 1996). In addition, the absence of negative associations between B. rubescens and edaphic

356 properties indicates that the soils of the study area do not present restrictions to their

357 establishment, and therefore favour the monodominance of the species.

358 Amaioua guianensis showed negative spatial association with Ca/Mg, Ca, Mg, K, and

359 gravel indicating that its spatial distribution is independent of fertility parameters and that this

360 species most likely prefers to occupy less drained locations. The soil A horizon in the study area

361 is shallow (~80 cm) with high concentrations of hydromorphic laterites, which can impede

362 drainage locally according to topographic position (Marimon-Junior, 2007). Botrel et al. (2002)

363 also described negative relationships of species from the family Rubiaceae with soil drainage in

364 a semi-deciduous seasonal forest of Southeastern Brazil. Hence, this result might be an

365 indication of the sensitivity of understory species to water restrictions (Tobin et al., 1999),

366 mainly in years of severe droughts recorded in the inventories over time (Zeng et al., 2008;

367 Lewis et al., 2011). On the other hand, positive spatial associations of A. guianensis with Fe may

368 indicate habitat preference linked to the benefits of this element in photosynthesis, production of

369 leaves, and flowering (Belkhodja et al., 1998; Molassiotis et al., 2006). In this case, the positive

370 spatial association with Fe might be a strategy to avoid reduced photosynthetic rates, since this

371 species occurs in the understory and has restricted access to lighting. However, Protium

372 pilosissimum (Burseraceae) shares the same forest layer with A. guianensis (Rubiaceae) and was

373 not associated to this element. Recently, Souza et al. (2016) have shown that phylogenetic

374 factors strongly control large-scale ecological variation in Amazon tree traits related to carbon

375 cycling and storage (demography, size, and wood density), yet the extent to which phylogeny is

376   a marker for variation in other nutrient processes in Amazon forests remains largely unknown.

377   Our study suggests that, for Fe at least, marked phylogenetically-associated niche differentiation

378   in nutritional requirements may exist at a remarkably fine spatial scale, even within the same

379   vertical strata and hence the same light environment.

380   Temporal changes in spatial associations of species according to edaphic properties

381   revealed marked spatial dynamics in the forest community, potentially related to population

382   imbalance and niche partitioning among life stages, corroborating with our initial hypothesis. It

383   thus appears that in our study site the relevance of edaphic properties in determining spatial

384   patterns of tree species may depend on the ontogenetic stage of individuals. Other work in

385   tropical ecosystems (Comita et al., 2007; Kanagaraj et al., 2011; Arieira et al., 2016) found that

386   the relationship of tree species with habitat decreases with ontogenetic advancement due to the

387   increase in intraspecific competition driven by density-dependent mortality. In our forest, the

388   positive spatial associations of Tetragastris altissima with Ca, Mg, Mn, Cu, Zn, and pH,

389   recorded only in the two last inventories, might be related to the intense demographic variations

390   (e.g., mortality and recruitment) of this population in this period. In this case, mortality of

391   individuals reduced intraspecific competition and led to greater spatial aggregation in the

392   population. On the other hand, the negative spatial association of Cheiloclinium cognatum with

393   Ca may be related to the direct competition with Protium pilosissimum and T. altissima were

394   positively associated with this element among the inventories.

395

396   4.3. Interspecific spatial patterns

397   The marked negative spatial association between species of the same forest layer, such as

398   Brosimum rubescens and Tetragastris altissima in the overstory, and Amaioua guianensis and

399   Protium pilosissimum in the understory, is evidence of niche overlap. Elsewhere, similar lighting

400   requirements might have induced competition among canopy species in a subtropical forest,

401　determining spatial repulsion between their individuals (Sühs and Budke, 2011). Similarly,

402　congeneric species in a temperate forest showed high level of interspecific competition

403　intensified by trophic similarities between them (Zhang et al., 2010). Yet, equally, in our

404　monodominant forest the positive association between species from different layers (e.g., B.

405　rubescens and P. pilosissimum; T. altissima and A. guianensis) suggests local competitive

406　exclusion. These positive and negative associations ensure that space sharing due to habitat

407　specialization of species and is consistent with previous findings in forest ecosystems (Martínez

408　et al., 2010; Lan et al., 2012; Liu and Slik, 2014). It is also possible that canopy species facilitate

409　the establishment of understory species in the areas below their treetops (e.g., nurse effects),

410　creating microenvironmental conditions that benefit positive interactions between them (Ren et

411　al., 2008). This type of interaction is common among tree species and might be one of the

412　determining factors of the high alpha-diversity found in tropical forests (Wright, 2002; Liu and

413　Slik, 2014). Conversely, it has been observed that tree monodominance might also inhibit the

414　establishment of understory species (Torti et al., 2001). In our study, the positive spatial

415　associations between layers observed in this forest suggest that the understory species analyzed

416　are specialists and adapted to this case of tree monodominance.

417　　　Changes in interspecific spatial associations of species among inventories might be

418　related to growth and recruitment of individuals over time. Juveniles show higher positive spatial

419　associations than negative compared to adults, which indicates that individuals in this life stage

420　have a wider range of niches and higher regeneration capacity (Hao et al., 2007). This fact

421　highlights the importance of the J-C effect, which changes interspecific spatial patterns of the

422　species according to the size of individuals and to the scale analyzed (Hao et al., 2007; Getzin et

423　al., 2014). Therefore, interspecific associations are subject to variations over time, according to

424　the demographic oscillations of species (life stages), and represent the natural spatial dynamics

425　of populations. Moreover, as observed in spatial distribution, these changes in interspecific

426 spatial associations might be related to the droughts that occurred in the region in 2005, 2007 and

427 2010 (Zeng et al., 2008; Lewis et al., 2011; Feldpausch et al. 2016). Xie et al. (2015) observed

428 that water stress increases positive associations in desert areas, and Miriti (2007) described

429 changes in interspecific associations of bushes after a severe drought. Overall the changes in

430 spatial associations over time suggest that drought disturbances have marked effects on the

431 temporal and spatial relationships of tree species in Amazon forests.

432

433 **5. Conclusions**

434   Temporal changes in intra- and interspecific spatial patterns of species in a

435 monodominant forest and their consistency with demographic variations after severe droughts

436 emphasize the potential sensitivity of Amazon forest ecosystems to this disturbance. The spatial

437 associations between species and edaphic properties analyzed here, as well as the maintenance of

438 these relationships over time (e.g., Amaioua guianensis and gravel; Brosimum rubescens and K)

439 indicate the relevance of habitat in determining intraspecific spatial patterns of tree species.

440 However, the absence of negative spatial associations for the monodominant species B.

441 rubescens suggests that the species is not subject to any edaphic restrictions for establishment,

442 and this helps to explain the maintenance of the monodominance. The marked spatial repulsion

443 and attraction between species in the same layer (e.g., A. guianensis and P. pilosissimum) and

444 between those from different layers (e.g., B. rubescens and P. pilosissimum) suggests that

445 structural arrangements of species assemblages in Amazon forests are determined, respectively,

446 by niche similarity and differentiation patterns. Overall, while monodominance was not favoured

447 by drought, the maintenance of the spatial patterns of B. rubescens and P. pilosissimum also

448 demonstrate resilience of this system in the face of severe droughts, as their monodominance

449 persisted.

450

451 **Author contributions**

452   FE and BSM conceived the study and wrote the manuscript. FE, BSM, BHMJr and OLP

453 designed the study. JCB, AEM, PSM and SMR contributed to data analysis. All authors apart

454 from JCB and AEM collected field data, and all contributed to editing, commented and approved

455 the manuscript.

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832 Table 1. Comparison of mean annual mortality (M) and recruitment (R) rates of the diameter
833 classes of the five most abundant species of trees evaluated among the periods 1996-2001, 2001-
834 2004, 2004-2010, and 2010-2013, in a Brosimum rubescens Taub. monodominant forest in the
835 transition zone Amazon rainforest-Cerrado. Acronyms: Amaioua guianensis (Ag); Brosimum
836 rubescens (Br); Cheiloclinium cognatum (Cc); Protium pilosissimum (Pp), and Tetragastris
837 altissima (Ta). The same uppercase and lowercase letters represent the same medians using the
838 Wilcoxon and Friedman test (Dunn, post hoc). Uppercase letters= mortality x recruitment;
839 lowercase letters= species.

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

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842 Table 2. Spatial associations of species tree with edaphic properties over time (1996, 2001, 2004,
843 2010, and 2013) in a Brosimum rubescens Taub. monodominant forest in the transition zone
844 Amazon rainforest-Cerrado, Brazil. The significance of the positive and negative (-) spatial
845 associations is represented in bold (bimodal alpha = 0.05). Acronyms: Gravel (Gra); Amaioua
846 guianensis (Ag); Brosimum rubescens (Br); Cheiloclinium cognatum (Cc); Protium pilosissimum
847 (Pp), and Tetragastris altissima (Ta).

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

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

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

|	Inventories				
	1996	2001	2004	2010	2013
Ag-Br	-0.18	-0.20	-0.14	0.10	0.16
Ag-Cc	-0.02	-0.09	-0.12	0.22	0.21
Ag-Pp	**-0.59**	**-0.48**	**-0.55**	-0.19	-0.12
Ag-Ta	-0.20	-0.05	-0.00	**-0.31**	0.06
Br-Cc	-0.09	0.02	-0.02	-0.13	-0.02
Br-Pp	**0.26**	**0.31**	**0.35**	0.10	**0.26**
Br-Ta	-0.11	**-0.26**	**-0.35**	-0.12	-0.11
Cc-Pp	0.15	0.14	0.11	-0.24	-0.15
Cc-Ta	-0.14	0.13	0.11	0.02	-0.07
Pp-Ta	-0.23	-0.05	-0.09	0.17	0.15
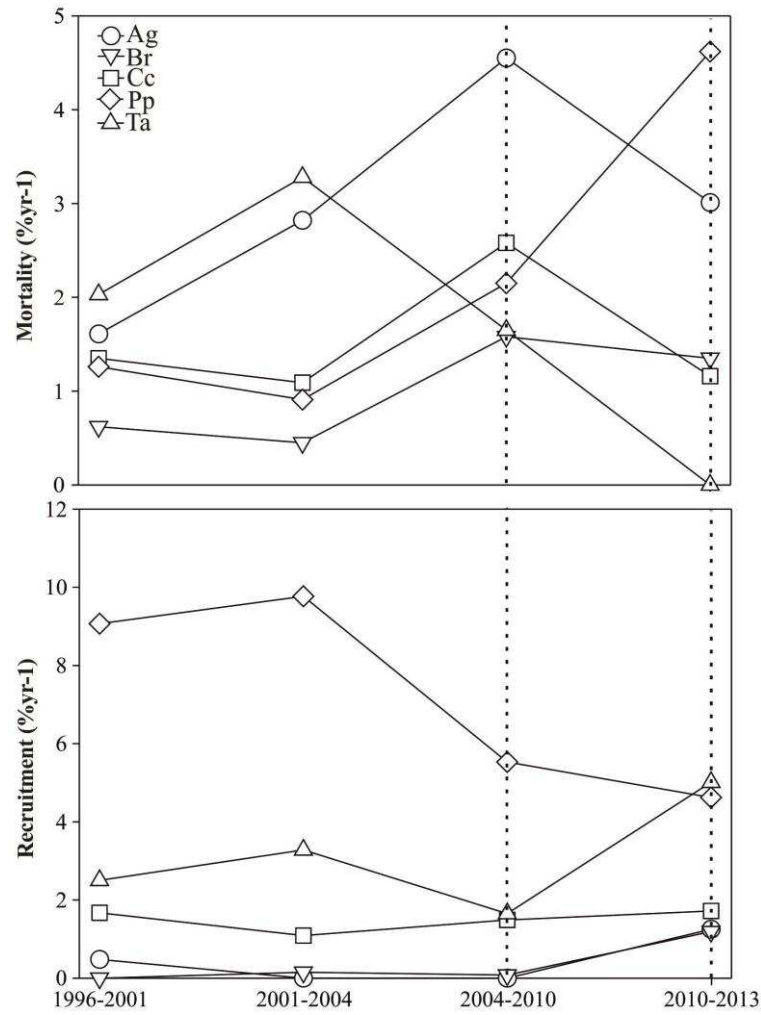
Figure 1. Mean annual rates of recruitment (lower panel) and mortality (top panel) of the five most abundant species of trees among the subplots in the periods 1996-2001, 2001-2004, 2004-2010, and 2010-2013, in a Brosimum rubescens Taub. monodominant forest in the transition zone Amazon rainforest-Cerrado, Brazil. No species varied significantly in mortality or recruitment rates among periods according to Repeated Measures ANOVA (p>0.05). Dashed lines indicate intense drought events. Acronyms: Amaioua guianensis (Ag); Brosimum rubescens (Br); Cheiloclinium cognatum (Cc); Protium pilosissimum (Pp), and Tetragastris altissima (Ta).
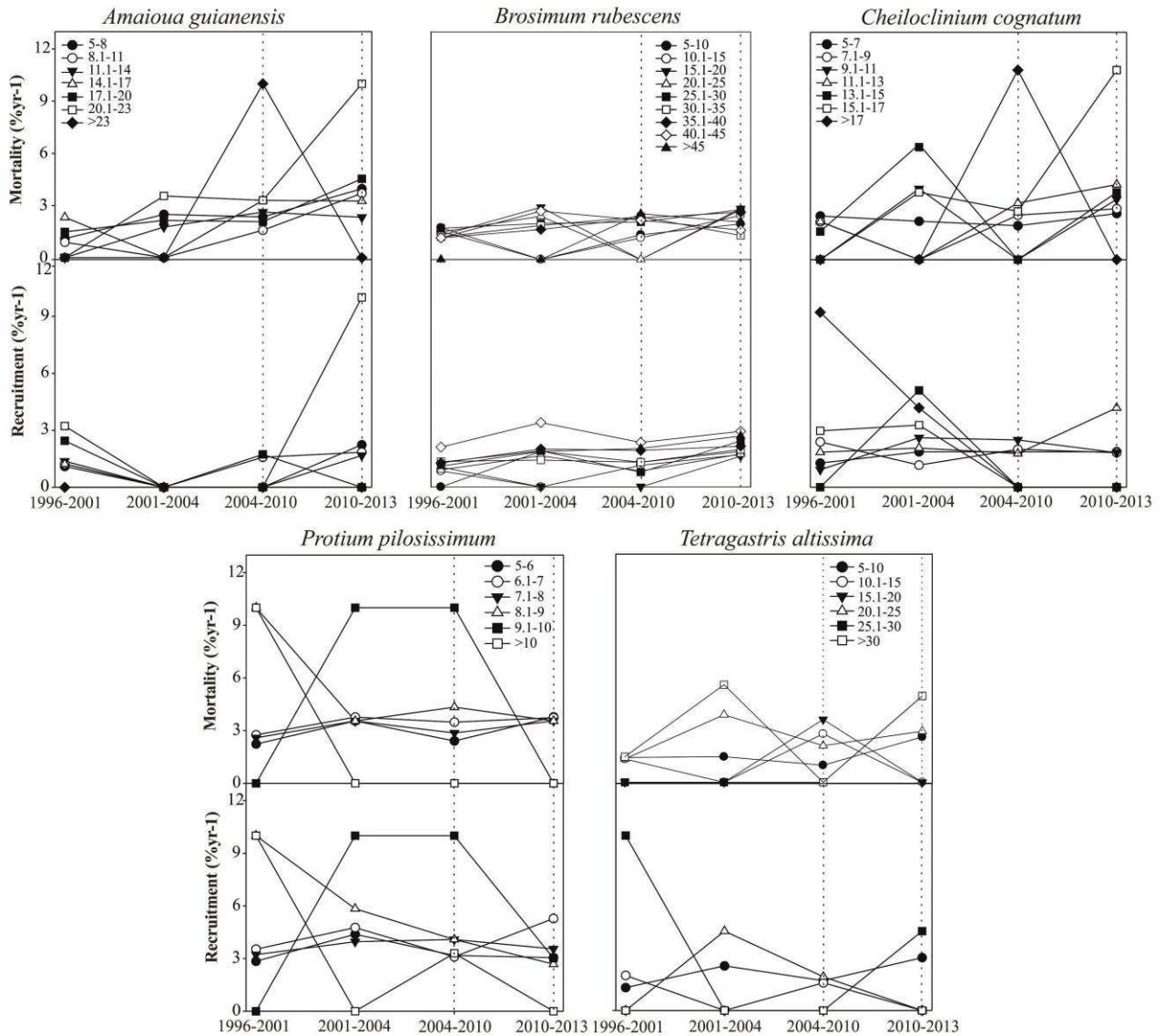
Figure 2. Mean annual mortality and recruitment rates of the five most abundant species of trees evaluated in different diameter classes (cm) in the periods 1996-2001, 2001-2004, 2004-2010, and 2010-2013, in a Brosimum rubescens Taub. monodominant forest in the transition zone Amazon rainforest-Cerrado. Dashed lines indicate intense drought events.
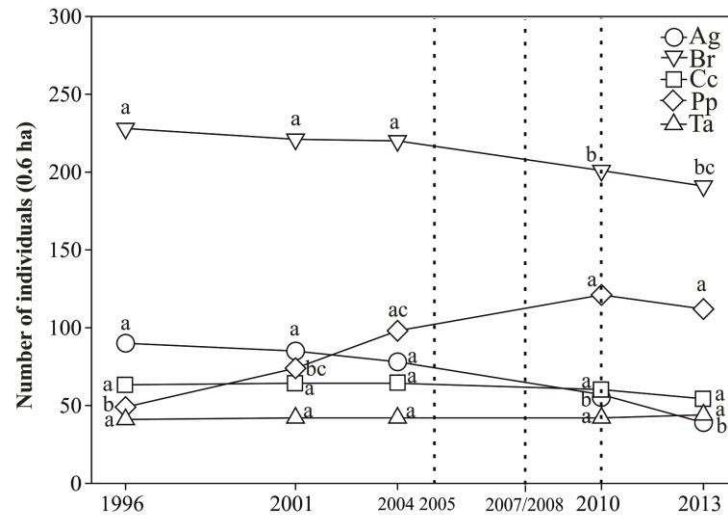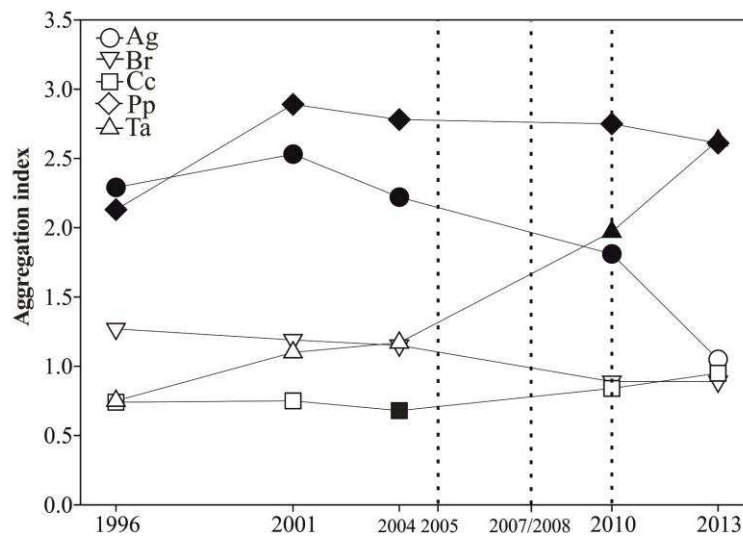
Figure 3. Number of individuals of the five most abundant species of trees over time (1996, 2001, 2004, 2010, and 2013) in a Brosimum rubescens Taub. monodominant forest in the transition zone Amazon rainforest-Cerrado, Brazil. Same letters represent significantly equal average density using ANOVA of repeated measures and Tukey's post hoc test. Dashed lines indicate intense drought events. Acronyms: Amaioua guianensis (Ag); Brosimum rubescens (Br); Cheiloclinium cognatum (Cc); Protium pilosissimum (Pp), and Tetragastris altissima (Ta).
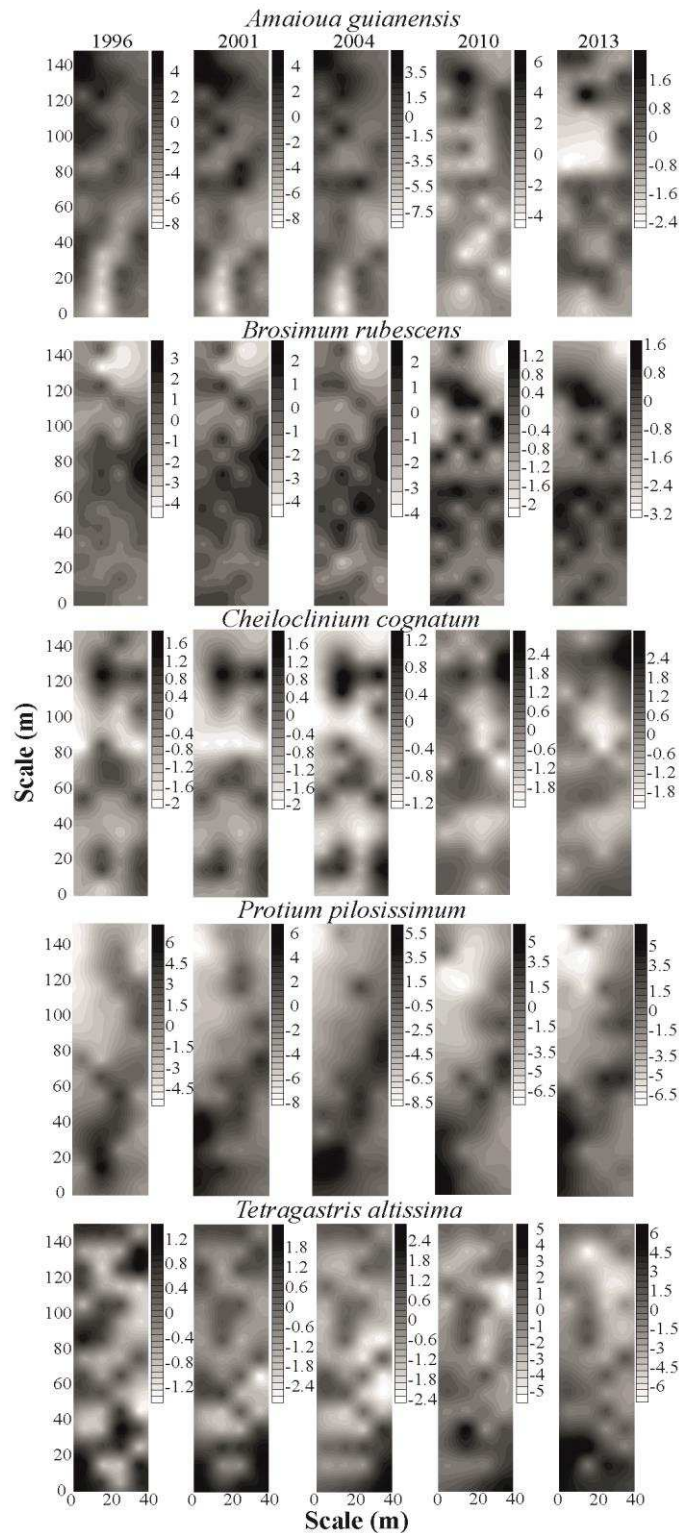

Figure 4. Spatial distribution of the five most abundant species of trees over time (1996, 2001, 2004, 2010, and 2013) in a Brosimum rubescens Taub. monodominant forest in the transition zone Amazon rainforest-Cerrado, Brazil. Significant Aggregation Index values (black) higher and lower than 1 indicates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

890 **Supplementary material**

891

892 Figure A.1. Kriging maps of spatial distribution (aggregation index values) of the five most
893 abundant species over time (1996, 2001, 2004, 2010, and 2013) in a Brosimum rubescens Taub.
894 monodominant forest in the transition zone Amazon rainforest-Cerrado, Brazil.
895
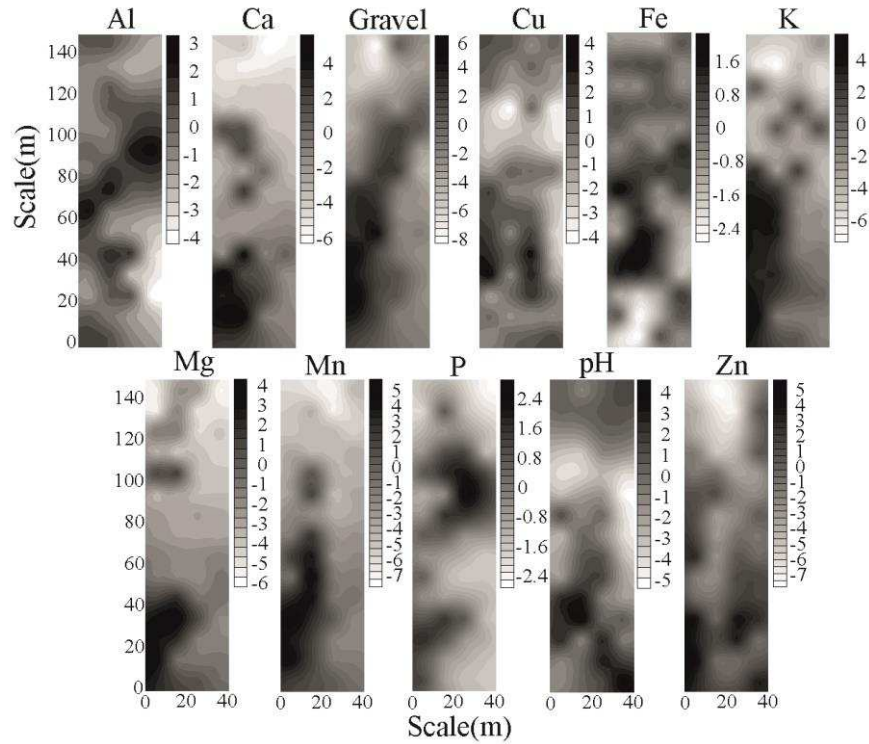
896

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

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901

902

903 Table A.1. Predictions by linear mixed effects models (GLMM) for temporal variation (1996-
904 2013) of mortality of the five species evaluated as a function of density, in a Brosimum
905 rubescens Taub. monodominant forest in the transition zone Amazon rainforest-Cerrado, Brazil.
906 The subplots represented the random effects.

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

907