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1 **Functional diversity and regeneration traits of tree communities in the Amazon-**
2 **Cerrado transition**

3
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38 **Abstract**

39 In central Brazil, there are strong gradients and discontinuities in vegetation structure and
40 composition between the forests of southern Amazonia, and the open savannas of South
41 America's Cerrado. These transitions are often controlled by disturbance processes, and
42 the ability of vegetation to respond to climatic and environmental changes may depend
43 on the regeneration traits of the different floras present. In this study we aim to assess the
44 regeneration traits of tree communities of the Amazon-Cerrado transition and to
45 understand how they differ among and within the markedly different vegetation types.
46 We sampled 39 one-hectare long-term monitoring plots that include typical cerrado
47 (TC=10), cerradão (CD=3), gallery forests (GF=3), floodplain forests (FF=6), seasonal
48 and open rainforests (SF=17). The regeneration traits assessed included dispersal
49 syndrome (zoochory, anemochory, and autochory), fruit consistency (dry and fleshy),
50 number of seeds per fruit, and diaspore dimensions (width and length). We found
51 differences among the vegetation types, in all regeneration traits. And these tended to be
52 aggregate by vegetation structure, being similar for cerrado and cerradão species, and
53 similar for SF, FF and GF (more forested vegetation). Vegetation types did not differ in
54 functional diversity, however, while regeneration traits among seasonal and open
55 rainforests were well-dispersed, in floodplain forests they were more clustered. Tree
56 species depend substantially on fauna (zoochoric species between 42 and 86% in
57 vegetation) for the dispersal across all habitats here, consisting of the dominant dispersal
58 strategy. By incorporating these strategies into the tree recruitment and establishment
59 study, we will be improving our understanding of the dynamic and tree species richness
60 of neotropical forests and savannas.

61

62 **Keywords:** functional trait, seed dispersal, fruit, forest, savanna, ecological strategy

63

64 **1. Introduction**

65 Regeneration traits are important elements in plant community ecology, affecting
66 the processes of dispersal, germination, colonization, and establishment of trees in the
67 environment (Vandelook et al., 2012; Romero-Saritamá and Pérez-Rúiz, 2016). The
68 regeneration in plant communities is the process whereby mature individuals of a
69 population are replaced by new individuals of the next generation through the
70 regeneration traits (i.e., seed production, fruit size, dispersal, and seedling emergence)

71 (Grubb, 1977). Species use distinct regeneration strategies as direct responses to different
72 selective pressures, which allows their coexistence in communities (Hutchings, 1986;
73 Houle, 1991). Hence, understanding the factors that affect forest regeneration is crucial
74 for practical restoration in the face of disturbance and for enabling the recovery of these
75 environments (Vieira and Scariot, 2006). Understanding the complex network of biotic
76 mechanisms that influence and control forest recovery is also key for a deeper
77 understanding of tropical forest ecology (Powers et al., 2009). For example, changes in
78 plant-pollinator interactions can affect seed dispersal and seedling recruitment,
79 potentially reducing population size or promoting local extinction (Girão et al., 2007).

80 Environmental conditions form the basis for the selective pressures that directly
81 influence the mechanisms responsible for plant regeneration (Houle, 1991; Grime, 2006).
82 Studies have highlighted how fire regimes, rainfall, temperature, resource availability
83 (light and nutrients), and the frequency and intensity of drought events are among the
84 main environmental factors that affect the regeneration of tropical vegetation types (e.g.
85 Vargas-Rodrigues et al., 2005). Consequently, the regeneration of tropical species results
86 from adaptation to abiotic factors, which directly affect species functional traits.
87 Nevertheless, there is potentially a wide range of regeneration strategies associated with
88 the environmental conditions of regions where communities are established (van Schaik
89 et al., 1993). Studies of regeneration traits in savanna and forest show that plant
90 regeneration strategies are strongly related to habitat, and this plays an important role in
91 community assembly (Ribeiro et al., 2015; Escobar et al., 2021).

92 Forest and savanna are influenced by different environmental filters, with fire
93 occurrence, groundwater depth, and high light availability in savannas (Hoffman et al.,
94 2009). And air humidity, soil moisture, canopy closure, and nutrient content increasing
95 towards the forest (Hoffman et al., 2004; Torello-Raventos et al., 2013). These sets of
96 environmental filters have been linked to describe what is currently known about
97 regenerative strategies in forests and savannas. In open savannas of the Cerrado, wind
98 dispersion predominates at the end of the rainy season and in the dry season (Kuhlmann
99 and Ribeiro, 2016) and pronounced post-fire resprouting (Scalon et al., 2020). While in
100 the tropical forests, dispersal by animals occurs much more distributed throughout the
101 year, with germination and seedling development under a closed canopy (van Schaik et
102 al., 1993; Ribeiro et al., 2015).

103 Vegetation in the Amazon-Cerrado transition separates the two largest South
104 American biomes, the Amazon and the Cerrado (Marques et al., 2019). Tree populations

105 in the Amazon-Cerrado transition are mostly composed of fast turnover species
106 (“hyperdynamic”, Marimon et al., 2014) but have also recently experienced net declines
107 in abundances due to land-use change and extreme climate events (e.g. Nogueira et al.,
108 2019; Marimon et al., 2020). How they regenerate will be a critical factor in determining
109 the ecological stability of a large area of forest in central South America. Different
110 patterns of regeneration may be expected among the different woody vegetation types in
111 the Amazon-Cerrado ecotone. Given that the region is characterized by complex
112 interactions among environmental factors (Marimon et al., 2006) and different vegetation
113 types are subject to different natural and anthropogenic environmental pressures. Several
114 vegetation types are found in the transition zone between Cerrado and Amazonian forests.
115 These include typical cerrado (typical savanna), cerradão (a dense and tall transitional
116 woodland formation) (Ratter et al., 1973), gallery forests (Marimon et al., 2002), and
117 floodplain forests (Marimon et al., 2015). Seasonal evergreen, seasonal semi-deciduous
118 (dry forests), and open rainforests are the true Amazonian forests in the transition zone.
119 (Ivanauskas et al., 2008). As a continuum from savanna vegetation of the Cerrado, passing
120 through transitional forests such as cerradão and dry forests to the rainforests in the
121 Amazonia. The environmental conditions in which these vegetation types differ provide
122 a great opportunity to investigate the relationship between habitat and regeneration traits.

123 In this study, we aimed to assess how functional diversity (a multitrait index) and
124 regeneration traits vary within and among the vegetation types of the Amazon-Cerrado
125 ecotone. We investigated and tested the following questions and hypotheses: a) *How do*
126 *regeneration traits differ between transitional vegetation types?* We expect that a higher
127 proportion of species bearing fleshy and large fruits would be found in moist forests, with
128 a greater proportion of wind-dispersed species with smaller diaspores in drier forests and
129 savannas. This is because environments with greater availability of water during the year
130 often have a higher proportion of species with fleshy fruits dispersed by animals (Howe
131 and Smallwood, 1982; Tabarelli et al., 2003; Correa et al., 2015); b) *Does regeneration*
132 *traits tend to cluster or diverge?* We expected that functional trait clustering would be
133 found, as phylogenetic and functional aggregation has been reported elsewhere in tropical
134 forests (Webb et al., 2002; Vamosi et al., 2009); c) *Which regeneration trait is the best*
135 *predictor?* We hypothesize that between our set of traits, fruit dimensions are the best
136 predictors. Since for zoochoric species, tall plants with large fruits may attract highly
137 mobile dispersers, which can take seeds long distances (Thomson et al., 2011). Thus,
138 influencing the seed dispersal range, which is strongly related to the local species

139 composition (Howe and Smallwood, 1982). For this purpose, we determined dispersal
140 syndrome, fruit consistency, number of seeds per fruit, fruit length, and fruit width for
141 196 tree species from a unique and complex set of vegetation types occurring in the
142 Amazon-Cerrado transition zone.

143 **2. Materials and methods**

144 *2.1 Study area*

145 We worked across the Amazon-Cerrado transition, with plots established from the
146 southern region of Pará State, skirting the southern edge of the Xingu Indigenous Land,
147 to the central-northern region of Mato Grosso State (Figure 1). Our analysis is based on
148 39 one-hectare long-term monitoring plots, classified as typical cerrado (TC=10),
149 cerradão (CD=3), gallery forests (GF=3), and floodplain forests (FF=6). For this study
150 we grouped the vegetation types: semideciduous seasonal forest, evergreen seasonal
151 forest, and open rainforest in a single class, named seasonal and open rainforests (SF=17).
152 Because these are the typical forest types and representatives of the peripheral region of
153 the Amazonia Forest in the transition zone with the Cerrado (Ratter et al., 1973; Pires and
154 Prance, 1985). The cerradão is a transitional forest, characterized by the presence of
155 species from both savanna and forest (Ratter et al., 1973) (Table 1). All the plots were
156 censused using RAINFOR protocols (e.g., Phillips et al., 2009; Marimon et al., 2014).

157 The climate of the region is tropical with dry winters (“Aw”) and monsoon
158 tropical (“Am”), according to the Köppen classification system (Alvares et al., 2013). The
159 average annual rainfall ranges from 1,511 to 2,353 mm, and the average annual
160 temperature varies from 24.1 to 27.3 ° C (Hijmans et al., 2005).

161

162 *2.2 Data collection*

163 Species lists from the most recent inventories (between 2014 and 2016) carried
164 out by the research team at the Plant Ecology Laboratory of the Mato Grosso State
165 University (UNEMAT) in Nova Xavantina were used. Data were deposited in the
166 ForestPlots.net forest monitoring database (Lopez-Gonzalez et al., 2011). In these
167 inventories, plants were included if the stem diameter was at least 10 cm, measured at
168 1.30 m (forest vegetation) or 0.30 m above ground level (savanna). Families were
169 classified according to the APG IV (Chase et al., 2016) system, and the Flora of Brazil
170 2020 (<http://floradobrasil.jbrj.gov.br/>) was consulted for identifying species. Voucher
171 materials have been deposited in the following herbaria: NX (UNEMAT - Mato Grosso

172 State University - Nova Xavantina, Mato Grosso State), UB (University of Brasilia,
173 Brasilia, Federal District), IBGE (Brazilian Institute of Geography and Statistics, Brasilia,
174 Federal District), and CEN (Embrapa Genetic Resources and Biotechnology, Brasilia,
175 Federal District).

176

177 *2.3 Regeneration traits*

178 Trait data were obtained from herbarium collections and available bibliography,
179 with values determined for each species present in the 39 plots studied. The regeneration
180 traits used were: dispersal syndrome, fruit consistency, number of seeds per fruit, fruit
181 length, and fruit width. Dispersal syndrome (zoochory, anemochory, and autochory), fruit
182 consistency (dry and fleshy), and the number of seeds per fruit were determined based on
183 diaspore characteristics (seed and fruit), which were obtained from field observations and
184 the specialized literature (Pott and Pott, 1994; Lorenzi, 1998; Barroso et al., 2000; Perez-
185 Harguindeguy et al., 2016).
186 Diaspore length and width data obtained from herborized samples available online (<http://splink.cria.org.br>, <http://fm1.fieldmuseum.org/vrrc>, <http://sweetgum.nybg.org/science/vh/>, and other virtual herbaria) were also used, and only samples collected within the bo
189 rders of the Mato Grosso State were selected. Five fruit replicates (five herbarium
190 specimens) per species were measured (Thompson et al., 1993), and a database was
191 created with the functional traits of the more dominant species that composed up to 80%
192 of the basal area of each plot, following the method recommended by Garnier et al.
193 (2004). The aim was to understand how the environment shapes vegetation characteristics
194 and how functional traits affect local productivity.

195

196 *2.4 Analyses*

197 To test for differences in regeneration traits between vegetation types, we
198 compared the functional traits using Generalized Linear Mixed Models (GLMM) in
199 `lme4` package (Bates et al., 2015), with the vegetation type as predictors (fixed effect)
200 and plots as random effect. We fitted the null model and an alternative model for each
201 trait and tested statistical similarity between the null model and the alternative model by
202 an ANOVA. To choose the best model, we used Akaike information criteria (AIC) for
203 the significant alternative models. We use the Tukey tests *a posteriori* for multiple
204 comparisons of values between groups (vegetation type) using the `multcomp` package

205 (Hothorn et al., 2008). We also performed an ordination based on a principal component
206 analysis (PCA) using the `vegan` package in a matrix consisting of the functional traits
207 of each species per vegetation type (Oksanen et al., 2017).

208 To verify if the regeneration traits tend to cluster or diverge, first we calculate the
209 Functional Diversity Index (FD), for this a functional dendrogram was built from a matrix
210 (species \times functional traits) transformed into a distance matrix. Gower distance was used
211 to treat categorical (dispersal syndrome and fruit consistency) and quantitative data
212 (number of seeds per fruit, fruit length, and fruit width) (Pavoine et al., 2009) in the `ade4`
213 (Dray et al., 2007) and `ape` packages (Paradis et al., 2004). Null models were used to test
214 whether functional traits were clustered or dispersed, and to test whether the observed
215 patterns of species coexistence differed from what would be expected by chance
216 regarding the regeneration traits. The null models were created by FD values of 1,000
217 communities built at random and compared based on the species pool of each vegetation
218 type. Next, the standardized effect size of FD was calculated and t-tests were performed
219 for samples, with the means of the standardized effect values being compared in relation
220 to the zero mean using the `Picante` package (Kembel et al., 2010): *Standardized effect*
221 *size (Z) = - (obsFD - rndFD)/sd.rndFD*. The obsFD is the observed FD (Functional
222 diversity index), rndFD is the FD mean of null communities, and sd.rndFD is the standard
223 deviation of the 1,000 random values of the FD (see Cianciaruso et al., 2012).

224 Standardized effect size values of FD higher than zero indicate functional
225 diversity higher than what would be expected by chance (functional clustering), and
226 values lower than zero indicate functional diversity lower than what would be expected
227 by chance (functional dispersion) (Webb, 2000).

228 To determine which regeneration traits were the best predictors among the set of
229 functional traits, we used the Bayesian average model with the `BMS` package (Zeugner
230 and Feldkircher, 2015), with the functional traits as explanatory variables and the
231 vegetation types as the response variable. We choose the hyperparameter on Zellner's (g-
232 prior) for the regression coefficients. The Bayesian average models are an extension of
233 the usual Bayesian inference methods, which use the Bayes theorem to produce posterior
234 models and parameters, allowing the model selection by the complete enumeration of the
235 model space (Hoeting et al., 1999; Fragoso et al., 2018). All analyses were performed in
236 the R program (R Core Team, 2018), with the significance level set at 5%.

237 **3. Results**

238 Regeneration traits were compiled for all 196 tree species found on the studied
239 sites. These included 60 species in the typical cerrado (TC), 27 in cerradão (CD), 22 in
240 gallery forests (GF), 23 in floodplain forests (FF), and 103 in seasonal and open
241 rainforests (SF). Fruit dimensions were smaller for seasonal and open rainforests species
242 (Fruit length = 2.17 ± 2 ; Fruit width = 1.34 ± 1.02) and larger for typical cerrado species
243 (Fruit length = 3.95 ± 3.48 ; Fruit width = 1.94 ± 1.28) (Figure 2 and Supplementary Table
244 1). Fruit lengths of species in seasonal and open rainforests were significantly shorter than
245 those in the cerradão and typical cerrado (Figure 2 and Supplementary Table 1). In
246 general, fruit length increase following a gradient of vegetation from the most forested
247 and dense vegetation (SF) to the savanna and open areas (TC).

248 The fruit width in seasonal and open rainforests species was only significantly
249 smaller than typical cerrado species (Figure 2 and Supplementary Table 1). Floodplain
250 forest species have a few numbers of seeds per fruit (1.83 ± 1.45) compared to other
251 vegetation types (Figure 2 and Supplementary Table 1).

252 Thus, the highest percentage zoochory (59 to 89%) were recorded in more forested
253 vegetation (SF, FF, and GF) and the lowest in typical cerrado (42.01 ± 11.71) and cerradão
254 (44.03 ± 5.27); these two vegetation types also showed the highest proportion of dry fruits
255 (TC = 53.75 ± 10.65 ; CD = 44.03 ± 5.27) (Figure 2 and Supplementary Table 1). Species
256 that were wind-dispersed (anemochoric) had significantly larger fruits than the autochoric
257 and zoochoric species in all vegetation types (Supplementary Table 4 and Supplementary
258 figure 1). However, when comparing species of the same dispersal type among vegetation
259 types, fruit dimensions were similar, for example, anemochoric species of typical cerrado
260 were similar in length to anemochoric species of seasonal and open rainforests
261 (Supplementary Table 4 and Supplementary Figure 1).

262 In ordination space, species tended to group based on their regeneration traits
263 instead of by the type of vegetation, forming functional groups structured by dispersal
264 syndrome and fruit type (percentage of variance explained, PC1 = 48% and PC2 = 16%)
265 (Figure 3). Three main clusters, represented by anemochoric species with dry fruits,
266 zoochoric species with fleshy fruits, and autochoric species, were observed (Figure 3).
267 We found a big division between more forested vegetation (GF, FF and SF), typical
268 cerrado (TC) and cerradão (CD). With clear occurrence of species of typical cerrado that
269 are an exception, standing with forest species. These tree species are: *Curatella*
270 *americana* L., *Guapira graciliflora* (Mart. ex J.A.Schmidt) Lundell, *Guapira noxia*

271 (Netto) Lundell and *Myrcia splendens* (Sw.) DC.. Savanna species with small fleshy fruits
272 dispersed by zoochory.

273 Vegetation types did not differ in functional diversity (FD index) of regeneration
274 traits (Figure 4). However, the functional diversity of seasonal and open rainforests and
275 of floodplain forests were different from what would be expected by chance, with *Z*
276 values significantly different from zero (Figure 5). For seasonal and open rainforests, the
277 mean *Z*-value was much lower than zero, which implies the presence of species with a
278 wide range of regeneration traits. By contrast, the mean of floodplain forests was higher
279 than zero, which is an indicator of communities formed by species with similar functional
280 traits (functional clustering).

281 The best regeneration traits model among the set of functional traits, for different
282 vegetation types, was composed of dispersal syndrome, with a posterior model
283 probability of 85% indicating that this is clearly the most important predictor (*Posterior*
284 *Inclusion Probabilities* / PIP = 0.97) (Figure 6 and Supplementary Table 6).

285

286 **4. Discussion**

287 Our results showed differences among the vegetation types in all the regeneration
288 traits examined. Which results in great variation in functional characteristics and
289 ecological strategies among the vegetation types of the Amazon-Cerrado ecotone. Our
290 hypothesis about variation of regeneration traits among vegetation types has been
291 partially confirmed with a higher proportion of species bearing fleshy and small fruits
292 dispersed by animals found in forest areas, and a greater proportion of wind-dispersed
293 species with big dry fruits in dry forests and savannas. Regarding community assembly
294 based on functional diversity, the seasonal and open rainforests showed overdispersion
295 of regeneration traits, in floodplain forests by contrast these were markedly clustered.
296 Contrary to our expectations, our results showed that dispersal syndrome (anemochory,
297 autochory, and zoochory) was the most effective variable among the set of regeneration
298 traits.

299

300 *4.1 Variation of regeneration traits among vegetation types*

301 These differences in functional traits highlight variability in re-colonization
302 capacity, competitive vigor, and response to disturbance (Romero-Saritama and Pérez-
303 Rúa, 2016; Cornelissen et al., 2003) throughout the Amazon-Cerrado transition. In this
304 case, heterogeneity in fruit size, consistency, and dispersal strategy indicates a spectrum

305 in terms of diaspore permanence in the soil, as large-sized fruits found in typical cerrado
306 species, in general, tend to remain in the soil in the seed bank for a shorter length of time,
307 forming a transient soil seed bank (Salazar et al., 2011). Other studies have also shown
308 variability in functional regeneration capacity between dry and evergreen forests
309 (Romero-Saritama and Pérez-Rúiz, 2016), savannas (García-Nuñez and Azócar, 2004),
310 and fragmented areas in the Atlantic Forest (Girão et al., 2007). The results of this study
311 show similar variability between different vegetation types at a broad spatial scale.

312 Species of the cerradão and typical cerrado have larger fruits than those in forest
313 vegetation. These fruits have higher exposure in the environment, requiring investment
314 in resistance adaptations (Romero-Saritama and Pérez-Ruiz, 2016). We also observed that
315 more forested vegetation had smaller fruits (SF, FF, and GF) which would suggest they
316 have a richer seed bank, also formed by fruits with seeds inside. Since smaller fruits have
317 a high capacity to contribute to the seed bank and attract dispersing agents, maintaining
318 a more distributed dispersion throughout the year (Marimon and Felfili, 2006). Cerrado
319 species are instead likely to rely on other types of regeneration strategies, such as
320 resprouting capacity. Resprouting capacity is more pronounced in savanna species
321 because it permits a rapid response to the impacts of fire and also a strategy for hydric
322 seasonality (Hoffmann et al., 2009). In general, within and between communities,
323 different sets of regeneration traits characterize the species, so that species with low
324 capacity to contribute to seed banks may have good resprouting or dispersal capacity over
325 long distances (Escobar et al., 2021).

326 Overall, a greater proportion of species with animal-dispersed seeds was found
327 than the wind-dispersed or self-dispersed species. Zoochory is usually the dominant
328 dispersal syndrome in tropical forests, and it is well represented even in environments
329 where fruits are seasonally scarce (Jordano et al., 2007). The dispersal peak for wind-
330 dispersed species occurs during the dry season, while animal-dispersed species takes
331 place throughout the year (van Schaik et al., 1993; Escobar et al., 2018). Thus, here as
332 elsewhere forest trees appear to depend strongly on animals for successful dispersal,
333 which may represent an adaptive advantage in reaching new environments where
334 seedlings can survive away from the zone closest to the parent tree, where they are more
335 likely to encounter reduce predation rates and less conspecific competition (Travesset et
336 al., 2014). Correa et al. (2015) found similar results in 1-ha plots when comparing
337 different vegetation types in neotropical forests in the Colombian Amazon, with zoochory
338 dominant in all plots, but with a high proportion of autochory in places with high levels

339 of disturbance. Regarding the consistency of fruits, a similar pattern was found as in other
340 studies, a predominance of dry fruits in dry forests and savannas and fleshy fruits in more
341 humid forests (Howe and Smallwood, 1982; Tabarelli et al., 2003; Vieira and Scariot,
342 2006).

343 The lowest number of seeds per fruit recorded for floodplain forest species may
344 reflect selective pressure in a harsh physical environment for ensuring the seed survive
345 (Jordano, 2014). Fruits with few large seeds increase the chances of seedling
346 establishment, especially when there are limited resources in the environment, reflecting
347 the general trade-off between dispersal and establishment (Parciak, 2002). On the other
348 hand, a large number of small seeds also favours dispersal away from the parent tree due
349 to their greater mobility. Seed number per fruit (seed output) is an important indicator of
350 potential seed production and is inversely related to the seed mass, reflecting per seed
351 resource investment (Henery and Westoby, 2001). In this context, the water present in
352 floodplain forests is an important abiotic filter in the seed production stage (Larson and
353 Funk, 2016), clearly selecting local species that invest resources in the production of few
354 seeds and probably of greater mass. The seeds of high production species are possibly
355 dispersed away from the parent tree because they are lighter and easily dispersed by wind
356 or animals (Thomson et al., 2011).

357

358 *4.2 Functional diversity and community assembly*

359 The functional diversity of regeneration traits did not differ among the vegetation
360 types of the Amazonian-Cerrado transition. Thus, the amplitude of regeneration traits and
361 the part of the niche space occupied by species are similar (Tilman, 2001; Mason et al.,
362 2005). Functional diversity may be interpreted as reflecting the diversity of niches and
363 ecological functions (Lavorel and Garnier, 2002). It was expected that the functional
364 diversity in forest vegetation types like SF, FF, and GF would be higher because, in these
365 areas, there is higher species richness and, according to Tilman et al. (2014), richness is
366 positively correlated with functional diversity. We did not find differences in the
367 functional diversity between vegetation types, possibly due to the type or quantity of
368 functional traits. Choosing more, or including other fruit or seed traits in the analysis (e.g.
369 seed mass, nutrient concentration in the fruits or partitioning the zoochory by type of
370 animal disperser) could have affected the functional diversity in the vegetation types by
371 increasing (or decreasing) the dimension of the functional space (Petchey and Gaston,
372 2002).

373 Considering that functional traits influence how species use the resources present
374 in the environment, complementarity in the use of resources may increase primary
375 productivity and enable more species to coexist (Tilman et al., 1997). Besides, different
376 responses from different species to environmental factors (e.g. fire and extreme climate
377 conditions) contribute to the maintenance of ecosystem function in the long-term (Grime,
378 1998). In this context, the functional variation that exists in the seasonal and open
379 rainforests of the Amazon-Cerrado transition may enhance the efficiency and
380 complementarity with which populations re-establish themselves, with lower
381 competition, leading to higher species richness and productivity.

382 On the other hand, the “insurance hypothesis” affirms that a community with
383 redundant species has greater resistance to disturbances. In these communities, important
384 ecosystem functions, such as seed dispersal and fruit set, are more likely to still be
385 performed even after species are lost (Yachi and Loreau, 1999). They may also contribute
386 ecosystem functions to other areas with fewer functional groups. In our study region,
387 seasonal and open rainforests are largely structured based on complementarity, whereas
388 floodplain forests have functional redundancy that ensures that dispersal and re-
389 establishment are more likely to be safely performed in environments subject to a certain
390 restricted set of physical conditions.

391 We expected that there would be functional clustering of regeneration traits in all
392 communities in which there were strong environmental filters, such as fire for the typical
393 cerrado (Cianciaruso et al., 2012) and water for gallery and floodplain forests (Marimon
394 et al., 2015). However, such clustering was only clearly found in floodplain forests, where
395 species are influenced by strong environmental filters as seasonal flooding, fire, and
396 drought (Maracahipes et al., 2014; Silva et al., 2018). This suggests that the regeneration
397 traits of the vegetation types of the Amazon-Cerrado transition show functional clustering
398 in the presence of severe environmental filters. Another factor that may have caused
399 functional clustering in addition to fire and flooding may have been a restricted pool of
400 dispersers due to flooding, for example reducing zoochory in which dispersal by birds is
401 important. The dispersal and frugivory network has a strong relationship with plant traits
402 so that changes in this interaction can restrict the number and identity of the dispersing
403 agents (González-Castro et al., 2015). It is also possible that the characters chosen here
404 were insufficient to detect patterns of environmental filtering in typical cerrado.
405 According to Cianciaruso et al. (2012), regeneration traits of fruits and seeds are not

406 affected by fire, and dispersal and pollination syndromes play a secondary role in the
407 regeneration of the cerrado, where the ability to resprout is the main strategy.

408 Regeneration traits play a key role in the maintenance of Amazon Forest
409 biodiversity via niche partitioning, as the traits of co-occurring species differ from those
410 expected from null models (Kraft et al., 2008; Paine et al., 2011). The traits analyzed
411 showed a strong relationship with the competitive vigor and colonization capacities of the
412 species, such as seed production, dispersal, germination, and emergence (Cornelissen et
413 al., 2003). Therefore, the observed functional dispersion reflected the role of competitive
414 hierarchies (Mayfield and Levine, 2010) in structuring forests of the Amazon-Cerrado
415 transition.

416

417 *4.3 The importance of dispersal syndrome for vegetation types*

418 The dispersal syndrome was the species regeneration trait that best explained the
419 differences in the regeneration functional structure between vegetation types. In fact,
420 different proportions of anemochory, autochory, and zoochory are fundamental to the
421 regeneration classification of vegetation types, especially in distinguishing forests (where
422 the proportion of zoochoric species is higher) from savannas (anemochory and zoochory
423 in similar proportions). Elsewhere, variations in the dispersal syndrome can be
424 characteristic markers of very different tropical vegetation types, perhaps, most notably
425 the fact that in humid forests fleshy fruits dispersed by animals are typical, while in
426 tropical dry forests it is the wind-dispersed fruits that often dominate (Howe and
427 Smallwood, 1982). This result is related to the metabolic cost for the production of fleshy
428 fruits, so that areas with greater availability of water (and nutrients), have a much greater
429 capacity to produce fleshy fruits as a resource for dispersing animals (Tabarelli et al.,
430 2003; Correa et al., 2015). Additionally, our results showed a drastic change in the
431 proportions of anemochory and zoochory between the vegetation types, following a
432 gradient of cover (savanna-forest). The complexity in the structure of the forested areas
433 increases the occurrence of frugivores mainly due to the contrast between the vegetation
434 and the fruits, favouring, for example, the dispersion by the birds (Camargo et al., 2013)
435 and also may limit wind flow, consequently, limiting wind dispersal (Escobar et al.,
436 2021). Thus, the zoochory proportions observed in this study for different types of
437 vegetation can be used as an indicator of the structural complexity of the environments
438 concerning the occurrence of dispersing animals. In this context, seasonal and open
439 rainforests are the most complex environments that best favour the presence of dispersers.

440 Overall, we found that regeneration strategies differ markedly from the use of
441 small, animal-dispersed fruits in forest vegetation types, to large often wind-dispersed
442 fruits in the savanna. These two functional groups of species represent two distinct
443 functional modes (“strategies”) of tree establishment and reproduction. The evaluated
444 traits were sufficient to distinguish the forest from savanna areas, but not to distinguish
445 among forest types. Here, we observed functional clustering (standardized effect size of
446 FD) that until then was in agreement for savanna vegetation but not yet registered for
447 floodplain forests that are also subject to the effect of fire. This helps to understand the
448 relationship between ecological processes and the diversity of regeneration strategies in
449 these forests. These results enhance our understanding of how these vegetation types will
450 respond to possible disturbances. With regional environmental changes and global
451 climate change strongly affecting the entire transitional region between South America’s
452 two largest biomes, such understanding can help us to better predict the stability of biomes
453 and the ability of different species and vegetation types to track these changes.

454

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466

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739

740 **Figure Legends**

741

742 **Figure 1.** Location of the 39 1-ha plots established in the Amazon-Cerrado transition. TC
743 = typical cerrado, CD = cerradão, GF = gallery forests, FF= floodplain forests, SF =
744 seasonal and open rainforests.

745

746 **Figure 2.** Raincloud plots showing the variation of the regeneration traits between
747 different vegetation types in the Amazon-Cerrado transition. The red dot represents the
748 mean for each vegetation and statistical differences are represented by different letters.
749 The Raincloud plot provides an overview of probability distribution and statistical
750 inference via medians and confidence intervals, combining box plot and violin plot. TC
751 = typical cerrado, CD = cerradão, GF = gallery forests, FF = floodplain forests, SF =
752 evergreen, seasonal and open rainforests.

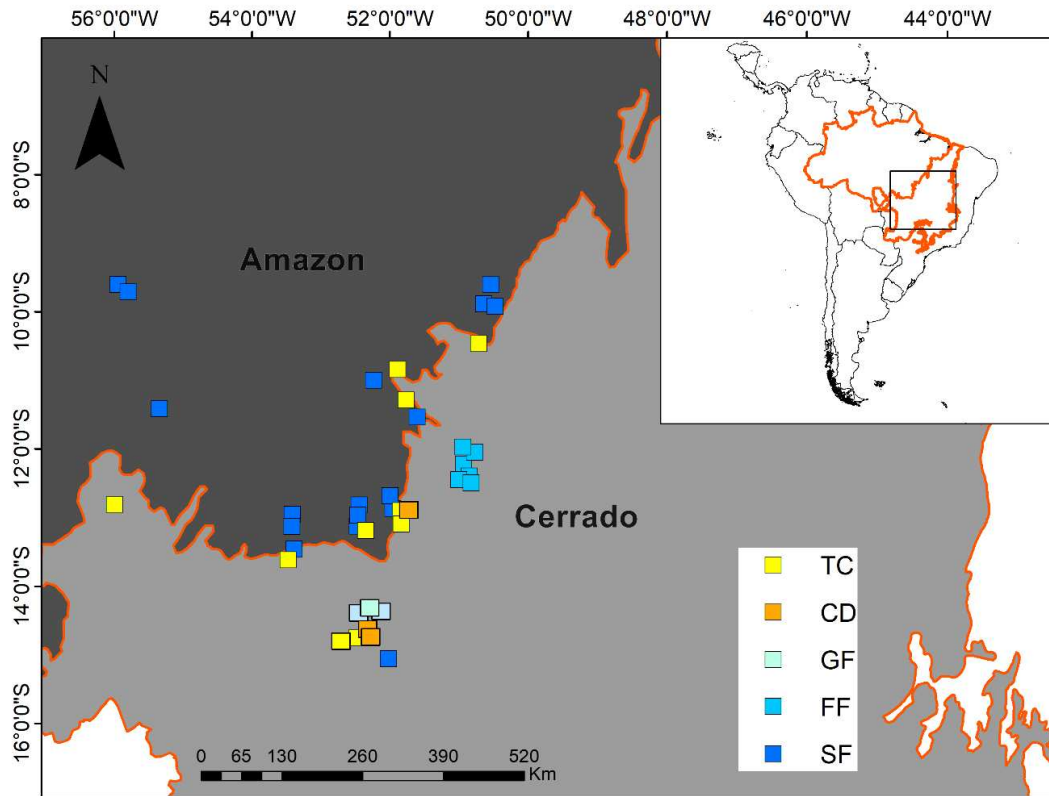
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754 **Figure 3.** Ordination produced by the analysis of the principal components of
755 regeneration traits and species found in the vegetation types of the Amazon-Cerrado
756 transition, using the first two dimensions. The traits closest to the axes showed higher
757 eigenvalues. Colored dots represent the species in each vegetation type. ANE =
758 anemochory, AUT = autochory, ZOO = zoochory, N/Seeds = number of seeds per fruit,
759 Length = fruit length, Width = fruit width. TC = typical cerrado, CD = cerradão, GF =
760 gallery forests, FF = floodplain forests, SF = seasonal and open rainforests. Details of the
761 position and length of the vectors are given in Supplementary Table 5 and Supplementary
762 Figure 2).

763
764 **Figure 4.** Box-plot showing the median, upper and lower quartile of functional diversity
765 calculated as FD index with no significant difference between different vegetation types
766 in the Amazon-Cerrado transition TC = typical cerrado, CD = cerradão, GF = gallery
767 forests, FF = floodplain forests, SF = seasonal and open rainforests.

768
769 **Figure 5.** Standardized effect size of functional diversity of regeneration traits in different
770 vegetation types in the Amazon-Cerrado transition. The * symbol indicates significant
771 non-zero values ($P < 0.05$). Confidence intervals = 95%. TC = typical cerrado, CD =
772 cerradão, GF = gallery forests, FF = floodplain forests, SF = seasonal and open
773 rainforests.

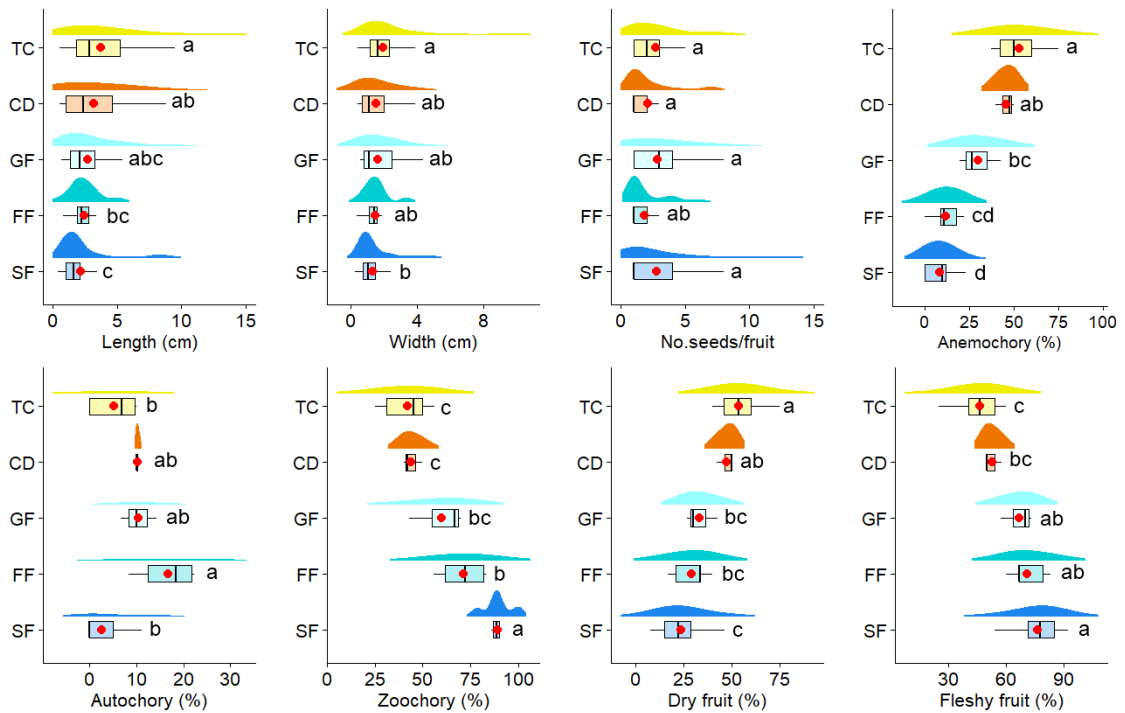
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775 **Figure 6.** A Bayesian average model of regeneration traits from different vegetation types
776 in the Amazon-Cerrado transition. Dispersion = dispersal syndrome, Fruit consist. = fruit
777 consistency, Width = fruit width, Length = fruit length, No. seeds = number of seeds per
778 fruit. The Y-axis contains the regeneration traits as predictors of vegetation types while
779 the X-axis shows an accumulated probability of models. Positive coefficients are
780 indicated by blue, negative coefficients by orange, and white indicates non-inclusion of
781 the respective predictor.

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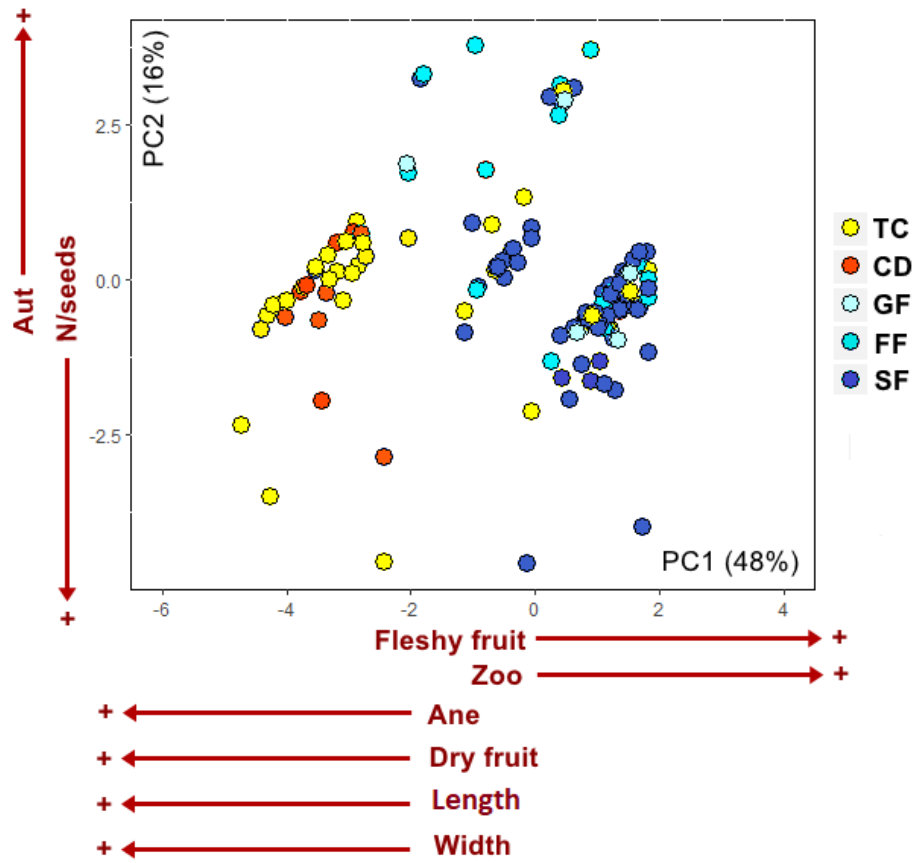
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Figure 1.



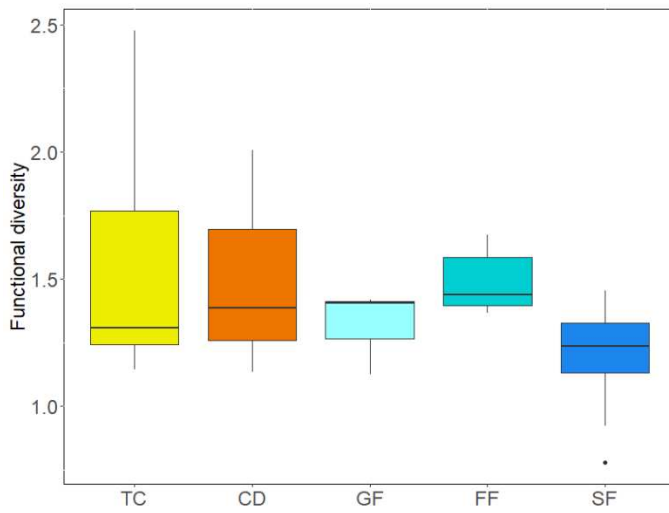
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Figure 2.



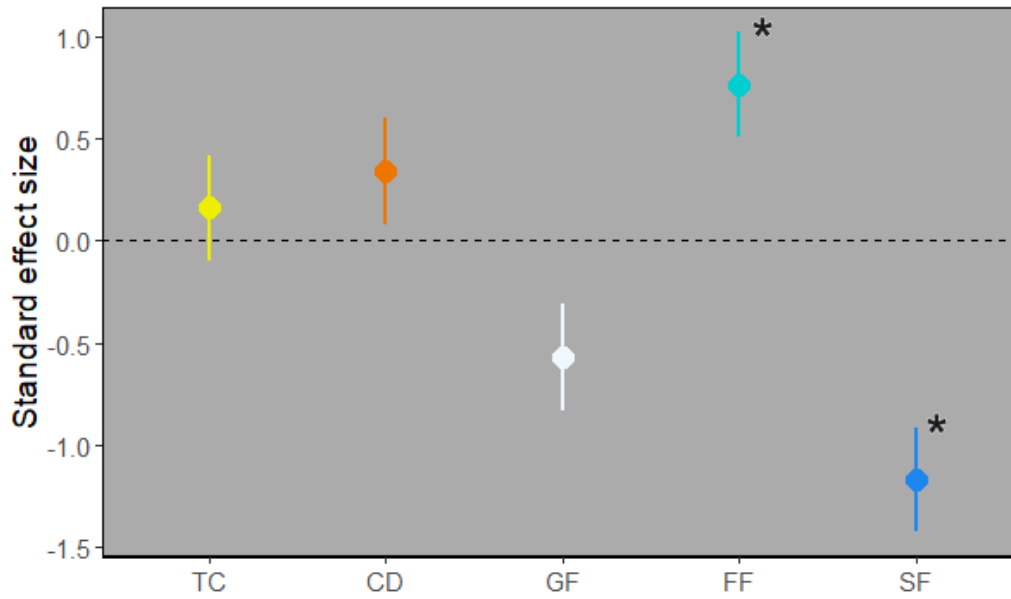
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Figure 3.



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Figure 4.



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Figure 5.



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Figure 6.

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804 **Table 1.** Structural parameters for vegetation types in in the Amazon-Cerrado transition.
805 H = mean tree height (m); LAI = mean leaf area index (m²/m²); BA = mean tree basal
806 area (m²/ha⁻¹); TD = mean tree density. The means were calculated using the values of
807 the plots of each vegetation type. The biome for vegetation type was defined by the
808 occurrence of plots (see Figure 1).

Vegetation type	Acroym	Biome	H	LAI	BA	TD
Typical cerrado	TC	Amazonia/Cerrado	5.80	1.6	8.49	404.8

Cerradão	CD	Cerrado	8.34	2.8	13.71	465.6
Gallery forest	GF	Cerrado	9.48	3.6	20.63	248.6
Floodplain forest	FF	Cerrado	10.67	3.4	25.25	811.5
Seasonal and open rainforests	SF	Amazonia/Cerrado	12.51	6.1	19.01	490.8

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