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1 **Tree diversity and above-ground biomass in the South America Cerrado biome and**  
2 **their conservation implications**

3

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32

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44 **Abstract** Less than half of the original two million square kilometers of the Cerrado  
45 vegetation remains standing, and there are still many uncertainties as to how to conserve and  
46 prioritize remaining areas effectively. A key limitation is the continuing lack of  
47 geographically-extensive evaluation of ecosystem-level properties across the biome. Here we  
48 sought to address this gap by comparing the woody vegetation of the typical cerrado of the  
49 Cerrado-Amazonia Transition with that of the core area of the Cerrado in terms of both tree  
50 diversity and vegetation biomass. We used 21 one-hectare plots in the transition and 18 in the  
51 core to compare key structural parameters (tree height, basal area, and above-ground  
52 biomass), and diversity metrics between the regions. We also evaluated the effects of  
53 temperature and precipitation on biomass, as well as explored the species diversity vs.  
54 biomass relationship. We found, for the first time, both that the typical cerrado at the  
55 transition holds substantially more biomass than at the core, and that higher temperature and  
56 greater precipitation can explain this difference. By contrast, plot-level alpha diversity was  
57 almost identical in the two regions. Finally, contrary to some theoretical expectations, we  
58 found no positive relationship between species diversity and biomass for the Cerrado woody  
59 vegetation. This has implications for the development of effective conservation measures,  
60 given that areas with high biomass and importance for the compensation of greenhouse gas  
61 emissions are often not those with the greatest diversity.

62  
63 **Key words:** Diversity-biomass; Richness; Carbon stocks; Core area; Transition; Neotropics

64 **Introduction**

65 As many as two hundred studies recognize the South American Cerrado savannas as a global  
66 center of diversity, largely on the basis of its 12,000-plant species which include many  
67 endemics (e.g. Mendonça et al. 2008; Brazilian Flora 2016). A likely driver of this high  
68 species richness is the heterogeneity of landscapes found within this region (Felfili et al.  
69 2005a; Mendonça et al. 2008). While the importance of this biodiversity has been recognized  
70 for at least two decades (e.g., Ratter et al. 1997; Silva and Bates 2002; Klink and Machado  
71 2005; Kier et al. 2005; Silva et al. 2006; BFG 2015), the importance of the Cerrado for  
72 ecosystem services such as carbon storage and hence climate mitigation is less appreciated  
73 (Grace et al. 2006), and the number and size of conservation units are still insufficient to  
74 avoid biodiversity losses (Françoso et al. 2015). In addition to establishing a more complete  
75 network of conservation areas covering the whole region, Bridgewater et al. (2004) also  
76 recommended a complementary regional focus to guarantee the adequate protection of  
77 geographical variations in species. Less than half the two million square kilometers originally  
78 occupied by the Cerrado are now intact (Sano et al. 2010; Lahsen et al. 2016); thus,  
79 understanding the distribution of remaining species diversity and carbon stocks within this  
80 region represents an urgent challenge for its conservation.

81 Most biodiversity and ecosystem ecology work in the Cerrado has focused on the core  
82 region, often relatively close to major population and academic centers such as Brasília  
83 (Federal District). The greatest research deficits lie well to the north and west of here  
84 (Miranda et al. 2014). In particular, while an extensive and complex transition exists between  
85 the Cerrado and the Amazon Forest (Ratter et al. 1973; Marimon et al. 2006, 2014), no study  
86 has yet compared the transitional vegetation with that of the core region using the  
87 standardized, fixed-area and quantitative inventory protocols required for a robust analysis of  
88 most ecosystem properties. Indeed, there has been little large-scale evaluation of structural

89 ecosystem-level properties at all across the Cerrado. In particular, for the key parameters of  
90 tree size, basal area and biomass—and hence above-ground carbon storage—the only studies  
91 we are aware of that included transition zone sites were based on only one or two sites. Yet,  
92 taking the published evidence together (Felfili et al. 1992; Castro and Kauffman 1998;  
93 Marimon-Junior and Haridasan 2005; Kunz et al. 2009; Marimon et al. 2014), it appears that  
94 the trees of the savanna formations in the Cerrado-Amazonia Transition might have greater  
95 basal area or biomass than similar formations in the core region of the Cerrado.  
96 Understanding how above-ground biomass varies among different areas of Cerrado and how  
97 this parameter responds to environmental and geographic factors will help reduce  
98 uncertainties in estimating carbon stocks and may contribute to greater reliability in  
99 conservation policies formulation. Forest biomass, for example, may be partly driven by  
100 climatic factors, such as precipitation and temperature (Silvertown et al. 1994; Larjavaara and  
101 Muller-Landau 2011), and topography, through its effects on water table levels (Fonseca and  
102 Silva Júnior 2004). Yet, this correlation may sometimes be weak and dependent on  
103 vegetation type (Stegen et al. 2011), while for the Cerrado core region the above-ground  
104 biomass of typical cerrado species may even be negatively correlated with precipitation  
105 (Miranda et al. 2014).

106 More generally, there are reasons to expect transition and core regions to differ  
107 ecologically beyond considerations of mean climate conditions. For example, the transition  
108 can have suboptimal environmental conditions relative to the core of the adjacent  
109 ecosystems, potentially reducing species richness (van der Maarel 1990). For similar reasons,  
110 the center-periphery hypothesis predicts that, due to harsher environmental conditions,  
111 peripheral populations should be smaller, less abundant and more fragmented, resulting in  
112 reduced demographic performance and genetic variation (Pironon et al. 2016). This would  
113 lead to the communities at the core being more stable and structurally distinct, while the more

114 unstable and fluctuating environments at the transition select for species and genotypes able  
115 to tolerate more variable conditions (Hardie and Hutchings 2010). Alternatively, Kark and  
116 van Rensburg (2006) suggested that precisely because populations in transitional regions are  
117 likely to include a wide range of taxa adapted to environmental instability, this would in fact  
118 result in them having greater species richness, and the potential to become centers for  
119 speciation.

120         These intriguing but conflicting viewpoints emphasize the potential existence of  
121 different patterns of diversity within the same biome, which need to be considered to develop  
122 effective conservation measures. In the specific case of the Cerrado, the picture remains  
123 unclear with respect to large-scale diversity patterns. Some studies have suggested that the  
124 core region of the Cerrado has relatively high species richness, due to its proximity to the  
125 center of species dispersal, whereas more peripheral regions are likely to be poorer in species  
126 despite the influence of adjacent biomes (Eiten 1972; Fernandes and Bezerra 1990; Rizzini  
127 1997; Castro et al. 1999). However, others have taken the view that the Cerrado-Amazonia  
128 Transition should have greater species richness than the core region, driven by their  
129 proximity to Amazonia (Ratter et al. 1973, 2003; Felfili et al. 2002; Marimon et al. 2006,  
130 2014). In parallel to the gap in Cerrado center–periphery studies noted above, what has been  
131 lacking so far is an evaluation of basic patterns of tree diversity using adequately replicated  
132 and fully standardized quantitative inventories across the biome.

133         While a better understanding of the distribution of plant diversity and biomass, and  
134 their environmental drivers across the Cerrado is necessary for adequate conservation  
135 planning, evaluating the diversity-biomass relationship itself is also important, both for the  
136 mitigation of climate change and for biodiversity conservation. A positive diversity-biomass  
137 relationship would indicate useful synergies between the goals of biodiversity protection and  
138 climate protection, while a negative one implies that difficult trade-offs become necessary

139 (Gardner et al. 2012). Several experimental studies elsewhere show that enhanced plant  
140 diversity can promote higher productivity and biomass, via mechanisms that include niche  
141 partitioning and species interactions that allow diverse communities to exploit resources  
142 more efficiently (e.g. Cardinale et al. 2012; Ruiz-Benito et al. 2014). However, within  
143 savanna ecosystems the covariation between ecosystem diversity and carbon properties is  
144 largely unstudied. Therefore, whether such mechanisms and relationships matter in the  
145 Cerrado, and any possible implications for conservation strategies, remains unknown.

146         Here, to help address these uncertainties in the geographical pattern, environmental  
147 drivers, and potential associations between Cerrado diversity and biomass, we conduct a  
148 large-scale analysis of these properties using distributed and standardized fixed-area  
149 quantitative ecological sampling plots. First, we investigate whether or not the structure and  
150 diversity of arboreal vegetation of the typical cerrado physiognomy (sensu Ribeiro and  
151 Walter 2008, a mixed arboreal-shrub vegetation with cover up to 50%) varies significantly  
152 between the Cerrado-Amazonia Transition and the core region. We then set out to evaluate  
153 the effects of potential climate drivers on typical cerrado structure, and the potential  
154 interaction between biomass and diversity. Our working hypotheses are (i) that the typical  
155 cerrado vegetation of the Cerrado-Amazonia Transition has greater basal area, biomass, and  
156 species diversity than at the core region, (ii) that biomass is influenced by climatic factors,  
157 such as precipitation and temperature, and (iii) that biomass is positively associated with  
158 diversity, independently of the potential influences of climate on biomass.

159

## 160 **Material and methods**

### 161 **Study areas**

162 We used data from standardized floristic and phytosociological surveys conducted across the  
163 central portion of the Cerrado (core area – CA) and the Cerrado-Amazonia Transition (TR),



164 i.e., the ecotone between the two largest biomes in South America (Fig. 1, Table S1). We  
165 used a zone of 150 km from the line that delimits the Cerrado and Amazonia to define the TR  
166 (IBGE 2004; Ivanauskas et al. 2008). We analyzed data from 39 permanent one-hectare plots  
167 installed in typical cerrado (cerrado stricto sensu) vegetation, 21 located in the TR and 18 in  
168 the CA (Fig. 1). We established plots in conservation units or in legal reserves of private  
169 properties in the Brazilian Federal District (CA), the Brazilian states of Mato Grosso (TR),  
170 Tocantins (CA), Bahia (CA), Goiás and Minas Gerais (CA), and in the Noel Kempff National  
171 Park in Bolivia (TR) (Fig. 1; Table S1). At each site, we selected the largest and best-  
172 preserved remnants of natural vegetation, within which we established plots randomly. In  
173 these areas, mean annual precipitation varied almost two-fold from 1043 mm to 1951 mm,  
174 and mean temperatures also ranged widely, from 19.3 °C to 26.9 °C (WorldClim 1.4; Hijmans  
175 et al. 2005).

176

### 177 **Data collection**

178 We identified and measured the diameter and total height of all woody plants with a diameter  
179 of at least 10 cm at a height of 30 cm from the ground, following standard protocols used in  
180 the Amazon forest (Phillips et al. 2010) and Cerrado (Felfili et al. 2005b). We identified  
181 species through comparison with voucher material available in herbaria, and consultation  
182 with specialists. The nomenclature was based on APG III (2009) and we confirmed the  
183 species names and synonymies using the Brazilian Flora (2016), with the flora package in the  
184 R environment (R Core Team 2018). We deposited botanical specimens in the permanent  
185 collections of Herbário NX (UNEMAT – Nova Xavantina campus, MT), Herbário UB  
186 (University of Brasília), Herbário IBGE (Brazilian Institute of Geography and Statistics),  
187 Herbário CEN (Embrapa Recursos Genéticos e Biotecnologia, Brasília, DF) and Herbario  
188 del Oriente Boliviano (USZ).

189 For each plot we calculated tree density (individuals/ha), mean tree height (m), mean  
190 tree diameter (cm), total basal area ( $\text{m}^2 \cdot \text{ha}^{-1}$ ) and total above-ground biomass ( $\text{Mg} \cdot \text{ha}^{-1}$ ),  
191 which were used as structural parameters of the vegetation. We estimated tree height from  
192 tree diameter for 10 of the TR plots using the model:

$$193 \quad H = a \times (1 - e^{-b \times D^c}),$$

194 where a, b and c are parameters of model and D is the tree diameter (Feldpausch et al. 2012).  
195 To assess the adequacy of this model, we compared height measurements from 3657 trees  
196 collected in the field with their estimated heights. The correlation between the field data and  
197 estimated heights was significant ( $r = 0.59$ ,  $p < 0.01$ ). We calculated above-ground biomass  
198 (hereafter biomass) from tree diameter using the Schumacher-Hall model:

$$199 \quad Y = \beta_0 D^{\beta_1} H^{\beta_2} \varepsilon,$$

200 where  $\beta_0$ ,  $\beta_1$ ,  $\beta_2$  are model parameters, D is tree diameter (at 30 cm from the ground), H is  
201 tree height and  $\varepsilon$  is the random error term (Schumacher and Hall 1933), with parameter  
202 values developed specifically for species of the typical cerrado physiognomy ( $\beta_0 = 0.03047$ ,  
203  $\beta_1 = 2.27159$ ,  $\beta_2 = 0.89748$ ; Rezende et al. 2006).

204 For each plot, we calculated species richness, Shannon information index ( $H'$ )  
205 (Shannon 1948), Fisher's log series  $\alpha$  (Fisher et al. 1943) and Pielou's evenness ( $J'$ ) (Pielou  
206 1969), which were used as diversity parameters (Magurran 2004). We also calculated, for  
207 each plot, the species richness rarefied to the same number of individuals in the smallest  
208 sample, i.e., 169 individuals based on the plot with the smallest number of trees (Hurlbert  
209 1971). All diversity parameters were calculated with the package vegan (Oksanen et al.  
210 2017).

211

212 **Statistical analyses**

213 To evaluate associations within structural and diversity parameters, we used the Pearson  
214 correlation coefficient. We assessed differences between CA and TR in structural and  
215 diversity parameters of the vegetation using boxplots and t-tests and, when such differences  
216 existed, we used Bayesian model averaging to identify the most important predictors of the  
217 two regions. In this analysis, structural and diversity parameters were used as explanatory  
218 variables and region (CA and TR) as the response variable. Bayesian model averaging, an  
219 extension of the usual Bayesian inference methods, models both parameter and model  
220 uncertainty using Bayes' theorem to produce parameter and model posteriors and, thus,  
221 allows for model selection by full enumeration of the model space when the number of  
222 predictors is not large (Hoeting et al. 1999; Fragoso et al. 2018). We conducted Bayesian  
223 model averaging with the BMS package (Zeugner and Feldkircher 2015).

224 To assess differences in the total (regional) pool of species between CA and TR, we  
225 built individual-based and sample-based species accumulation curves (Gotelli and Colwell  
226 2001). Further, to account for unseen species in our collection of sampled plots, we used  
227 abundance-based and incidence-based non-parametric estimators of species richness (Colwell  
228 and Coddington 1994; O'Hara 2005). Abundance-based estimators (Chao1 and ACE) were  
229 applied to the total counts of species in each region (CA vs. TR), while incidence-based  
230 estimators (Chao, Jackknife1, Jackknife2 and Bootstrap) were applied to the species frequencies  
231 in the plots for each region. Species accumulation curves and non-parametric estimators were  
232 calculated with the vegan package (Oksanen et al. 2017).

233 To investigate the relationships between biomass, diversity and climate, we used a  
234 modification of Bayesian model averaging to address model uncertainty in the presence of  
235 spatial autocorrelation, due to the inherent spatial dependencies among the observations  
236 (Legendre 1993). In this analysis, the spatial dependencies among observations are removed  
237 through a semiparametric spatial filtering approach based on selected eigenvectors extracted

238 from the spatial weight matrix (Tiefelsdorf and Griffith 2007). Considering the important  
239 effects that uncertainty in the type of spatial weight matrix (neighborhood relationships) can  
240 have on model parameter estimates, the spatial Bayesian model averaging method addresses  
241 both the uncertainty over model specification and the uncertainty regarding the choice of  
242 neighborhood relationships in the spatial regression model (Cuaresma and Feldkircher 2013).  
243 We implemented spatial Bayesian model averaging using package spatBMS (Feldkircher  
244 2010), using  $10^6$  iterations,  $10^5$  burn-in draws, the reversible-jump model-sampler algorithm,  
245 and default settings for the other parameters. We used eight different spatial weight  
246 matrices—k nearest-neighbors ( $k = 1, 2, 4$  and  $6$ ), Delaunay's triangulation, Gabriel graph,  
247 relative neighbor graph, and sphere of influence graph—built with package spdep (Bivand et  
248 al. 2013, Bivand and Piras 2015). To assess the adequacy of the spatial filtering, we  
249 compared P-values of the Moran's I (Moran 1950ab) test for spatial autocorrelation obtained  
250 from the 100 best models versus 100 ordinary least-squares models using the same  
251 predictors.

252 In the spatial Bayesian model averaging analysis, we used biomass as the response,  
253 and diversity and climate parameters as predictors. Prior to analysis, we selected diversity  
254 parameters based on a variance inflation factor (VIF) maximum threshold score of 4 (Quinn  
255 and Keough 2002), using package usdm (Naimi et al. 2014). This resulted in only species  
256 richness and Pielou's evenness being retained for analysis (results not shown). Further, we  
257 incorporated tree density and the distance from each plot to the line separating Amazonia  
258 from the Cerrado (IBGE 2004) as additional predictors, to control for any effects these  
259 parameters might have on biomass. We also ran a bivariate regression for both regions  
260 combined (CA and TR) to evaluate the relationship between biomass and climate parameters.  
261 The climate parameters consisted of temperature and precipitation, obtained from WorldClim

262 1.4, with a resolution of 30 s (Hijmans et al. 2005) and edited in the raster package (R Core  
263 Team 2018).

264 One TR plot (TR16 – Table S1), located within a protected area, had exceptionally high  
265 biomass (outlier) possibly due to the long-term protection from disturbances such as fire. The  
266 vegetation in this area is becoming denser and shifting from a savanna-like into a woodland  
267 physiognomy (Morandi et al. 2016), even though the habitat is still clearly consistent with  
268 that of the typical cerrado (Marimon-Junior and Haridasan 2005; Marimon et al. 2014). We  
269 retained this plot because it demonstrates the importance and effect of the establishment of  
270 protected areas but, to avoid potentially undesirable effects, we removed it from all  
271 regression analyses involving biomass.

272

## 273 **Results**

### 274 **Vegetation structure**

275 Summaries of vegetation structure parameters from each plot are in Table S2. Overall, the  
276 strongest correlations were between tree basal area vs. biomass, followed by density vs.  
277 biomass (Fig. S1). Tree height and total biomass were significantly higher in TR plots (Table  
278 1, Fig. S2). There were no differences between CA and TR plots in tree density, diameter and  
279 basal area (Table 1, Fig. S2). Bayesian model averaging indicated that, by and large, tree  
280 height was the best predictor of CA and TR plots: it had the largest standardized coefficient,  
281 with a 95% credibility interval that did not include zero, and the largest posterior inclusion  
282 probability (Table 2). Further, in all models containing height its coefficient was positive,  
283 indicating larger values in the TR, and the top model, including just height, concentrated 26%  
284 of the posterior model probabilities (Fig. 2). The remaining predictors had much lower  
285 standardized coefficients and posterior inclusion probabilities. The second-best model,  
286 including height and diameter, concentrated an additional 21% of the posterior model

287 probabilities, with the contribution of remaining models being much smaller (Fig. 2). In all  
288 but one model containing diameter, its coefficient was negative. Biomass, which had the  
289 second largest standardized coefficient, behaved similarly with a negative coefficient in all  
290 but one model (Table 2, Fig. 2). This indicates that, after accounting for differences in height,  
291 tree diameter and biomass are smaller in TR plots.

292

### 293 **Vegetation diversity**

294 We recorded 233 species in all plots combined, with 177 in the CA plots and 172 in the TR  
295 plots. Summaries of vegetation diversity parameters from each plot are in Table S2. The  
296 individual-based and sample-based species accumulation curves indicated that the CA has a  
297 larger species pool than the TR (Fig. 3). Likewise, all abundance-based and incidence-based  
298 non-parametric estimators indicated larger species richness in the CA (Table S3). Except for  
299 Pielou's evenness ( $J'$ ), the correlations between all diversity parameters were high (Fig. S3).  
300 There were no differences between CA and TR plots in tree diversity parameters (Table 1,  
301 Fig. S4). Overall, these results indicate higher regional diversity in the CA, but no differences  
302 in local (plot) diversity between CA and TR.

303

### 304 **Relationships between biomass, diversity and climate**

305 The spatial Bayesian model averaging analysis indicated that the spatial weight matrix based  
306 on the Gabriel graph had the highest posterior model probability (48.3%). By and large, tree  
307 density was the single best predictor of plot biomass: it had the largest standardized  
308 coefficient, with a 95% credibility interval that did not include zero, and the largest posterior  
309 inclusion probability (Table 3). In all models containing density, its coefficient was positive  
310 and the top model, including just density, concentrated 21% of the posterior model  
311 probabilities (Fig. 4). The remaining predictors had much lower standardized coefficients and

312 posterior inclusion probabilities. The second-best model, including density, richness, and  
313 evenness, concentrated an additional 17% of the posterior model probabilities, with the  
314 contribution of remaining models being much smaller (Fig. 4A). In all models containing  
315 species richness, the second-best predictor, its coefficient was negative (Table 3, Fig. 4A).  
316 The importance of the remaining predictors was much smaller. The incorporation of  
317 eigenvectors in the analysis successfully removed the spatial autocorrelation from the  
318 regression residuals (Fig. 4B). Summing up, the results indicate that after accounting for  
319 differences in density, species richness and biomass tend to be negatively correlated in the  
320 study plots. The results of bivariate regression indicated that, when evaluated separately,  
321 temperature is a good positive predictor of the biomass ( $r^2 = 0.21$ ,  $p < 0.01$ ; Fig. S5).

322

## 323 **Discussion**

324 We found that plots in typical cerrado vegetation of the Cerrado-Amazonia Transition  
325 (TR) had much greater biomass (58% more) than those of the core area (CA) of the Cerrado.  
326 By contrast, species richness and diversity are similar between the TR and CA. We also find  
327 that for typical cerrado trees there is no systematic relationship between species diversity and  
328 biomass. Thus, our first hypothesis, which suggested that the cerrados of the TR have greater  
329 tree size and ecosystem biomass and greater species diversity than the CA cerrados, was  
330 partly corroborated, given that only the structural variables differed as predicted. Our second  
331 hypothesis was supported, given that the climatic variables predict biomass. The species  
332 diversity-biomass relationship was weak and, if anything, negative, meaning that the third  
333 hypothesis was rejected. These findings are discussed in more detail below, together with an  
334 assessment of the implications for conservation.

335

## 336 **Structure**

337 The biomass and tree height in typical cerrado plots in the transition (TR) were all  
338 significantly greater than those recorded in the core area (CA) and in previous studies spread  
339 in the Cerrado biome (Castro and Kauffman 1998; Vale and Felfili 2005; Rezende et al.  
340 2006; Paiva et al. 2011; Miranda et al. 2014). Several small-scale (1 hectare) local studies in  
341 single sites within the TR had already indicated that the cerrados of this zone may have  
342 greater basal area than those of the more central regions of the Cerrado biome (Felfili et al.  
343 2002; Marimon-Junior and Haridasan 2005; Kunz et al. 2009; Marimon et al. 2014).  
344 However, this is the first time that a biome-scale study, which compares different regions  
345 directly with multiple, replicated plots, has detected such a pattern. The factors that affect the  
346 variation in biomass are discussed below.

347 From a conservation perspective, the clear structural differences between TR and CA  
348 cerrados are a new find, which has important implications. While the vegetation is defined as  
349 typical cerrado (Ribeiro and Walter 2008) in both cases, the unique structural characteristics  
350 found in each region should be considered for the development of habitat management  
351 practices. In other words, a conservation unit that protects typical cerrado in the core area  
352 will likely not be representative of the same physiognomy in the Cerrado-Amazonia  
353 Transition. This reinforces the position of Primack and Rodrigues (2001), who argued that  
354 conservation units should encompass physiognomies that are representative of environments  
355 on a wide geographic scale. In the specific case of the Cerrado-Amazonia Transition, the  
356 region also coincides with that of the 'arc of deforestation' (Fearnside 2005; Marimon et al.  
357 2014), where the landscape is dominated by agricultural frontiers, reinforcing the urgent need  
358 for the establishment of conservation units in this big region. In this context, the maintenance  
359 of private reserves is also an important strategy to conserve portions of cerrado along its wide  
360 geographic distribution.



361 The maps available on the site of the Mato Grosso State Environment Secretariat  
362 (SEMA: <http://www.sema.mt.gov.br/>) show that the unique state conservation unit of the TR  
363 that include Cerrado vegetation are all part of Morte-Araguaia river basin, which is subject  
364 to seasonal flooding (Marimon et al. 2015). In the Araguaia State Park for example, the  
365 predominant physiognomy is the murundus grassland, in which patches of typical cerrado are  
366 found only on the higher terrain, which is free of seasonal flooding. Throughout the state  
367 there is no fully protected area within a 200 km distance of the established limit between the  
368 Cerrado and Amazon biomes (IBGE 2016) in which the predominant vegetation is typical  
369 cerrado not subject to seasonal flooding (SEMA 2016). Given that TR cerrados are  
370 structurally different from those found in the CA, it is important to establish typical cerrado  
371 conservation units within the non-flooded areas of the TR.

372

### 373 **Species diversity**

374 While several previous studies have indicated that the typical cerrados of the TR have  
375 greater species diversity per unit area (alpha diversity) than those of the core area (Felfili et  
376 al. 2002; Ratter et al. 2003; Bridgewater et al. 2004), this was clearly not the case in our  
377 study in which well replicated, quantitative ecological sampling was conducted across both  
378 TR and CA. We conclude that tree species diversity does not vary notably between the  
379 central and outer regions of the Cerrado, even in the TR, where the contribution of the  
380 Amazonian flora increases (Eiten 1972; Ratter et al. 1973, 2003; Castro et al. 1999; Felfili et  
381 al. 2002; Bridgewater et al. 2004; Marimon-Junior and Haridasan 2005).

382 In a recent study it was stated that there is a greater overlap of species in the central  
383 portion of the Cerrado, which is reflected in higher species richness in the core area than in  
384 the border (Françoso et al. 2016). However, that study may have been influenced by  
385 sampling gaps, as the TR was under-represented. In addition, the above study was based on

386 binary presence-absence data, which may not be sufficiently robust given that population size  
387 is an important aspect of species diversity, and a fundamental parameter for the development  
388 of conservation measures (Felfili et al. 2005a; Mews et al. 2014).

389 While our results indicate that alpha diversity did not vary between the CA and TR, there  
390 is a suggestion that beta diversity was higher in the CA, possibly due to the more stable  
391 climate in this area (Werneck et al. 2012) which would be reflected in increased niche  
392 specialization (Moldenke 1975). Even so, neither our study nor previous work using different  
393 methods (Eiten 1972; Fernandes and Bezerra 1990; Rizzini 1997; Castro et al. 1999) strongly  
394 suggests that the TR is relatively species-poor or less diverse than the central area of the  
395 Cerrado. Marimon et al. (2014) observed that the vegetation of the transition zone, in  
396 addition to being hyperdynamic, is in disequilibrium, and Werneck et al. (2012) suggested  
397 that the lower diversity in the transition zone may reflect this instability. However, the  
398 instability normally observed in ecotones (e.g. van der Maarel 1990; Werneck et al. 2012;  
399 Pironon et al. 2016) does not appear to have affected tree species richness and diversity in the  
400 TR. For all these reasons, it is essential to consider both the TR and CA when designing  
401 conservation units, to guarantee the preservation of intrinsic vegetation properties of each  
402 region. As agricultural frontiers are still rapidly advancing within the TR (Marimon et al.  
403 2014), the complete absence of conservation units in typical cerrados is a significant concern.

404

#### 405 **Determinants of biomass variation**

406 In our study, tree density was the most important predictor of biomass variation. In other  
407 studies, precipitation and temperature were determinants of biomass in South African  
408 savannas (Scholes et al. 2002). In contrast with our results, however, Miranda et al. (2014)  
409 found a negative correlation between biomass and precipitation levels, albeit in an analysis in

410 which the TR was under-represented. Moreover, none studies referred here has used density  
411 as predictor of biomass.

412 Miranda et al. (2014) however suggest that biomass was greater in areas with reduced  
413 seasonality, which may also be relevant to the present study, given that TR cerrados are  
414 located in a region where the mean annual precipitation (1659 mm) is approximately 200 mm  
415 (14% – Table S1) higher than that in the CA (1446 mm), and seasonality is less pronounced  
416 (Keller-Filho et al. 2005; Alvares et al. 2013). This reinforces the effect of its proximity to  
417 the Amazon Forest (Felfili et al. 2002; Marimon-Junior and Haridasan 2005; Torello-  
418 Raventos et al. 2013), which may impact tree growth. Additionally, if we consider the results  
419 of the bivariate regression models, temperature and precipitation have a direct effect on  
420 biomass, with the TR contributing most to this tendency.

421

#### 422 **Diversity-biomass relationships and implications for conservation**

423 We observed no positive diversity vs. biomass relationship across all plots. It is notable that  
424 the lack of correlation between biomass and diversity metrics remains despite the fact that  
425 only biomass is associated with temperature and to precipitation, and this clearly argues  
426 against their being a positive effect of tree species diversity on carbon storage within the  
427 Cerrado. It is interesting to note that these findings parallel a recent report from across the  
428 tropical moist forest biome (i.e., Amazonia, Africa, Southeast Asia), for which there is also  
429 no detectable relationship between community diversity and carbon storage except at the very  
430 smallest scales (0.04 ha) (Sullivan et al. 2017). Torello-Raventos et al. (2013), analyzing the  
431 structural and floristic data from three continents, observed that there is not necessarily a  
432 congruence between floristic and structural groupings for vegetation types in the forest-  
433 savanna transition zone. Therefore, to the extent that positive diversity-function mechanisms

434 and relationships might exist, within the two largest tropical biomes on Earth they do no  
435 translate into a significant effect on carbon storage.

436 As a practical consequence, it cannot be assumed that efforts made to conserve the  
437 diversity of typical cerrado will have clear co-benefits (cf. Day et al. 2013) for climate  
438 protection, since the areas with higher diversity do not necessarily coincide with those with  
439 highest biomass. According to Gardner et al. (2012), when this relationship is inverse or  
440 nonexistent, as in the case of the Cerrado, then decisions on the conservation of carbon stocks  
441 or species diversity will imply difficult trade-offs for institutions responsible for the  
442 conservation of biodiversity and the reduction of greenhouse gases. For the Cerrado the  
443 implications seem clear—it is necessary to carefully design a biome-wide conservation  
444 network that can protect both high levels of species diversity and also store large stocks of  
445 carbon, and not assume that protection for one purpose automatically guarantees the other.

446 As we have already argued, there is clearly now a deeply concerning gap in the  
447 protection of TR cerrado. Furthermore, the similar tree species richness and diversity  
448 observed in the typical cerrado of the CA and TR, together with the greater tree heights and  
449 biomass in the TR, are consistent with the notion that populations of transition zones may be  
450 better adapted to environmental instability and impacts, and would be more capable of  
451 persisting through periods of climate change (Kark and van Rensburg 2006), were they to  
452 survive direct removal as part of Brazil's agricultural revolution. While the high  
453 environmental heterogeneity of the Cerrado (Felfili et al. 2005a; Mendonça et al. 2008; BFG  
454 2015) cannot be overlooked in the planning of the network of conservation units  
455 (Bridgewater et al. 2004), it is clearly vital to increase protection of the TR, threatened as it is  
456 by intense anthropogenic pressures that may provoke the disappearance of this unique and  
457 valuable environment.

458

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699 **Figure Captions**

700

701 **Fig. 1** Geographic location of 39 one-hectare plots of typical cerrado in the core area of the  
702 Cerrado (brown circles) and at the Cerrado-Amazonia Transition (green circles) in South  
703 America. Shading indicates the ranges of Cerrado and Amazonia. Lines represent country  
704 boundaries

705

706 **Fig. 2** Bayesian model averaging of vegetation structure parameters for 39 one-hectare plots  
707 of typical cerrado in the core region of the Cerrado and at the Cerrado-Amazonia transition.  
708 The Y-axis contains the predictors of core vs. transition plots, while the X-axis is scaled by  
709 the posterior model probabilities. Colors indicate predictor inclusion in each of the 32 models  
710 assessed (the full set of possible models). Positive coefficients are indicated by blue, negative  
711 coefficients by red, and white indicates non-inclusion of the respective predictor

712

713 **Fig. 3** Individual-based (top) and sample-based (bottom) species accumulation curves for  
714 trees from 39 one-hectare plots of typical cerrado in the core region of the Cerrado and at the  
715 Cerrado-Amazonia transition. The continuous lines represent the mean and the shaded areas  
716 the 95% confidence interval

717

718 **Fig. 4** Spatial Bayesian model averaging of tree above-ground biomass, diversity and climate  
719 parameters for 39 one-hectare plots of typical cerrado in the core region of the Cerrado and at  
720 the Cerrado-Amazonia transition. Above-ground biomass represents plot totals. Distance to  
721 transition boundary represents linear distance from each plot to the line separating Amazonia  
722 from the Cerrado (IBGE 2004). The Y-axis contains the predictors of total tree above-ground  
723 biomass in plots, while the X-axis is scaled by the posterior model probabilities. Colors  
724 indicate predictor inclusion in each of the 32 models assessed. Positive coefficients are  
725 indicated by blue, negative coefficients by red, and white indicates non-inclusion of the  
726 respective predictor

1 **Table 1** Summary statistics of vegetation structure and diversity parameters for 39 one-hectare plots of typical cerrado in the core region of the  
 2 Cerrado and at the Cerrado-Amazonia transition. Values indicate mean  $\pm$  one standard deviation and t-test statistics. Tree height and diameter  
 3 represent plot means, whereas basal area and above-ground biomass represent plot totals. n: number of plots sampled

Parameter	Core area (n= 18)	Transition (n= 21)	t	P
<b>Vegetation structure</b>				
Density (individuals.ha <sup>-1</sup> )	304.3 $\pm$ 71.7	355.5 $\pm$ 152.3	-1.372	0.181
Height (m)	4.5 $\pm$ 0.5	5.8 $\pm$ 0.5	-8.454	< 0.001
Diameter (cm)	14.4 $\pm$ 0.7	14.9 $\pm$ 1.6	-1.155	0.258
Basal area (m <sup>2</sup> .ha <sup>-1</sup> )	5.6 $\pm$ 1.7	6.9 $\pm$ 3.1	-1.590	0.122
Above-ground biomass (Mg.ha <sup>-1</sup> )	20.4 $\pm$ 6.5	32.4 $\pm$ 16.5	-3.052	0.005
<b>Vegetation diversity</b>				
Species richness	45.6 $\pm$ 11.4	45.6 $\pm$ 12.0	-0.004	0.997
Rarefied species richness	37.4 $\pm$ 7.3	37.0 $\pm$ 8.3	0.162	0.872
Shannon information index ( <i>H'</i> )	3.0 $\pm$ 0.4	3.1 $\pm$ 0.4	-0.945	0.351
Fisher's log-series $\alpha$	15.3 $\pm$ 4.5	14.4 $\pm$ 4.3	0.641	0.525
Pielou's evenness ( <i>J'</i> )	0.80 $\pm$ 0.07	0.83 $\pm$ 0.05	-1.606	0.117



1 **Table 2** Bayesian model averaging of vegetation structure parameters for 39 one-hectare plots of typical cerrado in the core region of the  
 2 Cerrado and at the Cerrado-Amazonia transition. PIP: posterior inclusion probabilities, i.e., sum of posterior model probabilities for all models  
 3 wherein a predictor was included; PostMean: standardized coefficients averaged over all models; PostSD: standard deviations of standardized  
 4 coefficients; CondPosSign: sign certainty, i.e., posterior probability of a positive coefficient expected value conditional on inclusion; 95%  
 5 PostCI: 95% credibility interval of the posterior probability distribution. Tree height and diameter represent plot means, whereas basal area and  
 6 above-ground biomass represent plot totals

Parameter	PIP	PostMean	PostSD	CondPosSign	95% PostCI
Height (m)	1.000	0.874	0.161	1.000	0.3691 – 0.7576
Diameter (cm)	0.386	-0.067	0.129	0.067	-0.1642 – 0.0798
Density (individuals.ha <sup>-1</sup> )	0.301	0.094	0.222	1.000	-0.0005 – 0.0038
Above-ground biomass (Mg.ha <sup>-1</sup> )	0.274	-0.142	0.395	0.136	-0.0743 – 0.0088
Basal area (m <sup>2</sup> .ha <sup>-1</sup> )	0.235	0.035	0.365	0.520	-0.1935 – 0.3599

7

1 **Table 3** Spatial Bayesian model averaging of tree above-ground biomass versus diversity and climate parameters for 39 one-hectare plots of  
 2 typical cerrado in the core region of the Cerrado and at the Cerrado-Amazonia transition. PIP: posterior inclusion probabilities, i.e., sum of  
 3 posterior model probabilities for all models wherein a predictor was included; PostMean: standardized coefficients averaged over all models;  
 4 PostSD: standard deviations of standardized coefficients; CondPosSign: sign certainty, i.e., posterior probability of a positive coefficient  
 5 expected value conditional on inclusion; 95% PostCI: 95% credibility interval of the posterior probability distribution. Above-ground biomass  
 6 represents plot totals. Distance to transition boundary represents linear distance from each plot to the line separating Amazonia from the Cerrado  
 7 (IBGE 2004).

Parameter	PIP	PostMean	PostSD	CondPosSign	95% PostCI
Density (individuals.ha <sup>-1</sup> )	1.000	0.697	0.111	1.000	0.4914 – 0.9210
Species richness	0.462	-0.133	0.171	0.000	-0.5038 – 0.0910
Pielou's evenness ( <i>J'</i> )	0.273	0.037	0.084	0.916	-0.0628 – 0.2583
Temperature (°C)	0.198	0.026	0.079	1.000	-0.1237 – 0.2532
Precipitation (mm)	0.174	0.009	0.052	0.816	-0.1109 – 0.1772
Distance to transition boundary (km)	0.148	0.002	0.057	0.485	-0.1660 – 0.2192

Figure 1







