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Temporal changes in species composition, diversity, and woody vegetation structure of savannas in the Cerrado–Amazon transition zone

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ABSTRACT

Vegetation in the transition between tropical forest and savanna is hyperdynamic and there is evidence that in the absence of fire, forest advances over savanna. Between 2008 and 2013 we evaluated changes in species composition and diversity and in the structure of the woody vegetation of savanna physiognomies in the transition between the Cerrado and Amazon biomes that were fire free for 11 years. The physiognomies form a gradient from savanna woodland (Typical Cerrado - TC), to low woodland (Dense Cerrado - DC), to woodland (locally called *Cerradão* - CO). We hypothesise that: 1) the more open physiognomies (TC and DC) are more dynamic compared to the closed physiognomy (CO); and 2) in the absence of fire vegetation tends to become more forested. We found that: 1) TC was more dynamic (e.g. greater increases in richness, diversity, and abundance of plants and basal area) than CO and DC; 2) The three physiognomies experienced an increase in basal area and abundance of individuals, but only certain key species contributed to these increases. These results indicate that the open physiognomies were more dynamic than the closed physiognomies, and in the absence of fire the savanna physiognomies became more forested and accumulated biomass.

Keywords: alternative stable states, biodiversity, Brazilian savanna, conservation, mortality, recruitment

Introduction

Transition zones between biomes tend to be temporally dynamic, with distinct plant communities expanding and retracting over time (Staver *et al*. 2011 a; b; Gowda *et al*. 2012; Joly *et al*. 2012). There have been numerous reports over the past 40 years on the advance of tropical forests during more humid periods and the expansion of savanna habitats during drier periods (Ratter *et al*. 1973; Marimon *et al*. 2006; 2014). Stevens *et al*. (2017) evidenced ongoing increases in plant densities and basal area of savanna vegetation (woody encroachment) in transition regions within tropical forests in South America, Africa, and Australia. Favier *et al*. (2004) showed, in a modelling study, that forest expansion over savanna occurs by three processes: 1. advance of the forest edge over savanna; 2. formation of clumps in savanna and subsequent coalescence with the forest; and 3. afforestation of savanna (woody encroachment, according to Stevens *et al*. 2017). The last process, which occurs especially in the absence of fire (Staver *et al*. 2011 a; b; Stevens *et al*. 2017), has been observed primarily in the vast area of the forest–savanna transition in central and northern Mato Grosso, Brazil (Marimon *et al*. 2006; 2014; Mews *et al*. 2011 a; b). This region is characterised by an intricate and complex interaction between the two ecosystems (Askew *et al*. 1970), which provides an excellent opportunity to monitor temporal and spatial patterns and understand

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the response of forests and savannas to changes in the climate and the increasing intensification of land use and fire frequency.

The transition zone between the Cerrado and Amazon forests is formed by a mosaic of vegetation types, with characteristics of both forest and savanna (Ratter *et al.* 1973; Ackerly *et al.* 1989; Marimon *et al.* 2006), and the influence of both biomes on species composition (Pinto & Oliveira-Filho 1999; Méio *et al.* 2003; Françoso *et al.* 2016). This mosaic is heterogeneous, with varying structure, species composition, and dimensions within the transition zone (Marimon *et al.* 2006; Torello-Raventos *et al.* 2013).

In Mato Grosso State, the transition between the Cerrado and the Amazon Forest extends over a large area (Ackerly *et al.* 1989), which coincides with the 'arc of deforestation' (Nogueira *et al.* 2008; Domingues & Bermann 2012), and is composed of seasonal perennial and semi-deciduous forests with characteristics distinct from the forest habitats of either the Cerrado or Amazon (Marimon *et al.* 2006; Balch *et al.* 2008; 2010; Hoffmann *et al.* 2012). Distinct savanna physiognomies (*sensu* Ribeiro & Walter 2008) can also be found in the region, including the woodland (*Cerradão*), low woodland (Dense Cerrado), savanna woodland (Typical Cerrado), open scrub (Sparse Cerrado), rocky field (Rocky Cerrado), palm swamp (*Vereda*), and savanna parkland, also known as the Murundu (Askew *et al.* 1970; Eiten 1975; Marimon-Junior & Haridasan 2005; Maracahipes *et al.* 2011; Mews *et al.* 2011 a; b; Marimon *et al.* 2014). We focus on the first three because they represent a gradient of tree density and height (Maracahipes-Santos *et al.* 2015) and offer a good opportunity to evaluate the rapid changes in vegetation of the Cerrado–Amazon transition zone.

Research in this region suggests that the vegetation is hyperdynamic (see Marimon *et al.* 2014), since forest formations are quickly advancing over the savanna ones (Ratter 1992) by roughly 7 km in 40 years (Marimon *et al.* 2006). The substitution of savanna by forest may begin with the consolidation (increasing density) and increasing basal area of the savanna formations, which may become more forested over time with changes in structure associated with a shift in species composition (Durigan & Ratter 2006; Geiger *et al.* 2011; Honda & Durigan 2016). However, Almeida *et al.* (2014) did not find significant structural changes in *Cerrado sensu stricto* in the central portion of the Cerrado biome during a period of 27 years. Also, Roitman *et al.* (2008) found a small annual increment in biomass, over a 13-year period, of a savanna in transition with the semi-arid Caatinga biome. This suggests that the savannas in transition with tropical forests are more dynamic and accumulate more biomass than those savannas in the central portion of the Cerrado biome or in transition with the semi-arid biome.

Assuming that the savanna formations of the Cerrado–Amazon transition zone are being gradually replaced by forest formations as previously discussed, we compared the changes in the species composition and diversity as well as the structure of the woody vegetation in three savanna physiognomies (*sensu* Eiten 1975) in order to better understand these temporal changes: a woodland (*Cerradão* - CO), a low woodland (Dense Cerrado - DC), and a savanna woodland (Typical Cerrado - TC). Because three physiognomies were protected from fire for 11 years before the experiment, we tested the following hypothesis: 1) the more open physiognomies (here TC and DC) are more dynamic compared with the closed physiognomy (here CO); 2) in the absence of fire, the savanna vegetation tends to become more forested by an encroachment process. We also discuss our results regarding the 'alternative stable states' theory proposed by Staver *et al.* (2011 a; b) and Murphy & Bowman (2012), which argues that savanna vegetation tends to become more forested in appropriate climatic and edaphic conditions and in the absence of fire.

Materials and methods

Study area

This study focused on three sites (also studied by Maracahipes-Santos *et al.* 2015 — check that study for site localisation) with distinct savanna physiognomies: woodland/locally called *Cerradão* (CO) (12°49'26.8"S 51°46'06.0"W), low woodland/locally called Dense Cerrado (DC) (12°49'07.6"S 51°46'12.3"W), and savanna woodland/locally called *cerrado sensu stricto* (TC) (12°50'02.5"S 51°45'55.9"W) (Fig. 1). These sites are located in the municipality of Ribeirão Cascalheira in the Cerrado–Amazon transition of eastern Mato Grosso State, Brazil. The climate is seasonal, with a rainy season between October and March, and a dry season between April and September (Alvares *et al.* 2013). For details on differences in diversity, floristic composition and structure, and relation to vegetation of the three physiognomies, see Maracahipes-Santos *et al.* (2015; 2017).

Data collection

In April 2008, at each site we established a one-hectare plot (100 m × 100 m), divided into 25 permanent contiguous subplots of 20 m × 20 m. We recorded, identified, and marked with aluminum tags all woody plants with a DBH 1.30 m (diameter at 1.30 m above ground) of at least 10 cm. We adopted this limit of inclusion because these data are part of a global network that samples sites of forest and forest transition around the world (ForestPLot.net; Lopez-Gonzalez *et al.* 2011). We also measured the diameter of all the stems of each individual below the minimum sampling height (Moro & Martins 2011) to calculate the quadratic diameter. In April 2013, we re-measured all surviving individuals and included new recruits (individuals that had reached the minimum diameter) in the sample. We identified

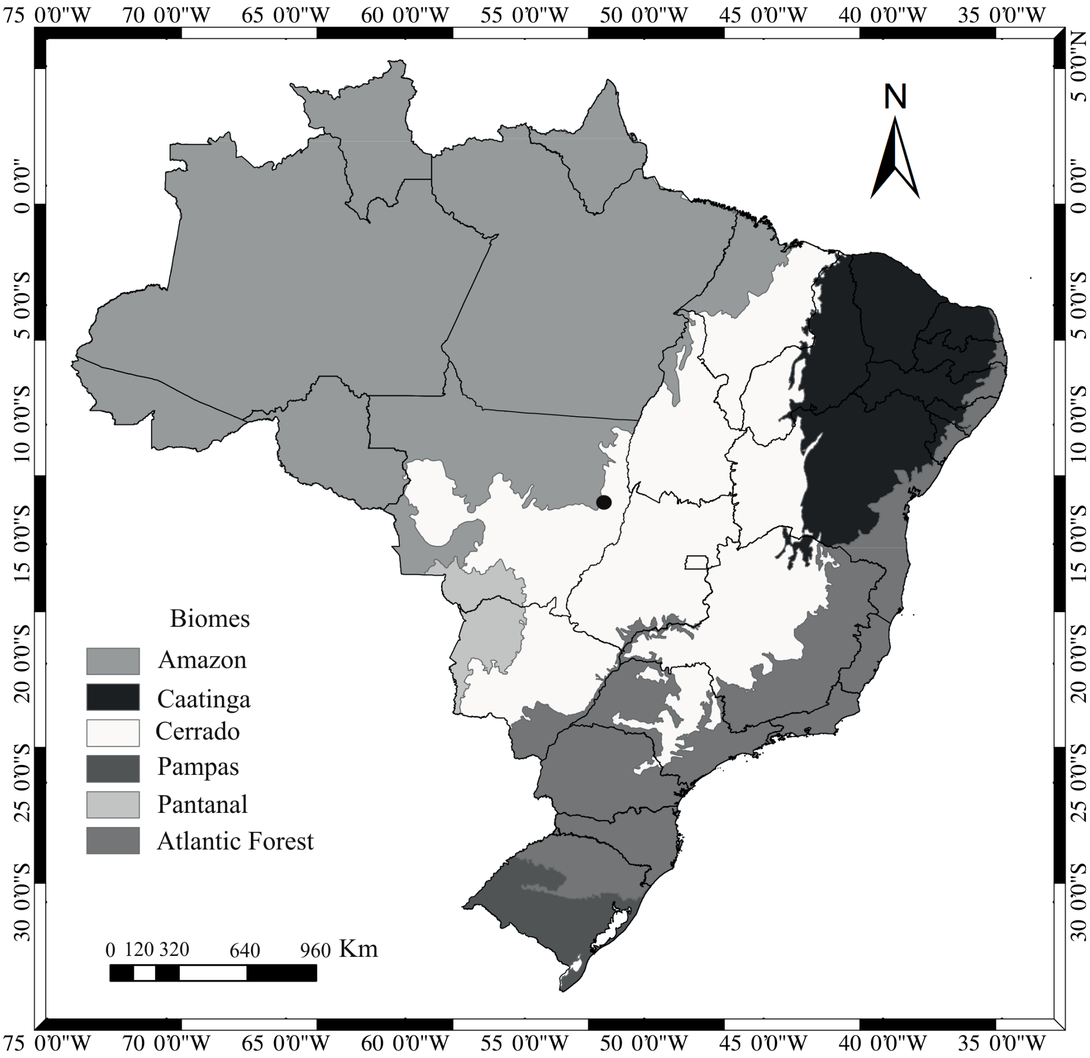

Figure 1. Location of the three Cerrado sites (●) surveyed in the Cerrado–Amazon transition, Ribeirão Cascalheira, Mato Grosso State, Brazil.

the species in the field according to the classification system of the Angiosperm Phylogeny Group (APG IV 2016), and we revised and updated the nomenclature of the rate based on the Brazilian List of Plant Species (http://floradobrasil.jbrj.gov.br/).

Data analysis

To evaluate whether the three phytophysiognomies (woodland – CO; low woodland – DC; savanna woodland – TC) formed distinct groups, we applied Principal Coordinates Analysis (PCoA) to the data from 2008, with a second analysis for the data from 2013, based on the species composition and abundance, using the Bray–Curtis distance coefficient (Felfili *et al.* 2011; Legendre & Legendre 2012). We tested the significance of the groups formed by the PCoA using ANOSIM with Bonferroni correction (Clarke & Warwick 1994). We ran these analyses in the *vegan* package (Oksanen *et al.* 2017) of the R environment, version 3.2.3 (R Core Team 2017). Since these analyses indicated the formation of three consistent groups, all other analyses were based on the comparison of CO, DC, and TC. We compared species richness between years and among physiognomies based on a rarefaction analysis of the number of individuals, with 1,000 randomisations (Gotelli & Colwell 2001). This approach is used to compare communities considering the number of individuals recorded in the smallest sample (Gotelli & Colwell 2001; Magurran 2011). This analysis was run in the PAST (*PAleontological STatistics*) programme, version 2.15 (Hammer *et al.* 2001).

We compared species diversity among the three savanna physiognomies and between survey years based on diversity profiles generated by a Rényi exponential series (Tóthmérész 1995). This technique is effective when there is no reliable criterion for the selection of diversity indices, given that it generalises the weight the different indices confer on rare (less abundant) species (Melo 2008). Alpha represents a family of diversity indices (alpha = 0 shows species richness).

This analysis was also run in PAST, version 2.15 (Hammer *et al.* 2001).

We used the Wilcoxon test to compare the mean density (per subplot), mean diameter (per individual), and basal area (per subplot) among years at each site. We applied the non-parametric Kruskal–Wallis analysis of variance (Zar 2010) to the analysis of these same variables among sites in the same year. Non-parametric analyses were applied due to the lack of normality of the residuals or homogeneity of variances, even after the log- transformation of the data. In both cases, the Mann–Whitney test was used for *post hoc* pairwise comparisons. These analyses were also run in PAST, version 2.15 (Hammer *et al.* 2001). All the analyses described above were also conducted between survey years (2008 and 2013) for each physiognomy and among the physiognomies (CO, DC, and TC) for each year.

For each physiognomy, we calculated the mean annual mortality and recruitment rates according to Sheil *et al.* (1995; 2000), and the replacement time (turnover) for the number of individuals and basal area according to Korning & Balslev (1994). For the annual recruitment and mortality rates, we applied the correction factor proposed by Lewis *et al.* (2004), which allowed reliable comparisons over distinct time intervals. We compared these rates among sites using the non-parametric Kruskal–Wallis analysis of variance (Zar 2010), except for the replacement times, because the data were insufficient (for the physiognomy of TC, we recorded mortality in only two subplots).

Results

The groups (physiognomies) established prior to the study on the basis of species composition and vegetation structure were confirmed by the analyses in both 2008 (Fig. 2A) and 2013 (Fig. 2B), based on the results of the ANOSIM (2008: $R = 0.38$, $p = 0.001$; 2013: $R = 0.43$, $p = 0.001$; Bonferroni correction: $p < 0.001$ for both years). However, in 2008, the subplots of all three phytophysiognomies were more widely dispersed (Fig. 2A), while in 2013 the groups were better defined. This is mainly due to the reduction in the proportion of species shared between CO and DC (23.8 in 2008 and 13.0 in 2013) and between DC and TC (6.3 in 2008 and 2.8 in 2013) (Tab. 1).

In 2008, we recorded 945 individuals distributed in 63 species, 45 genera, and 27 families at the three sites, while in 2013, we registered 1,061 individuals belonging to 69 species, 51 genera, and 30 families, with a clear tendency for increasing densities and species richness in all three physiognomies, except for low woodland (DC) (Tab. 1). The highest increase in the abundance of individuals (39.4 %) and species richness (36.7 %) between 2008 and 2013 was recorded in the savanna woodland (TC) (Tab. 1).

Estimated species richness did not vary between 2008 and 2013 in the CO (woodland) and DC, although an increase in richness was observed between years in the TC (Fig. 3A-C). This resulted in an increase in the species richness of the TC, which was initially much lower than that of the CO and DC, to a more similar level in 2013 (Fig. 3D, E).

We observed no clear changes in species diversity in the CO between 2008 and 2013, a minor reduction in the DC, and an increase in the TC (Fig. 4A- C). These changes resulted in the species diversity of the TC becoming more similar to that of the other physiognomies, due, in particular, to the increase in absolute species richness (alpha = 0 in Fig. 4D, E).

The increase in the species diversity in the TC was due to the inclusion of eight individuals of *Tachigali vulgaris* (species absent in 2008) and 11 other species represented by one to three individuals (see Fig. 4D, E). The abundance of other species also increased, such as *Emmotum nitens* (7 individuals in 2008 and 15 in 2013), *Eugenia gemmiflora* (10 and 15) and *Qualea parviflora* (13 and 23). The more discreet changes in species diversity observed in the CO and DC were related to the well-balanced equitability of these physiognomies, that is, the better distribution of the individuals among the species (Fig. 4D, E). However, the pattern of diversity in the TC shifted considerably between the two survey years (Fig. 4D, E), once the large number of species (12) (Tab. 1) recruited in this physiognomy promoted more equitable distribution of the most abundant species (Fig. 4D, E).

Some species also increased considerably in abundance (by at least three individuals) in all three physiognomies (*Tachigali vulgaris* and *Emmotum nitens*) in the CO and DC (*Myrcia splendens*), CO and TC (*Roupala montana*), or in a single vegetation type, i.e., the CO (*Pterodon pubescens*, *Qualea grandiflora*, and *Eriotheca gracilipes*), DC (*Mouriri elliptica*), or TC (*Qualea parviflora*, *Eugenia gemmiflora*, *Mezilaurus crassiramea*, *Bowdichia virgilioides*, *Xylopia aromatica*, and *Stryphnodendron rotundifolium*). On the other hand, a reduction in abundance (of at least three individuals) was recorded only in the CO (*Machaerium acutifolium*, *X. aromatica*, *Aspidosperma multiflorum*, and *Curatella americana*) and DC (*Pouteria ramiflora*). One species — *E. nitens* — presented a positive change in basal area in all three phytophysiognomies, while the basal area of *T. vulgaris* increased in both the CO and the TC, and some species increased only in the CO (*Xylopia sericea*, *P. pubescens*, and *M. splendens*) or TC (*Q. parviflora*, *M. crassiramea*, and *E. gracilipes*). A clear loss of basal area was recorded only for *M. acutifolium* in the CO. Overall, the gains in species diversity, abundance, and basal area were invariably greater than the losses in all three physiognomies. In addition, greater gains and smaller losses were recorded in the TC in comparison with the CO and DC.

We also recorded a lower annual rate of mortality and a higher annual rate of recruitment in the TC in comparison with the CO and DC (Tab. 2). As a result, the TC presented the greatest net changes in comparison with the other two vegetation types, both in the number of individuals and

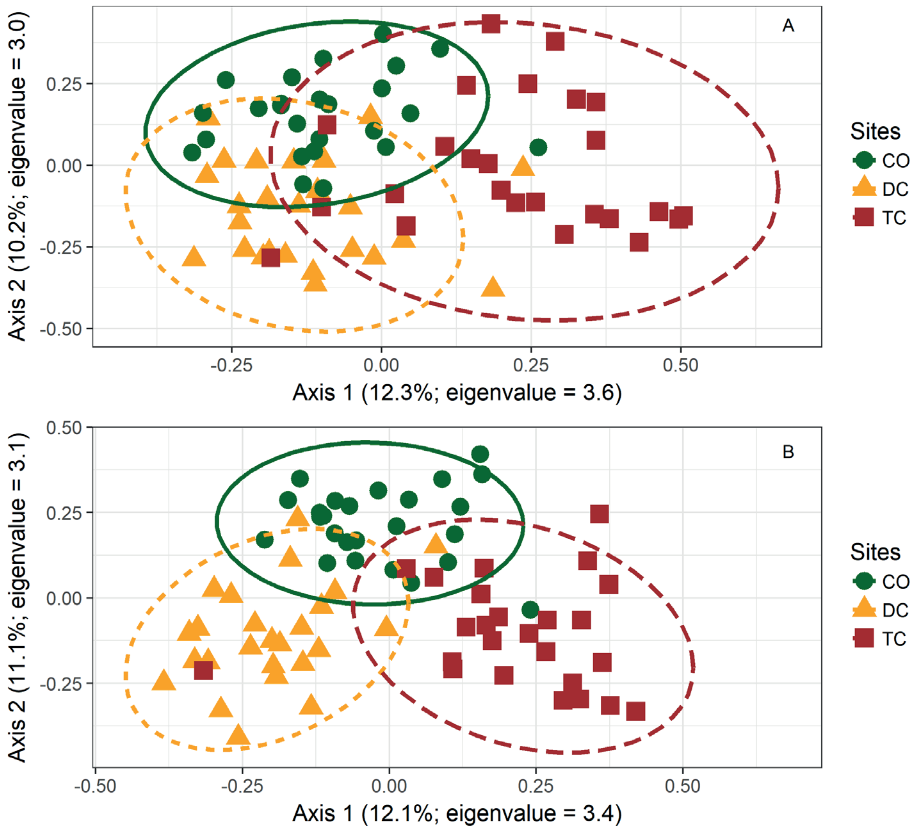

Figure 2. Principal Coordinates Analysis for the species composition and tree abundance (2008 and 2013) in the three Cerrado physiognomies sampled in the Cerrado–Amazon transition, Ribeirão Cascalheira, Mato Grosso State, Brazil. CO = woodland (●); DC = low woodland (Δ); TC = savanna woodland (■); **A**. 2008 and **B.** 2013.

Table 1. Structural parameters, species richness (2008 and 2013), and exclusive and shared species recorded in the woody vegetation surveyed in the three Cerrado physiognomies in the Cerrado-Amazon transition, Ribeirão Cascalheira, Mato Grosso state, Brazil. CO = Woodland; DC = Low woodland, and TC = Savanna woodland.

Parameters	2008	2013	2008	2013	2008	2013
	CO	CO	DC	DC	TC	TC
Number of individuals	411	436	364	388	170	237
Number of species	47	49	45	45	30	41
Number of genera	36	39	35	36	26	31
Number of families	22	23	23	23	19	20
Number of species ▲	2	-	3	-	1	-
Number of genera ▲	1	-	2	-	1	-
Number of families ▲	1	-	2	-	1	-
Number of species ▼	-	4	-	3	-	12
Number of genera ▼	-	4	-	3	-	6
Number of families ▼	-	2	-	2	-	2
Exclusive species (%)	**2008**			**2013**		
CO	12 (19.0)			12 (17.4)		
DC	6 (9.5)			7 (10.1)		
TC	6 (9.5)			11 (15.9)		
Shared species (%)	**2008**			**2013**		
CO-DC-TC[*]	20 (31.7)			27 (39.1)		
CO-DC[#]	15 (23.8)			9 (13.0)		
CO-TC[#]	0 (0.0)			1 (1.4)		
DC-TC[#]	4 (6.3)			2 (2.9)		

▲ Species recorded in 2008, but absent in 2013 (outgrowth); ▼ Species recorded in 2013, but absent in 2008 (ingrowth); * Considering the three physiognomies, # Only between two compared physiognomies.

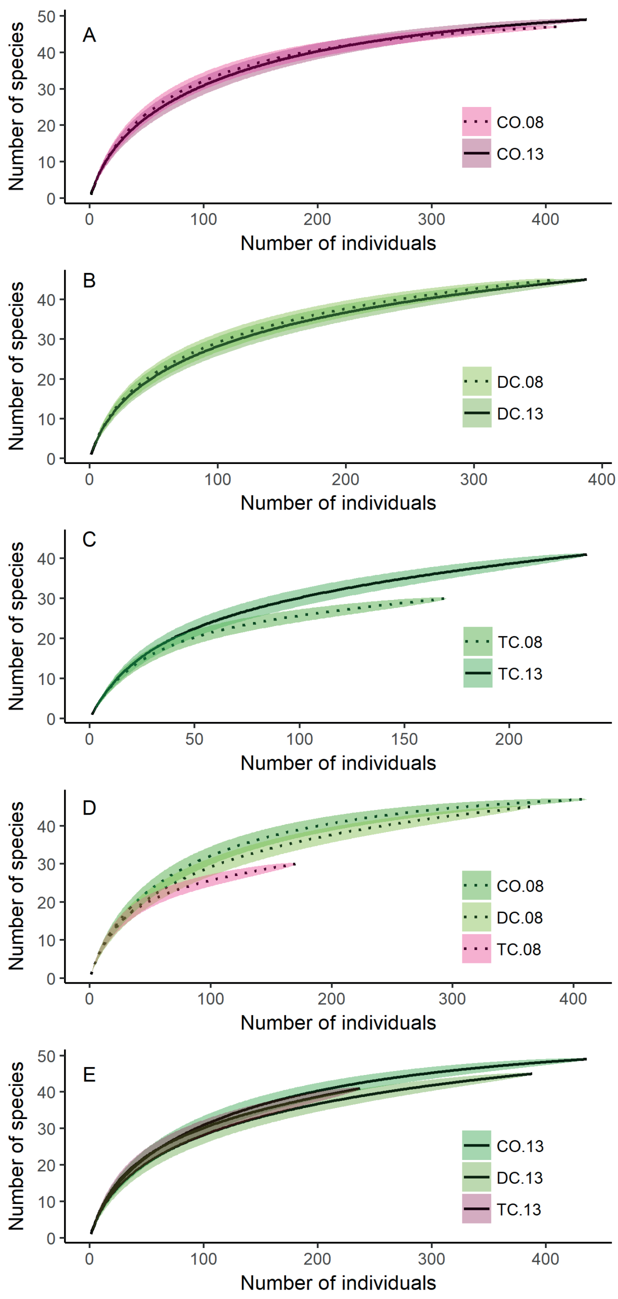

Figure 3. Rarefaction curve for the plant species of the three Cerrado physiognomies surveyed in 2008 (08 = *dotted line*) and 2013 (13 = *solid line*) in the Cerrado–Amazon transition, Ribeirão Cascalheira, Mato Grosso State, Brazil. The 95 % confidence interval is shaded in grey. CO = woodland; DC = low woodland; TC = savanna woodland.

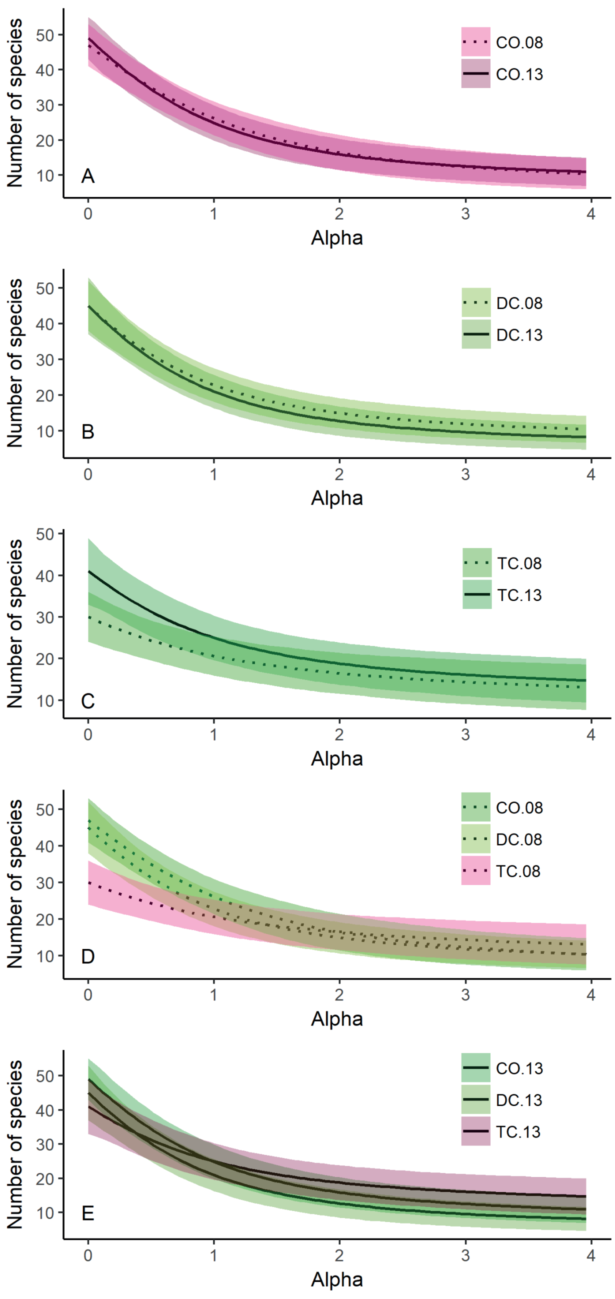

Figure 4. Tree species diversity profiles recorded in the three Cerrado physiognomies in 2008 (08 = *dotted line)* and 2013 (13 = *solid line*) in the Cerrado–Amazon transition, Ribeirão Cascalheira, Mato Grosso State, Brazil. CO = woodland; DC = low woodland; TC = savanna woodland.

basal area, which increased at a much higher rate than in the CO or DC (Tab. 2).

All three physiognomies presented an increase in abundance and basal area between the surveys in 2008 and 2013 (see Tab. 3). The abundance and basal areas were similar in the CO and DC plots, and higher than those recorded in the TC in both years. Only the mean diameter did not vary between years in the same physiognomy, neither among the three physiognomies in either year (Tab. 3).

Discussion

We show in this study that 1) the savanna formations of the Cerrado–Amazon transition zone are more dynamic than the forest formations, given that the low tree and scrub woodland (savanna woodland – TC) presented the greatest positive changes in species richness, diversity, composition, and structure of the woody vegetation in comparison with the intermediate (low woodland – DC) and forested (woodland – CO) physiognomies. The TC also shows lower mortality and a higher recruitment rate, net change, and turnover in terms of both the number of individuals and basal area; 2) the three physiognomies are increasing significantly in basal area and abundance of individuals. Here we first discuss the greatest dynamic in TC in relation to the DC and CO, before proceeding to discuss the changes in vegetation structure by the afforestation or encroachment process, in the absence of fire, as proposed by Favier *et al.* (2004), Staver *et al.* (2011 a; b), Murphy & Bowman (2012), and Stevens *et al.* (2017) in savanna–forest transitions. We were not able to test the other two processes proposed by Stevens *et al.* (2017) (advance of forest border over savanna; formation of clumps in savannas and additional coalescence with the forest), so we suggest conducting future studies to test these two processes.

Species richness, which was lowest in the TC in 2008 in comparison with the other physiognomies, equalled that in 2013, through the rapid recruitment of new species and reduced losses through mortality in the TC. In relation to other parameters, the higher rates of change observed in the TC reduced the differences between 2008 and 2013, but did not make the TC any more similar to the two other physiognomies. In the case of the diversity profile, for example, while the changes were more pronounced in the TC, the general pattern in the three physiognomies remained unaltered between years. Even so, the recruitment of new species in the savanna woodland, together with the increase in density of some species, altered the pattern of diversity in this physiognomy, emphasising its more dynamic characteristics. It is important to note that the changes observed in the present study occurred over a period of only five years, which is considered a short-term scale of time for woody vegetation of Cerrado habitats (Felfili 1995; Felfili *et al.* 2005). However, the results provide some support for the operational hypothesis, given that the greatest increases in density, species richness, and exclusive species were recorded in the TC, while little difference was found between the woodland and the low woodland.

However, changes in species composition in each physiognomy did not promote evident changes in CO, DC, and TC similarity, as indicated by the ordination analysis for the years 2008 and 2013, and by small changes, between 2008 and 2013, in the proportion of species unique to each physiognomy or shared between the three physiognomies. Given that all three sites are subject to the same climatic conditions, are at the same altitude, and are on the same type of soil, in terms of its physical properties and granulometry (Maracahipes-Santos *et al.* 2017), the distinct parameters found in the TC in comparison with the CO and DC appear to reflect the intrinsic properties of the three physiognomies. This dynamic nature of the vegetation is related primarily to the presence of fast-growing species, such as *Tachigali vulgaris*, which are thus extremely important, not only for the recuperation of basal area in degraded habitats (Reis *et al.*

Table 2. Parameters of the dynamics of the woody vegetation surveyed in the three Cerrado physiognomies in the Cerrado-Amazon transition, Ribeirão Cascalheira, Mato Grosso state, Brazil. CO = Woodland; DC = Low woodland; TC = Savanna woodland. Mean values accompanied by the same letter are not statistically different (lines), according to the Kruskal-Wallis parameter (*H*), at 5%.

Parameter	2008–2013			Kruskal-Wallis	
	CO	DC	TC	H	P
Number of Individuals					
Mean annual mortality rate (% year^{-1})	2.89^{a}	1.93^{a}	0.52^{b}	25.48	< 0.001
Mean annual recruitment rate (% year^{-1})	3.99^{b}	3.29^{b}	7.51^{a}	16.24	< 0.001
Net rate of change (% year^{-1})	1.04^{b}	1.29^{b}	6.87^{a}	23.88	< 0.001
Replacement time (years)	23.45	31.79	77.74	-	-
Basal area					
Net rate of change (% year-^{1})	1.93^{b}	1.50^{b}	5.86^{a}	32.61	< 0.001
Replacement time (years)	34.30	40.39	146.81	-	-

Table 3. Comparisons of the abundance (number of individuals per 20 m × 20 m subplot), basal area (20 m × 20 m subplots) and diameter of the stems (DBH ≥ 10 cm) of the woody vegetation sampled in the Cerrado-Amazon transition, Ribeirão Cascalheira, Mato Grosso state, Brazil. Comparisons between years were based on the Wilcoxon test, and the Kruskal-Wallis analysis of variance was used to compare the three physiognomies. *P* = significance. Uppercase letters indicate similarities or differences among physiognomies (columns) and lowercase letters, similarities or differences between years (lines).

Physiognomy	Abundance (no. ind.)		*P*	Basal area (m^{2}.ha^{-1})		*P*	Diameter (cm)		*P*
	2008	2013		2008	2013		2008	2013	
Woodland	16.4 ± 3.2^{Ab}	17.4 ± 3.2^{Aa}	**0.030**	0.29 ± 0.06^{Ab}	0.32 ± 0.06^{Aa}	**0.001**	14.3 ± 4.2^{Aa}	14.6 ± 4.3^{Aa}	0.099
Low woodland	14.6 ± 5.6^{Ab}	15.5 ± 5.7^{Aa}	**0.047**	0.25 ± 0.11^{Ab}	0.27 ± 0.12^{Aa}	**0.004**	14.4 ± 4.0^{Aa}	14.4 ± 4.1^{Aa}	0.217
Savanna woodland	6.8 ± 3.7^{Bb}	9.5 ± 4.5^{Ba}	**0.001**	0.13 ± 0.09^{Bb}	0.17 ± 0.10^{Ba}	**0.001**	14.7 ± 5.0^{Aa}	14.3 ± 4.9^{Aa}	0.297
P	**< 0.001**	**< 0.001**	--	**< 0.001**	**< 0.001**	--	0.847	0.354	--

2015), but also for natural processes in well-preserved areas, such as that of the present study. In the transition region between the Cerrado and the Atlantic with low frequency of fires (a burn in a period of 35 years), the changes in vegetation structure of the savanna are mediated by 5 species out of a total of 85 forest species (Geiger *et al*. 2011). This reinforces the importance of a few key species for the vegetation densification process (see the discussion below).

Studies of savanna and woodland formations in Brazil (*e.g.* Pinheiro & Durigan 2009; Franczak *et al*. 2011; Mews *et al*. 2011a; Gomes *et al*. 2014) and other parts of the world (*e.g.* Warman & Moles 2009; Mitchard *et al*. 2011; Palla *et al*. 2011) have typically found more discreet changes in species composition and structure than those recorded in the TC in the present study. However, Marimon *et al.* (2014) did also record a pattern of accelerated change in different physiognomies in the Cerrado–Amazon transition zone. These findings indicate that savannas in zones of contact with forests are highly dynamic, due to potential for the exchange of species between the biomes (see Ratter *et al.* 2003; Marimon *et al*. 2006; 2014; Honda & Durigan 2016; Stevens *et al*. 2017). The Cerrado–Amazon transition zone is located in a region with higher rainfall rates than the central portion of the Cerrado biome (Silva *et al.* 2008), despite recent years of low precipitation (Balch *et al.* 2008; Coe *et al*. 2013). In particular, Marimon *et al.* (2006) concluded that this region is suffering a progressive substitution of its savanna vegetation by forest formations. This is consistent with the situation found in the present study, given the marked increase in density and basal area recorded in these physiognomies, even over a relatively short interval of time (five years). In this case, the savanna formations of the Cerrado in transition with Amazon forests may act as an important carbon sink. However, Marimon *et al.* (2006; 2014) concluded that deforestation and other anthropogenic disturbances in the region, such as the increasingly frequent burn-offs, may be reverting the inherent process of the accumulation of biomass in this transition region.

Other evidence that savanna formations tend to become more forested formations in the absence of fires is that the two species that increased their densities in the three physiognomies (*Tachigali vulgaris* and *Emmotum nitens*) are dominant in woodland of the Cerrado biome and the region in which the present study was conducted (Furley & Ratter 1988; Moreira 2000; Marimon-Junior & Haridasan 2005; Solórzano *et al*. 2012), but occur in lower densities in savanna formations (Costa & Araújo 2001; Marimon-Junior & Haridasan 2005). These two species have a high basal area, are typically arboreal, and occupy the upper vertical stratum of this physiognomy (Marimon-Junior & Haridasan 2005; Franczak *et al*. 2011; Reis *et al*. 2015). *T. vulgaris* is still a pioneer and fast-growing species (Reis *et al*. 2015), considered of great importance for the dynamics of the vegetation (Franczak *et al*. 2011; Reis *et al*. 2015) and accumulation of biomass in the study region (Reis *et al*. 2015). This causes *T*. *vulgaris* and *E*. *nitens* to be considered two key species in the process of vegetation densification in the transition region between the Cerrado and the Amazon. Despite the evidence discussed above, only longer-term studies can confirm whether the current trend of densification will lead to the establishment of forest formations where savannas currently exist.

We showed here that in low fire frequency (the three physiognomies have been protected from fire for at least 11 years), we noticed vegetation densification and increase in basal area, as well as higher rates of recruitment than mortality. This result corroborates the theory of *different alternative stable states* among climate, soils, and fire proposed by Staver *et al.* (2011 a; b) and Murphy & Bowman (2012). According to this theory, savanna vegetation tends to become more forested in appropriate climatic and edaphic conditions and in the absence of fire. However, the region where this study was conducted is under high burning frequencies in the last decades (Silvério *et al*. 2013), which can reverse or impede the natural process of densification, increase of basal area, and establishment of more forest formations. This is because fires decrease the density, basal area, and, consequently, biomass of the *Cerrado stricto sensu* (Gomes *et al*. 2014; Lenza *et al*. 2017) in much of the woodlands (Reis *et al*. 2015). Still, the three species that increased their densities between 2008 and 2013 in at least two of the three physiognomies (*Tachigali vulgaris*, *Emmotum nitens*, *Roupala montana*) are immediately affected by fires. For example, *T. vulgaris* presented high mortality rates after burning in woodland (Moreira 2000; Reis *et al*. 2015) and *Cerrado stricto sensu* (Mews *et al*. 2013); *R. montana* is always cited as one of the most sensitive species to fires in different physiognomies of the Cerrado (Moreira 2000; Hoffmann & Solbrig 2003; Mews *et al*. 2013); and *E. nitens* also has its densities and basal area reduced after burning in woodland (Reis *et al*. 2015) and *Cerrado stricto sensu* (Mews *et al*. 2013). So, it is necessary to protect these frequent fire areas in order to preserve the functional role of this transitional vegetation in decreasing greenhouse emissions into the atmosphere.

The vegetation and other environmental features of the study area were investigated in the 1960s and 1970s by the team of the Xavantina-Cachimbo Expedition, which documented an extremely rich landscape, and suggested that this transition region is not static (Ratter *et al*. 1973). The richness and preservation of local ecosystems, the long history of research, the accelerated dynamics, and the increase in the basal area of the vegetation over the past few decades all make this area, together with a few other remnants of the savanna of eastern Mato Grosso State, major points of interest for the conservation of these environments and research into the interaction between climate and vegetation in the transition zone between the Cerrado and the Amazon. Given this, the small-scale patterns observed in the present study should be analysed in more detail on a regional scale and over a much longer interval of time.

We conclude that the typical savanna formations may undergo more marked and rapid changes than the intermediate and forested formations of the region of the Cerrado–Amazon transition in central Brazil. Based on these findings, we expect that the savanna formations will reveal more clearly the gradual advance of the forest vegetation in the transition zone, as suggested in previous studies. We also recommend that future studies focus on the changes in other features of the plant community, such as its functional and phylogenetic diversity.

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