Savanna turning into forest: concerted vegetation change at the ecotone between the Amazon and Cerrado biomes

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Abstract: In the Cerrado-Amazon ecotone in central Brazil, recent studies suggest some encroachment of forest into savanna, but how, where, and why this might be occurring is unclear. To better understand this phenomenon, we assessed changes in the structure and dynamics of tree species in three vegetation types at the Cerrado-Amazon ecotone that are potentially susceptible to encroachment: open cerrado (OC), typical cerrado (TC) and dense woodland (DW). We estimated changes in density, basal area and aboveground biomass of trees with diameter ≥10 cm over four inventories carried out between 2008 and 2015 and classified the species according to their preferred habitat (savanna, generalist, or forest). There was an increase in all structural parameters assessed in all vegetation types, with recruitment and gains in basal area and biomass greater than mortality and losses. Thus, there were net gains between the first and final inventories in density (OC: 3.4-22.9%; TC: 1.8-12.6%; DW: 0.2-8.3%), in basal area (OC: 8.3-18.2%; TC: 2-12.7%; DW: 2.3-8.9%), and in biomass (OC: 10.6-16.4%; TC: 1-12%; DW: 5.2-18.7%). Furthermore, all vegetation types also experienced net gains in forest and generalist species relative to savanna species. A decline in recruitment of savanna species was a likely consequence of vegetation encroachment and environmental changes. Our results indicate, for the first time based on quantitative and standardized multi-site temporal data, that concerted structural changes caused by vegetation encroachment are occurring at the ecotone between the two largest biomes in Brazil.

Keywords: Encroachment, environmental group, keystone species, structure, vegetation dynamics.

1 Introduction

On the Southern border of the Amazon, there is an extensive ecotone (also known as 'Zone of Ecological Tension') approximately 4,500 km long between the two largest biomes in South America, the Cerrado savanna and the Amazon forest (Marimon et al. 2006). At long centennial and millennial time-scales, the concerted advancement and retreat of the two largest South American biomes occurs due to natural climate changes, with hot and humid periods alternating with cold and dry periods and reflecting to a large degree the movements of the intertropical convergence zone (ITCZ) (Mayle 2000). Because the ITCZ responds to continuously changing climate forcing, it may be expected that forest and savanna in Southern Amazonia also exist in a state of permanent tension and movement (e.g., Ratter 1992). The current Southern Amazon climate is potentially more humid than at any time in the Holocene (Mayle et al. 2000) and, potentially as a consequence of this, several studies have suggested that the Amazon forests are naturally advancing into savannas in the Cerrado (Ratter et al. 1973; Ackerly et al. 1989; Ratter 1992; Marimon et al. 2006; Morandi et al. 2015). This process potentially parallels recent changes in other savanna-forest transitions in Africa (Cole 1992; Khavhagali & Bond 2008; Veenendaal et al. 2015) and Australia (Cole 1992; Kershaw 1992) and might also help to explain the hyperdynamic condition of the vegetation in the ecotone, with high rates of tree recruitment and mortality (Marimon et al. 2014; Morandi et al. 2015).

However, climatic changes are not the only important influence on the forest-savanna ecotone and other processes may also influence the structure of the vegetation here. This includes changes in the frequency of fire, especially where management may be suppressing cerrado fires (Durigan and Ratter 2006; Moreira 2000; Geiger et al. 2011). Additionally, the recent unprecedented rise in atmospheric carbon dioxide is expected to favor C3 plants over C4 grasses, as more CO_2 may preferentially increase the water use efficiency of C3 plants (Phillips et al. 2009; Kerbauy 2012). These multiple factors may impact the species composition (Khavhagali and Bond 2008), structural dynamics, density of individuals, basal area, aboveground biomass (Phillips et al. 2009; Marimon et al. 2014; Morandi et al. 2015), occurrence of fire-tolerant plants (Miranda et al. 2002; Henriques 2005) and vegetation encroachment (Khavhagali and Bond 2008), and contribute to the high biodiversity of the region (Marimon et al. 2014; Oliveira et al. 2016).

In some communities, such as savanna areas of typical and open cerrado and forest areas, such as the dense woodland, succession usually occurs according to the climax-gradient model (Whittaker 1953; Eiten 1972; Ratter 1992; Henriques 2005). These authors suggest that although vegetation formations can be identified as relatively stable communities adapted to maximize resource use in terms of biological productivity, there is no single, absolute

vegetation climax state across large areas. Rather, 'climax composition' has meaning only relative to a site's precise position along multiple environmental gradients, including local topographic, edaphic, and hydrologic factors. Hence, according this model, plant vegetation is likely to change dynamically over time in response to continuous variations in availability of different resources and frequency of disturbances.

There are multiple processes occurring at the ecotone between the Amazon and Cerrado biomes with potential to drive changes in vegetation composition and structure. The region has undergone rapid deforestation, which may lead to localized drying and vulnerability of remaining forest fragments resulting from agriculture, grazing and urban activities (Fearnside 2005; Nogueira et al. 2008). Habitat fragmentation can lead to declines in biodiversity, invasion of exotic species, soil erosion, pollution of aquifers, ecosystem degradation, increase in fires, imbalance of the carbon cycle and other elements related to regional climate changes (Fearnside 2005; Klink and Machado 2005; Bonini et al. 2014, 2018), most of which may be expected to degrade remaining forests. Furthermore, the same region has experienced a multi-decadal warming trend and a marked increase in dry season intensity and length (e.g., Marengo et al. 2013). This process may be a consequence of anthropogenic climate change (e.g., Li et al. 2009) and is contributing to increases in Amazon tree mortality (Phillips et al. 2009; Brienen et al. 2015) and reductions in growth (Feldpausch et al. 2016). Thus, several powerful and in some cases opposing factors are influencing vegetation dynamics in this transition zone. Determining which of them are the most influential currently requires careful analysis, including on-the-ground monitoring of vegetation dynamics.

In sum, the factors that determine current changes in the Cerrado-Amazon ecotone are many and varied, and poorly known in terms of their relative importance for remaining natural vegetation. Our objective is to assess changes in the structure and composition of tree species in permanent sample plots in savannas (typical and open cerrado, known in Brazil as 'Cerrado Típico' and 'Cerrado Ralo') and forests (dense woodland, known locally as 'Cerradão') in the Cerrado-Amazon ecotone. We aimed to answer the following questions: (1) Are there detectable changes in structural parameters (density, basal area and aboveground biomass) over time? (2) Is the composition of these systems changing, in terms of an increase in forest tree species in savanna sites? Our working hypotheses are: (1) there is vegetation encroachment, as measured by an increase in structural parameters (density, basal area and aboveground biomass) and (2) there is an increase in the number of forest species through the suppression of savanna species.

2 Material and methods

2.1 Study area and data collection

The study was carried out in the eastern region of the state of Mato Grosso, in the Cerrado-Amazon ecotone. We delimited two dense woodland areas, a forest vegetation known as 'cerradão' in Brazil (DW-1 e DW-2), two typical cerrado areas (TC-1 and TC-2) and one open cerrado area (OC-1). The dense woodland ('cerradão') has savanna and forest species with a fairly continuous tree cover that varies between 50-90% and mean species height from 8 to 15 m. Typical cerrado ('cerrado típico') has scattered trees and shrubs with woody cover ranges between 20-50% and mean species height from 3 to 6 m, while open cerrado ('*cerrado ralo*') is a less dense community with widely scattered woody elements than typical cerrado with a tree cover between 5-20% and mean species height from 2 to 3 m (Ribeiro and Walter 2008).

The study sites are located at Fazenda Santa Marta, in the municipality of Ribeirão Cascalheira, and in the Bacaba Municipal Park, in Nova Xavantina (Fig. 1). In each area, we set up 1-ha permanent plots and sampled the vegetation in 2008, 2011, 2013 and 2015 as part of the UK-led TROBIT (Tropical Biomes in Transition) and RAINFOR (Red Amazônica de Inventários Florestais) projects and the Brazil-led PELD (Projeto Ecológico de Longa Duração) project, co-ordinated by UNEMAT-Nova Xavantina. We numbered, identified and measured the height and the diameter at breast height (*DBH* at 1.3 m) of all individuals with $D \geq 10$ cm using standard protocols (e.g. Phillips et al. 2010). Based on the specialized literature (Mendonça et al. 2008) and field experience of some members of the present study, we also classified each species according to the habitat (or physiognomy) of its preferred occurrence: forest, savanna or generalist (when it occurs in both).

2.2 Data analysis

We calculated tree density, basal area ($g = (\pi/4).d^2$), where d= *DBH* (diameter at breast height of each individual) and total aboveground biomass of each study area, this latter parameter following Scolforo et al. (2008). We calculated the average annual rates of tree recruitment and mortality (Sheil et al. 1995; 2000), the gain and loss in basal area (Guimarães et al. 2008) as well as the turnover rate of individuals (Phillips & Gentry 1994). To compare variations between areas and over time in tree density, basal area and aboveground biomass and habitat-preferences of species, we used repeated measurements ANOVA, followed by a Tukey post hoc tests (Zar 2010). We tested assumptions of homogeneity of variances and normality of residuals with Levene and Shapiro-Wilk tests, respectively. To quantify temporal changes in species composition, we apply NMDS ordination based on Bray-Curtis similarity measure. We also conducted linear regression analyses to examine the temporal relationship in

density, basal area and aboveground biomass. We carried out the analyses and graphs with the "vegan" (Oksanen et al. 2016), "MASS" (Venables and Ripley), "gridExtra" (Baptiste Auguie 2016) and "ggplot2" package (Wickham 2009) in the program R (R Core Team, 2016). We considered 5% significance level for all analyses.

3 Results

Between the first (2008) and the following inventories (2011, 2013 and 2015), both in dense woodland areas and in typical and open cerrado areas, there was a constant or significant increase in density ($F_{12,360}$=12.57, p<0.01), basal area ($F_{12,360}$=9.80, p<0.01) and aboveground biomass ($F_{12,360}$=15.02, p<0.01), except for one area of dense woodland (DW-1) which tended to decrease in density (Fig. 2, Table S1). When analysed instead by linear regression, all typical and open cerrado areas clearly increase in all parameters (stem density, basal area and aboveground biomass) and dense woodland areas in terms of basal area and aboveground biomass, with R^2 values close to or exceeding 0.9 (Table S5). Throughout, the two areas of typical cerrado (TC-1 and TC-2) had density, basal area and aboveground biomass values similar to those found in dense woodland DW-2 (Fig. 2, Table S1). Among all the areas studied, we highlight the open cerrado (OC-1) as showing a progressive and significant increase in all parameters throughout all inventories, with the greatest relative increases (Fig. 2, Table S1). The DW-1 site had particularly large basal area and aboveground biomass gains after 2011. Across all plots and in all intervals sampled, the recruitment rates and gain in basal area were higher than mortality rates and loss in basal area, except for dense woodland between 2011 and 2015. Finally, both the typical cerrado and the open cerrado had higher stem turnover rates than those of dense woodland areas (Table S1).

When we analyzed the data according to the species' preferred habitat of occurrence, we observed a tendency for savanna species density to be constant or decrease over time, except for TC-1 and OC-1 ($F_{12,360}$=2.40, p<0.01; Table S2 and Fig. 3). By contrast, there was an increase in basal area ($F_{12,360}$=10.20, p<0.01) and aboveground biomass ($F_{12,360}$=7.48, p<0.01) of forest and generalist species ($F_{12,360}$=3.28, p<0.01; $F_{12,360}$=6.57, p<0.01, respectively), in particular in the open cerrado site (OC-1). As well as the relationship between forest species structural parameters with calendar year was very strong, with an R^2 between 0.8 and 0.9, mainly in aboveground biomass (Table S5). In OC-1 site, generalist species increased in terms of their contribution to vegetation structure since 2011, while forest species did so since 2013, although savanna species still dominate the vegetation (Fig. 3, Table S2 e S5). Nevertheless, all areas showed considerable floristic similarity among them and over time (Fig. S1).

In general, the recruitment rate and gain in basal area were also higher than the mortality rate and loss in basal area (Table S3). However, for savanna species the mortality rate was higher than recruitment in woodland areas. On the other hand, the rates of recruitment and gain in basal area for forest species were higher than their mortality rates and losses in basal area in all areas (Table S3). Overall, when we analyzed the communities over time in terms of the stem density and basal area of each ecological group, we observed clear increases in forest and generalist species, not only in the Cerrado vegetation but also in dense woodland areas (Table S3).

4 Discussion

Our study found an increase in density, basal area and aboveground biomass, both in typical and open cerrado as well as in dense woodland. Although the finding that vegetation is becoming denser over time corroborates our first hypothesis, this changes isn't abrupt and not all the sites are becoming forest-like. However, there is a tendency that all savanna sites, as the parameters assessed in typical cerrado (TC-1 e TC-2) having similar values to those of the dense woodland (DW-2), to become a forest-like if the current trends are maintained. Furthermore, other indicators of encroachment such as vegetation dynamics generally showed higher recruitment than mortality rates and higher gain than loss in basal area, indicative of a future marked natural change in structure. While other studies on the Cerrado-Amazon transition have already detected localized changes at single sites or with semi-quantitative assessments (Ratter et al. 1973; Ratter 1992; Marimon et al. 2006; Morandi et al. 2015), this is the first time that quantitative and standardized data corroborated the vegetation encroachment hypothesis over longer temporal scales and considering multiple types of savanna vegetation.

The excess of tree recruitment over mortality can result in an increase of tree stem density, while the excess of growth rates over death rates can result in increasing tree basal area and biomass. Therefore, in these sites at least, vegetation has a tendency to become markedly denser and, consequently, there is a tendency to favor the establishment and growth of forest species in what are savanna habitats. As an example, while we observed that stem density hasn't changed in dense woodland (DW-1 and DW-2) over the years and nor did it change in typical cerrado (TC-2) between 2013 and 2015, in all cases the basal area and aboveground biomass did increase, indicating that the vegetation is tending to become denser. Among the factors that may contribute to the process of vegetation encroachment, we highlight the increase in the availability of resources, such as carbon dioxide (e.g., Lewis et al. 2004; Phillips et al. 2009), changes in the frequency of fires (e.g., Geiger et al. 2011; Durigan & Ratter 2006) in most of the areas, and the increase in rainfall (Gloor et al. 2013, Castanho et al.

2016). These factors can favor the advancement or withdrawal of the forest over the savanna (Ratter et al. 1973; Ratter 1992; Marimon et al. 2014) or speed up the natural dynamics of the vegetation. These changes in dynamics may also favor the establishment and acceleration of individual tree life cycles, especially those of instrinsically fast developing taxa, such as *Tachigali vulgaris* (Morandi et al. 2015).

While the overall composition of species in savanna systems remains predominantly savanna species, there is still a markedly tendency for savanna species to decline and forest species parameters to increase over time. We observed an increase in basal area and aboveground biomass mainly in generalist and forest species in all areas and a decrease in savanna species in the dense woodland (DW-1 and DW-2) and TC-2. A driver here may be the absence of fire in these areas for at least 15 years, favoring recruitment over mortality rate and the establishment of generalist and forest species. Other studies have reported the replacement of savanna with forest species after fire suppression in the Cerrado biome (Moreira 2000; Henriques & Hay 2002; Hoffmann & Moreira 2002; Mews et al. 2011; Durigan & Ratter 2006, 2016). However, apparently our results show that vegetation may recover biomass and stem numbers very quickly after fire. For example, TC-1 showed a decline due to the fire that affected the area soon after the first inventory (2008), but soon afterwards we found an increase in density, basal area and aboveground biomass of generalist species (inventory of 2013) as well a further increase in basal area and biomass of forest species in the inventory of 2015. Hence, within a short period after the fire there was a increase in the density of generalist and savanna species, but not of forest species. This can indicate that the vegetation seems to be resilient to the impacts of fire, but that non-forest species dominate post-fire recovery in these areas.

Earlier work by Marimon et al. (2014) revealed dense woodland to be 'hyperdynamic' in the sense of having exceptionally fast recruitment and mortality of stems, results which are corroborated here and extended also to open and typical cerrado. The marked dynamism of these vegetation types, geographically closen to the Amazon (Marimon et al. 2010; Marimon et al. 2014) corroborates the hyperdynamism of the whole Cerrado-Amazon ecotone (Marimon et al. 2014). The increase in forest taxa is one driver of this hyperdynamism, and at least superficially consistent with a positive relationship between rainfall and biomass accumulation (Costa et al. 2010; Brando et al. 2014; Baker et al. 2014; Veenendaal et al. 2015). Yet, while Amazon rainfall has increased recently in some localities (e.g. Gloor et al. 2013), in our region there have been a sequence of strong droughts. Apparently in the ecotone, biomass has proven resistant to recent climate changes, and this increase is likely driven by other factors such as

the increase in atmospheric carbon dioxide (e.g., Phillips et al. 1998), change in fire regimes (Abreu et al. 2017), or both.

Other factors may also be favoring the species studied in the possible encroachment of the vegetation by the increase in canopy cover (Yarranton & Morrison 1974; Silva et al. 2013; Veenendaal et al. 2015) and the accumulation of leaf litter, consequently of soil nutrients (Yarranton & Morrison 1974; Connell & Slatyer 1977; Marimon Junior & Haridasan 2005; Silva et al. 2013; Passos et al. 2014; Oliveira et al. 2016). These factors are related to vegetation establishment and productivity, as well as the accumulation of organic matter and higher microbial activity in the soil (Haridasan 2001). Such conditions can favor generalist and forest species, as they tolerate low light environments (Silva et al. 2013) and usually require higher availability of nutrients in the cycling system (Peltzer et al. 2010), as observed in the present study. Our results indicate that transitional habitats, including savannas, deserve greater attention to their ecology and conservation because of the intense interactions between species, which can alter the structure and dynamics of the entire habitat (Miranda et al. 2014).

Indeed, the occurrence of generalist and forest species such as *Emmotum nitens*, *Hirtella glandulosa*, *Tachigali vulgaris* (Ratter et al. 1973; Ratter 1992; Marimon et al. 2006; Morandi et al. 2015) and *Xylopia sericea* (Table S4) can be a tendency of changing in vegetation can occur along the time. *E. nitens*, *H. glandulosa* and *Vochysia haenkeana*, have been classified as connectors of riparian forest, dense woodland and transitional vegetation on the Southern edge of the Amazon (Oliveira-Filho & Ratter 1995). Moreover, *X. sericea* is a species typical of forest habitats, and is typically absent from savanna (Ratter et al. 1973; Marimon et al. 2006). Finally, special attention should be given to *T. vulgaris*, known as a key species at early phases of the successional process on the Southern edge of the Amazon, and which can favor community dynamics and floristic compositional changes (Moreira 2000; Morandi et al. 2015). These dominant species - with high density and basal area in multiple savanna inventories in the transition zone – may be considered keystone species in the process of vegetation encroachment and hence potential 'ecosystem engineers' that can favor the increased occurrence of other forest species over time (Ratter et al. 1973; Ratter 1992; Marimon et al. 2006; Vidotto et al. 2007; Morandi et al. 2015) by facilitation processes (Yarranton & Morrison 1974; Connell & Slatyer 1977; Durigan & Ratter 2006) (Table S4).

It is important to point out that our observations have occurred over a relatively short sampling period of seven years. The encroachment in the structural vegetation recorded in the savanna communities can be clearly favoring carbon accumulation (Ratajczak et al. 2012; Pellegrini et al. 2016). While savanna species remain abundant and species-rich, the changes indicate the potential for afforestation over time. Nevertheless, this process results in a clear

dilemma for conservationists, with implications for climate changes and preservation of savanna species, as for example management of fire in Cerrado protected and non-protected areas can have large impacts on both carbon storage and biodiversity (Durigan and Ratter 2016). There is an apparent trade-off – let these lands absorb carbon dioxide but lose savanna biodiversity, or actively manage them via increased fire to protect savanna diversity. The long-term consequences and implications of this tradeoff however remain unknown (Pellegrini et al. 2016) and should be better assessed, especially in this critical ecotone between the two largest biomes in South America.

Our study observed in the savannas sites and dense woodland has a tendency to be similar in structural changes over time. The results showed here suggest that many savannas in the Cerrado-Amazon ecotone can be currently undergoing a process of becoming a denser vegetation, even in the face of a regionally warming and drying climate. For example, despites of our results the grass-dominated open cerrado (OC-1) in 2008, is already better classified as a typical cerrado only seven years later (2015). Hence, if the current trends are maintained, open and typical cerrado can be likely to change into forest-like vegetation, and dense woodland can become a taller and denser forest. Finally, our work suggests the need for further studies to test whether and precisely how a facilitation process is driving the overall encroachment, and specifically the establishment of forest species. Deeper understanding of facilitation here may be critical for improved understanding of the full ecological and conservation processes involved in the complex vegetation dynamics at the transition between the Brazilian savanna and Amazon forest.

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Fig. 1 Geographic location of the study areas in dense woodland, DW-1 (●) and DW-2 (■), and savannas of typical cerrado, TC-1 (○) and TC-2 (□), and open cerrado, OC-1 (◊), and in the Cerrado-Amazon ecotone, Mato Grosso, Brazil.

Fig. 2 Density (a), Basal area (b), and Aboveground biomass (c) (average ± standard error) of tree species in dense woodland (DW; green continuous line), typical cerrado (TC; red dashed line), and open cerrado areas (OC; orange dotted line), in the Cerrado-Amazon ecotone.

Fig. 3 Density, Basal area, and Aboveground biomass (average ± standard error) of tree species in different scale in Y axis. All parameters are classified according to their preferred habitat of occurrence: savanna (a-c), generalist (d-f), and forest (g-i), in dense woodland (DW; green continuous line), typical cerrado (TC; red dashed line), and open cerrado areas (OC; orange dotted line), in the Cerrado-Amazon ecotone.

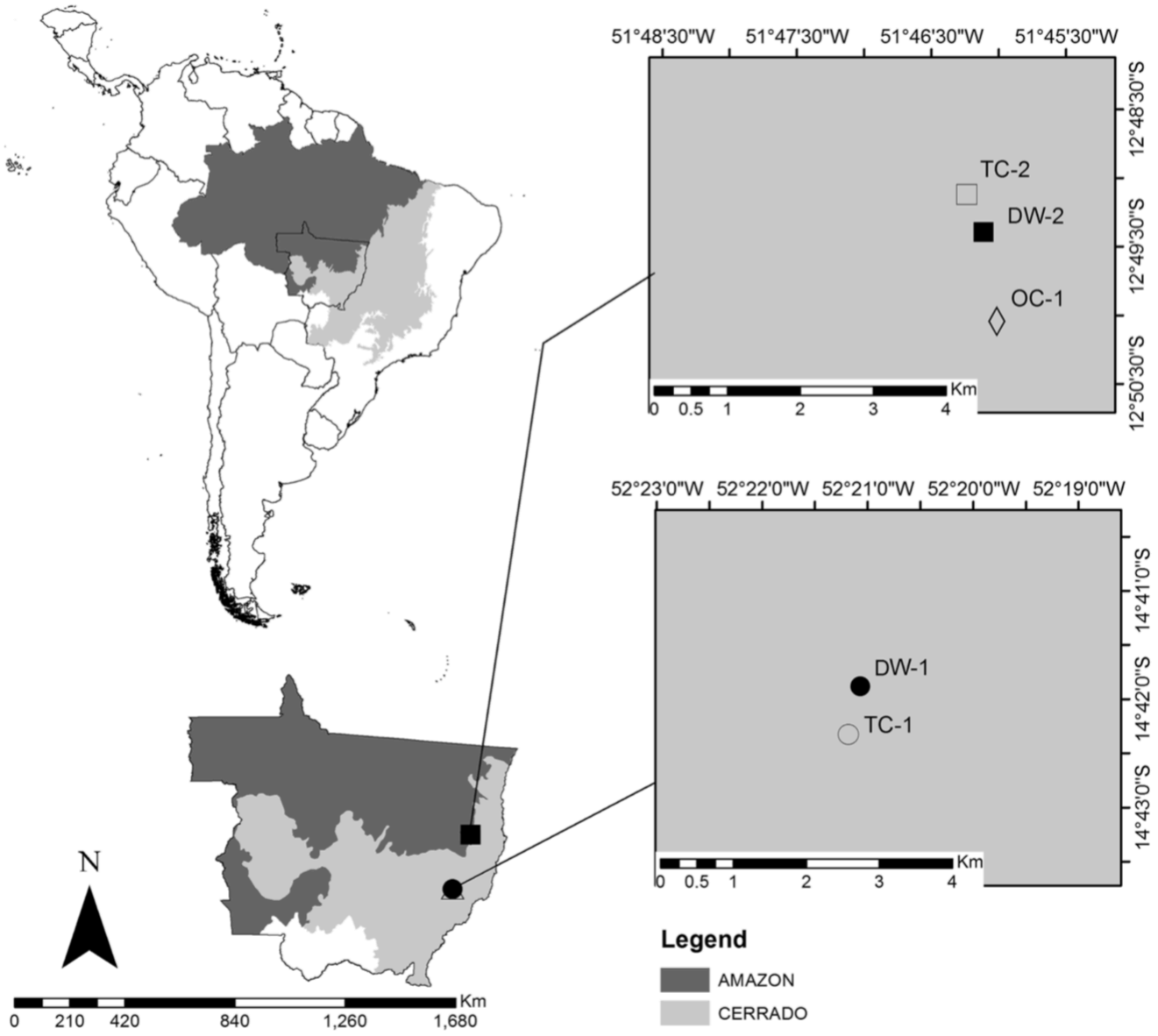
51°48'30"W
51°47'30"W
51°46'30"W
51°45'30"W
12°48'30"S
12°49'30"S
12°50'30"S
TC-2
DW-2
OC-1
0 0.5 1 2 3 4 Km
52°23'0"W
52°22'0"W
52°21'0"W
52°20'0"W
52°19'0"W
14°41'0"S
14°42'0"S
14°43'0"S
DW-1
TC-1
0 0.5 1 2 3 4 Km
N
0 210 420 840 1,260 1,680 Km
Legend
AMAZON
CERRADO

Figure 1

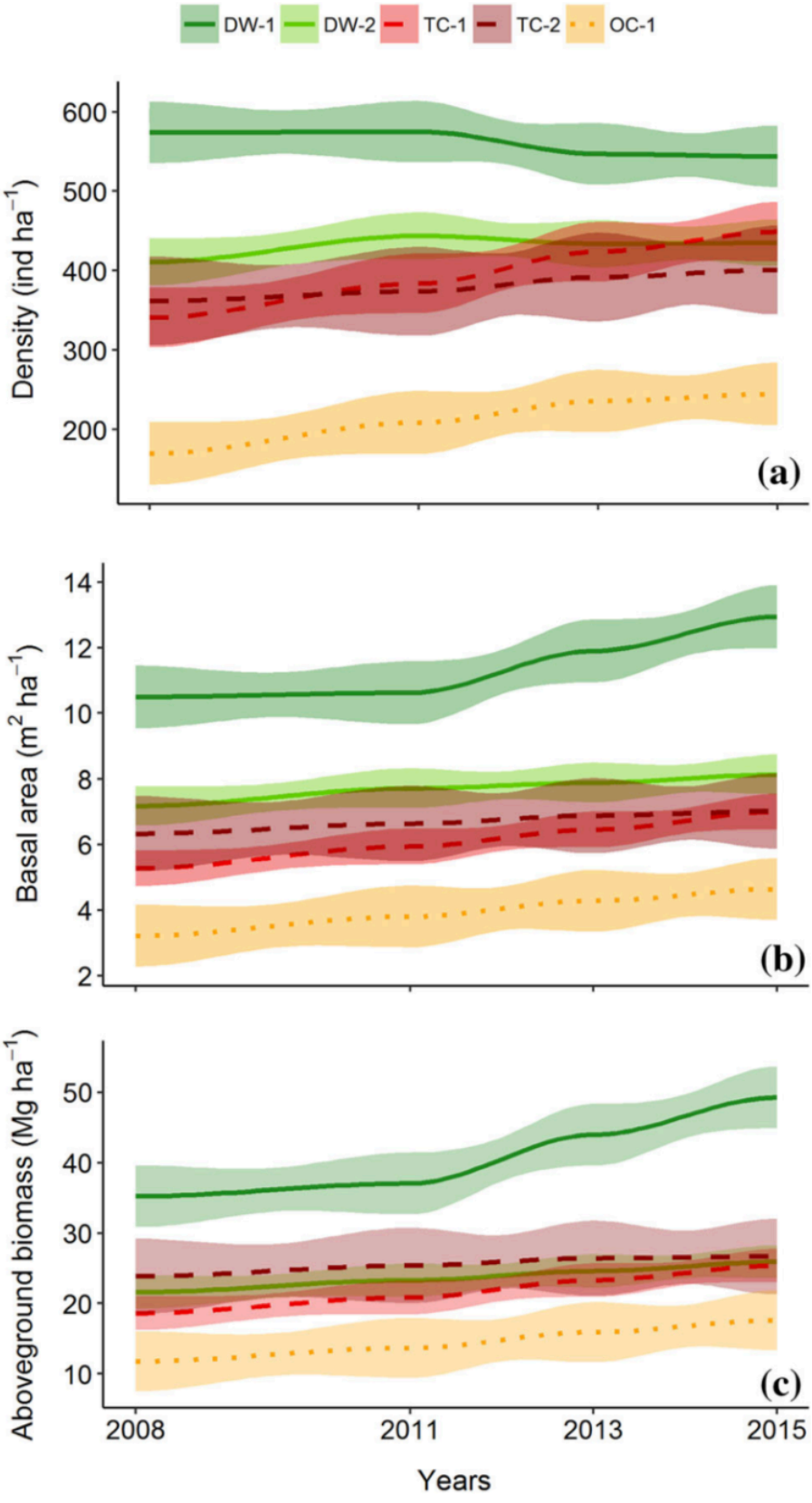
DW-1
DW-2
TC-1
TC-2
OC-1
Density (ind ha^{-1})
600
500
400
300
200
(a)
Basal area (m^2 ha^{-1})
14
12
10
8
6
4
2
(b)
Aboveground biomass (Mg ha^{-1})
50
40
30
20
10
(c)
2008
2011
2013
2015
Years

Figure 2

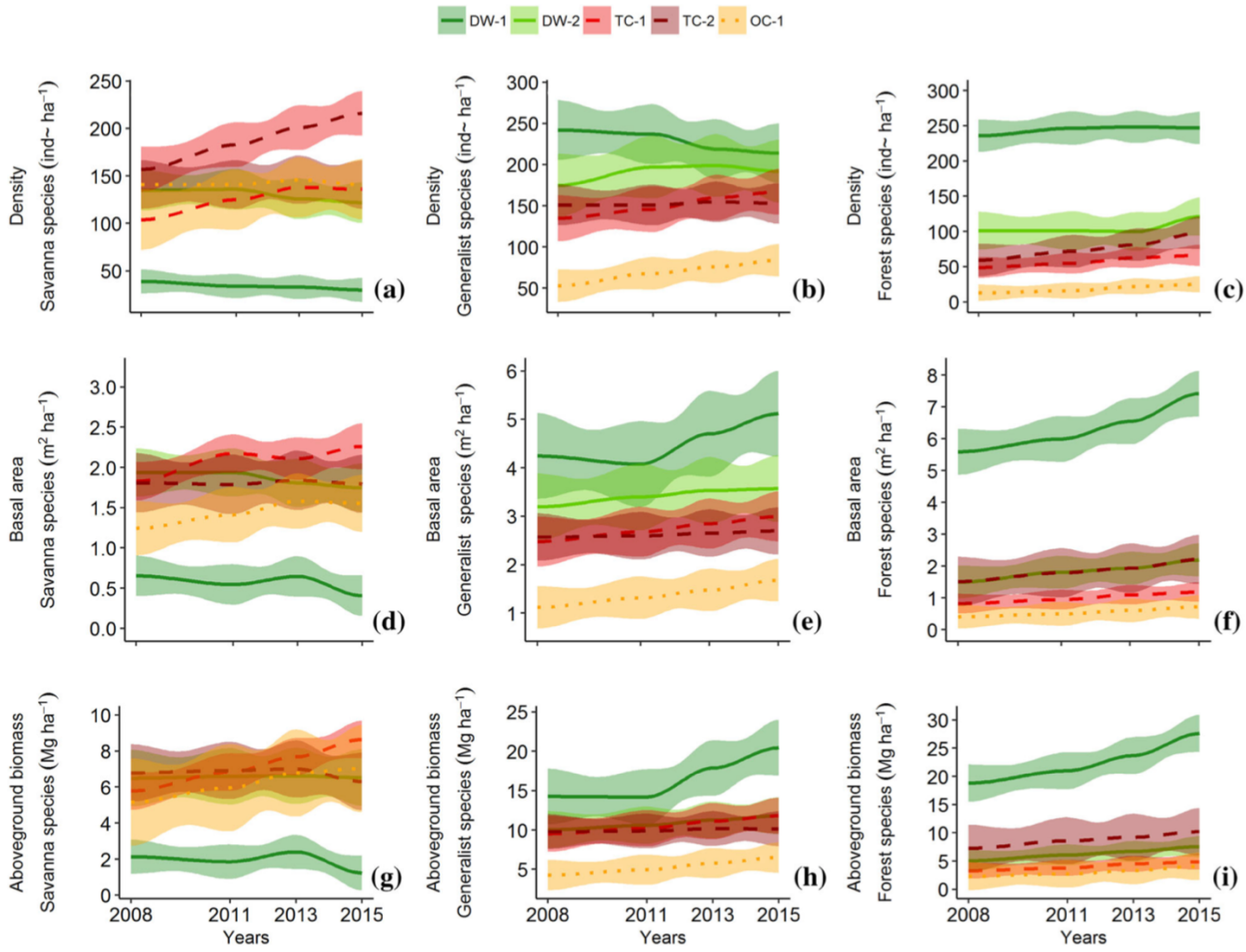
DW-1
DW-2
TC-1
TC-2
OC-1
Density
Savanna species (ind~ ha^{-1})
Density
Generalist species (ind~ ha^{-1})
Density
Forest species (ind~ ha^{-1})
Basal area
Savanna species (m^2 ha^{-1})
Basal area
Generalist species (m^2 ha^{-1})
Basal area
Forest species (m^2 ha^{-1})
Aboveground biomass
Savanna species (Mg ha^{-1})
Aboveground biomass
Generalist species (Mg ha^{-1})
Aboveground biomass
Forest species (Mg ha^{-1})
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
2008
2011
2013
2015
Years

Figure 3

Supplemental Information

Figure S1 Nonmetric multidimensional scaling (NMDS) plots summarizing the floristic patterns showing temporal trajectories for abundance from 2008 to 2015 in dense woodlands (DW-1 and DW-2), typical cerrado (TC-1 and TC-2) and open cerrado (OC-1) in Cerrado-Amazônia ecotone.

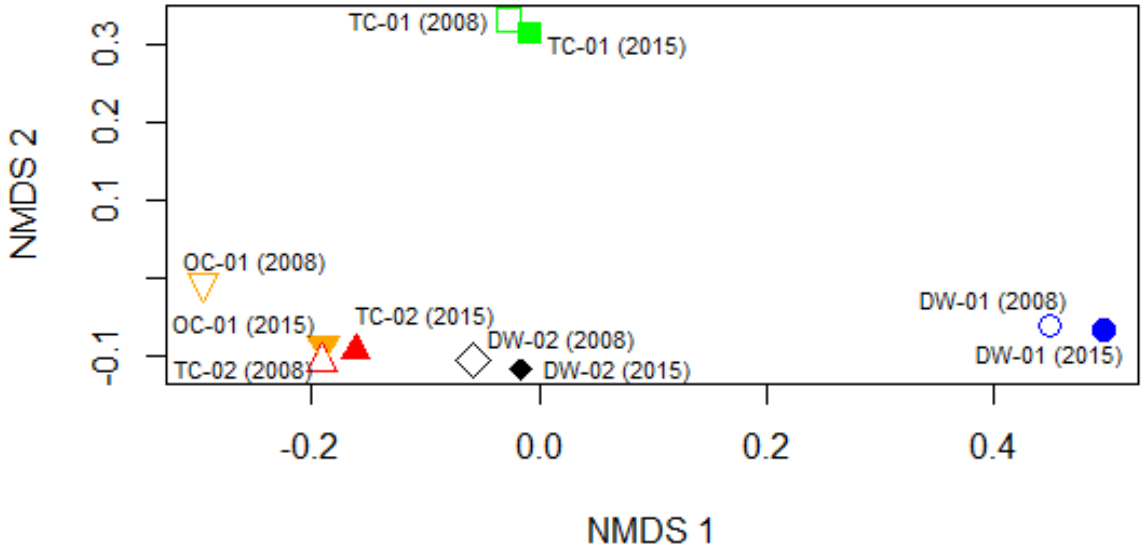

Table S1 Density, Basal area, and Aboveground biomass (average ± standard error) of tree species in areas of dense woodland (DW), typical cerrado (TC) and open cerrado (OC) in the Cerrado-Amazon ecotone. Uppercase letters represent the comparison between areas (horizontal line) and lowercase letters, the comparison between inventories (years) (vertical line) for each area.

		DW-1	DW-2	TC-1	TC-2	OC-1
Density (ind ha^{-1})	2008	$574^{A,a}$±20.89	$411^{B,a}$±15.95	$341^{B,a}$±17.9	$362^{B,a}$±27.99	$170^{C,a}$±18.54
	2011	$575^{A,a}$±19.53	$444^{B,b}$±14.81	$384^{B,b}$±19.2	$374^{B,a}$±29.7	$209^{B,b}$±20.05
	2013	$547^{A,a}$±17.76	$434^{B,b}$±15.34	$424^{B,c}$±18.68	$392^{B,b}$±28.42	$236^{C,c}$±20.77
	2015	$544^{A,a}$±19.65	$435^{B,b}$±13.07	$449^{B,d}$±19.87	$401^{B,b}$±26.28	$245^{C,d}$±20
Basal area (m^2 ha^{-1})	2008	$10.50^{A,a}$±0.39	$7.18^{B,a}$±0.3	$5.27^{B,a}$±0.24	$6.33^{B,a}$±0.57	$3.22^{C,a}$±0.45
	2011	$10.62^{A,a}$±0.43	$7.71^{B.,b}$±0.28	$5.94^{B,b}$±0.27	$6.64^{B,a}$±0.6	$3.8^{C,b}$±0.47
	2013	$11.9^{A,b}$±0.50	$7.89^{B,b}$±0.32	$6.46^{B,c}$±0.3	$7.1^{B,b}$±0.59	$4.28^{C,c}$±0.49
	2015	$12.95^{A,c}$±0.59	$8.14^{B,b}$±0.3	$7.00^{B,d}$±0.3	$7.32^{B,b}$±0.56	$4.64^{C,d}$±0.49
Aboveground Biomass (Mg ha^{-1})	2008	$35.23^{A,a}$±1.5	$21.62^{B,a}$±1.16	$18.62^{B,a}$±1.01	$23.86^{B,a}$±2.58	$11.78^{C,a}$±1.96
	2011	$37.06^{A,a}$±1.77	$23.31^{B,a}$±1.11	$20.85^{B,a}$±1.17	$25.4^{B,a}$±2.78	$13.69^{C,b}$±2.07
	2013	$43.98^{A,b}$±2.47	$24.62^{B,b}$±1.27	$23.32^{B,b}$±1.28	$26.44^{B,b}$±2.77	$15.93^{C,c}$±2.21
	2015	$49.29^{A,c}$±2.84	$25.92^{B,c}$±1.2	$25.37^{B,c}$±1.32	$26.69^{B,b}$±2.65	$17.63^{C,d}$±2.32

Table S2 Density, Basal area, and Aboveground biomass (average ± standard error) of tree species in areas of dense woodland (DW), typical cerrado (TC), and open cerrado (OC) classified according to the species' preferred habitat of occurrence (savanna, generalist and forest) in the Cerrado-Amazon ecotone. Uppercase letters represent the comparison between areas (horizontal line) and lowercase letters, the comparison between inventories (years) (vertical line) for each area.

			DW-1	DW-2	TC-1	TC-2	OC-1
Density (ind ha^{-1})	Savanna	2008	$39^{A,a}$±6.3	$135^{B,a}$±10.7	$157^{B,a}$±10.85	$141^{B,a}$±11.89	$104^{C,a}$±15.05
		2011	$34^{A,a}$±6.75	$136^{B,a}$±10.61	$183^{C,b}$±11.88	$141^{B,a}$±12.9	$125^{B,b}$±16.83
		2013	$33^{A,a}$±6.24	$126^{B,b}$±10.84	$202^{C,c}$±12.06	$146^{B,a}$±13.44	$138^{B,b}$±16.21
		2015	$30^{A,a}$±6.12	$122^{B,b}$±11.11	$219^{C,c}$±13.25	$141^{B,a}$±13.06	$136^{B,b}$±15.95
	Generalist	2008	$242^{A,a}$±19.51	$175^{B,a}$±18.2	$135^{B,a}$±12.16	$151^{B,a}$±13.27	$53^{C,a}$±9.05
		2011	$237^{A,a}$±18.43	$197^{A,b}$±20.63	$146^{B,a}$±13.52	$151^{B,a}$±12.12	$68^{C,b}$±10.05
		2013	$219^{A,b}$±17.27	$199^{A,b}$±19.01	$159^{A,b}$±14.71	$155^{A,a}$±12.16	$76^{B,c}$±10.05
		2015	$214^{A,b}$±17.79	$192^{A,b}$±18.75	$163^{A,b}$±14.79	$153^{A,a}$±12.1	$84^{B,d}$±10.4
	Forest	2008	$293^{A,a}$±18.56	$101^{B,a}$±15.17	$49^{B,a}$±6.99	$70^{B,a}$±15.14	$13^{C,a}$±5.23
		2011	$304^{A,a}$±17.42	$111^{B,a}$±16.78	$55^{B,a}$±7.36	$82^{B,a}$±15.51	$16^{C,a}$±5.93
		2013	$295^{A,a}$±16.26	$109^{B,a}$±15.2	$63^{B,a}$±7.51	$91^{B,b}$±14.5	$22^{C,a}$±6.18
		2015	$300^{A,a}$±17.73	$121^{B,b}$±12.72	$66^{B,a}$±8.02	$107^{B,b}$±14.54	$25^{C,a}$±5.59
Basal area (m^2 ha^{-1})	Savanna	2008	$0.65^{A,a}$±0.13	$2.48^{B,a}$±0.24	$1.97^{B,a}$±0.15	$2.24^{B,a}$±0.23	$1.68^{B,a}$±0.3
		2011	$0.54^{A,a}$±0.12	$2.5^{B,a}$±0.24	$2.31^{B,b}$±0.16	$2.25^{B,a}$±0.24	$1.98^{B,b}$±0.34
		2013	$0.65^{A,a}$±0.15	$2.42^{B,a}$±0.26	$2.50^{B,c}$±0.17	$2.29^{B,a}$±0.24	$2.19^{B,c}$±0.35
		2015	$0.40^{A,b}$±0.09	$2.37^{B,b}$±0.26	$2.81^{B,d}$±0.17	$2.11^{B,b}$±0.23	$2.24^{B,c}$±0.35
	Generalist	2008	$4.24^{A,a}$±0.40	$3.2^{B,a}$±0.34	$2.48^{B,a}$±0.23	$2.57^{B,a}$±0.25	$1.12^{C,a}$±0.2
		2011	$4.07^{A,a}$±0.39	$3.4^{A,a}$±0.36	$2.68^{A,a}$±0.26	$2.6^{A,a}$±0.24	$1.32^{B,b}$±0.21
		2013	$4.70^{A,a}$±0.46	$3.53^{B,a}$±0.35	$2.85^{B,b}$±0.27	$2.65^{B,a}$±0.24	$1.48^{C,b}$±0.23
		2015	$5.11^{A,b}$±0.5	$3.57^{B,a}$±0.33	$3.00^{B,c}$±0.28	$2.7^{B,a}$±0.25	$1.68^{C,c}$±0.24
	Forest	2008	$5.59^{A,a}$±0.29	$1.5^{B,a}$±0.23	$0.83^{B,a}$±0.14	$1.51^{B,a}$±0.37	$0.41^{B,a}$±0.16
		2011	$5.99^{A,a}$±0.35	$1.8^{B,b}$±0.28	$0.95^{B,a}$±0.15	$1.82^{B,b}$±0.41	$0.52^{B,a}$±0.18
		2013	$6.54^{A,b}$±0.35	$1.9^{B,b}$±0.28	$1.10^{C,b}$±0.77	$1.91^{B,b}$±0.39	$0.61^{C,b}$±0.19
		2015	$7.41^{A,c}$±0.42	$2.2^{A,c}$±0.25	$1.19^{A,b}$±0.83	$2.21^{A,c}$±0.4	$0.72^{A,b}$±0.21
Aboveground Biomass (Mg ha^{-1})	Savanna	2008	$2.14^{A,a}$±0.49	$6.49^{A,a}$±0.74	$6.23^{A,a}$±0.52	$6.98^{A,a}$±0.8	$5.68^{A,a}$±1.05
		2011	$1.86^{A,a}$±0.45	$6.60^{A,a}$±0.76	$7.31^{A,b}$±0.51	$7.09^{A,a}$±0.85	$6.48^{A,b}$±1.12
		2013	$2.39^{A,a}$±0.61	$6.62^{A,a}$±0.82	$8.12^{A,c}$±0.58	$7.18^{A,a}$±0.82	$7.35^{A,b}$±1.25
		2015	$1.23^{A,b}$±0.30	$6.53^{A,a}$±0.83	$8.98^{A,d}$±0.59	$6.54^{A,b}$±0.78	$7.51^{A,b}$±1.22
	Generalist	2008	$14.26^{A,a}$±1.39	$14.59^{A,a}$±1.59	$9.54^{A,a}$±1.08	$9.79^{A,a}$±1.18	$5.72^{A,a}$±1.18
		2011	$14.18^{A,a}$±1.38	$15.85^{A,a}$±1.73	$10.33^{A,a}$±1.28	$9.90^{A,a}$±1.12	$6.35^{A,a}$±1.22
		2013	$17.87^{A,b}$±1.91	$20.73^{A,b}$±2.36	$11.77^{A,b}$±1.36	$10.22^{A,a}$±1.16	$7.39^{A,b}$±1.3
		2015	$20.43^{A,c}$±2.25	$23.87^{A,c}$±2.65	$11.87^{A,b}$±1.46	$10.24^{A,a}$±1.18	$7.73^{A,b}$±1.26
	Forest	2008	$18.83^{A,a}$±1.27	$5.09^{A,a}$±0.83	$3.94^{A,a}$±0.69	$7.58^{A,a}$±1.97	$4.15^{A,a}$±1.73
		2011	$21.01^{A,a}$±1.54	$6.11^{A,a}$±0.97	$4.52^{A,a}$±0.74	$8.96^{A,a}$±2.22	$4.88^{A,a}$±1.91
		2013	$23.71^{A,b}$±1.67	$6.73^{A,a}$±1.00	$5.38^{A,a}$±0.73	$9.62^{A,a}$±2.17	$5.88^{A,a}$±2.01
		2015	$27.61^{A,c}$±2.00	$7.58^{A,b}$±0.9	$5.83^{A,b}$±0.74	$10.65^{A,b}$±2.24	$7.09^{A,b}$±2.32

Table S3. Recruitment rates (RR), mortality (MR), gain in basal area (GBA), loss in basal area (LBA) and turnover (TO) to arboreal species in dense woodland (DW), typical cerrado (TC) and open cerrado (OC) in the Cerrado-Amazon ecotone. The parameters were distributed in total area and preferred habitat of occurrence: savanna, generalist and forest throughout the inventories of 2008, 2011, 2013, and 2015. The rates values are expressed in % year^{-1}.

		DW-1			DW-2			TC-1			TC-2			OC-1		
		2008 - 2011	2011 - 2013	2013 - 2015	2008 - 2011	2011 - 2013	2013 - 2015	2008 - 2011	2011 - 2013	2013 - 2015	2008 - 2011	2011 - 2013	2013 - 2015	2008 - 2011	2011 - 2013	2013 - 2015
Total Area	RR	2.8	1.0	1.9	4.2	2.6	3.2	5.3	5.7	5.7	2.8	3.4	3.6	7.0	6.8	5.6
	MR	1.3	4.1	2.1	1.7	3.7	3.0	1.5	0.9	2.9	1.8	1.1	2.7	0.4	0.7	2.4
	TO	2.1	2.5	2.0	2.9	3.1	3.1	3.4	3.3	4.3	2.3	2.2	3.1	3.7	3.8	4.0
	GBA	4.2	9.5	9.3	5.1	2.3	3.8	8.4	7.3	3.0	3.3	4.6	5.0	11.0	11.0	7.3
	LBA	3.0	6.7	2.4	0.6	1.3	1.3	0.5	3.3	3.6	0.5	1.4	3.5	0.1	0.1	0.6
Savanna	RR	1.9	1.5	0	1.0	0.4	0	7.0	2.2	3.7	2.2	3.1	1.8	5.9	6.0	1.5
	MR	5.4	4.4	4.7	0.5	4.1	1.6	2.2	1.7	5.3	2.2	1.4	3.8	0	1.2	2.6
	TO	3.7	3.0	2.3	0.7	2.3	0.8	4.6	1.9	4.5	2.2	2.3	2.8	3.0	3.6	2.0
	GBA	3.6	6.8	6.6	11.0	5.4	13.4	3.3	4.0	5.2	8.5	9.7	13.8	12.0	16.4	14.8
	LBA	11.4	2.5	4.4	0.8	1.8	2.2	2.9	0	0	0	4.3	2.4	1.6	0	2.9
Generalist	RR	3.9	0.9	1.7	6.7	3.8	3.4	3.3	0	0.7	1.6	2.0	1.7	8.0	5.4	5.5
	MR	1.4	10.5	2.9	2.9	3.4	5.2	0.7	0.3	1.7	1.6	0.7	2.6	0.6	0	0.7
	TO	2.6	5.7	2.3	4.8	3.6	4.3	2.0	0.2	1.2	1.6	1.3	2.1	4.3	2.7	3.1
	GBA	6.3	3.8	19.2	6.7	4.2	3.6	3.9	3.6	0.8	2.9	3.5	4.3	10.1	8.8	11.7
	LBA	4.6	5.4	15.2	1.9	1.8	3.3	3.1	3.0	0.2	2.9	1.6	4.9	0	0	0.7
Forest	RR	2.1	0.5	2.1	4.1	2.8	6.0	5.1	0.9	0.9	6.5	6.2	8.8	9.1	14.7	12.8
	MR	0.7	4.9	1.3	1.0	3.7	0.9	1.4	0	0.9	1.4	1.2	1.1	2.6	0	7.1
	TO	1.4	2.7	1.7	2.5	3.2	3.4	3.2	0.4	0.9	4.0	3.7	5	5.9	7.4	9.9
	GBA	6.5	5.5	18.0	1.5	0.8	0.3	1.6	5.1	4.7	2.8	3.2	1.7	10.4	8.9	2.5
	LBA	3.5	4.0	12.6	1.2	4.9	2.4	0.6	4.7	2.7	3.0	1.5	10.0	0	0.5	1.6

Table S4. Density (D) and basal area (BA) of the tree species with highest occurrence (Oc) in density (D) or indicators (In) of habitat change (savanna-forest). The species are distributed in their respective areas (DW = dense woodland, TC = typical cerrado, and OC = open cerrado) and preferred habitat of occurrence (Hab): savanna (S), generalist (G), and forest (F) in the Cerrado-Amazon ecotone. The density is expressed in ind ha^{-1} and basal area, in m^2 ha^{-1}.

Areas	Species	Hab	Oc	D 2008	D 2011	D 2013	D 2015	BA 2008	BA 2011	BA 2013	BA 2015
DW-1	*Hirtella glandulosa*	F	D, In	138	143	140	141	2.76	2.96	3.25	3.36
	Tachigali vulgaris	G	D, In	74	78	74	76	1.25	1.25	1.53	2.61
	Emmotum nitens	F	D, In	34	35	34	34	0.81	0.83	0.92	1.20
	Xylopia aromatica	G	D	52	41	34	30	0.85	0.68	0.72	0.46
	Myrcia splendens	G	D	31	29	29	27	0.54	0.53	0.63	0.41
	Eriotheca gracilipes	F	In	21	19	18	19	0.35	0.39	0.42	0.72
	Vochysia haenkeana	F	In	3	6	7	7	0.04	0.07	0.10	0.19
DW-2	*Xylopia sericea*	F	D	68	69	66	71	1.04	1.22	1.29	1.41
	Mezilaurus crassiramea	S	D	40	40	38	37	0.93	0.94	0.91	0.88
	Pterodon pubescens	G	D	30	45	47	50	0.65	0.83	0.89	0.99
	Bowdichia virgilioides	G	D	29	30	29	29	0.52	0.53	0.53	0.51
	Pouteria ramiflora	G	D	19	22	29	25	0.50	0.50	0.50	0.51
	Emmotum nitens	F	In	16	21	22	29	0.23	0.31	0.34	0.45
	Eriotheca gracilipes	F	In	8	9	11	11	0.13	0.15	0.18	0.19
	Tachigali vulgaris	G	In	1	7	9	10	0.03	0.07	0.13	0.22

	Vochysia haenkeana	F	In	2	2	2	2	0.02	0.03	0.03	0.04
	Hirtella glandulosa	F	In	-	1	1	1	-	0.01	0.01	0.01
TC-1	*Qualea parviflora*	S	D	35	46	54	56	0.42	0.55	0.65	0.68
	Eriotheca gracilipes	F	D, In	21	23	24	24	0.41	0.47	0.53	0.55
	Aspidosperma tomentosum	G	D	20	20	21	20	0.25	0.25	0.24	0.25
	Strychnos pseudoquina	G	D	18	17	18	16	0.34	0.34	0.34	0.34
	Qualea grandiflora	S	D	18	23	23	27	0.21	0.27	0.28	0.33
	Roupala montana	G	In	17	20	22	25	0.37	0.39	0.40	0.44
	Emmotum nitens	F	In	6	6	10	12	0.13	0.14	0.19	0.22
	Hirtella glandulosa	F	In	1	-	-	-	0.01	-	-	-
	Tachigali vulgaris	G	In	-	-	7	9	-	-	0.08	0.10
TC-2	*Emmotum nitens*	F	D, In	56	68	76	92	1.27	1.53	1.64	1.95
	Pouteria ramiflora	G	D	46	44	43	42	0.88	0.84	0.83	0.82
	Mouriri elliptica	S	D	29	26	32	32	0.60	0.57	0.61	0.59
	Bowdichia virgilioides	G	D	23	23	23	22	0.50	0.51	0.53	0.53
	Roupala montana	G	D, In	21	22	23	23	0.31	0.34	0.36	0.36
	Hirtella glandulosa	F	In	1	1	1	1	0.01	0.02	0.02	0.02
	Eriotheca gracilipes	F	In	1	-	-	-	0.03	-	-	-
	Tachigali vulgaris	G	In	-	-	3	5	-	-	0.03	0.07
OC-1	*Mezilaurus crassiramea*	S	D	20	24	24	23	0.40	0.45	0.47	0.45
	Eugenia dysenterica	S	D	17	18	18	19	0.26	0.28	0.29	0.30
	Bowdichia virgilioides	G	D	16	17	19	21	0.38	0.40	0.42	0.45
	Qualea parviflora	S	D	13	17	23	24	0.23	0.29	0.37	0.41
	Eugenia geminiflora	S	D	10	14	15	15	0.11	0.15	0.15	0.16
	Emmotum nitens	F	In	7	10	15	16	0.07	0.13	0.21	0.25
	Roupala montana	G	In	6	7	10	9	0.10	0.12	0.16	0.16

Eriotheca gracilipes	F	In	5	6	6	6	0.33	0.37	0.40	0.45
Tachigali vulgaris	G	In	-	5	7	10	-	0.07	0.15	0.25
Vochysia haenkeana	F	In	-	-	-	1	-	-	-	0.01

Table S5 Density, Basal area, and Aboveground biomass of tree species total and classified according to the species' preferred habitat of occurrence (Hab): savanna, generalist and forest in areas of dense woodland woodland (DW), typical cerrado (TC), and open cerrado (OC) in the Cerrado-Amazon ecotone.

Areas	Parameters	Hab	R	R^2	Slope	F	P
DW-1	Density (ind ha^{-1})	Total	0.4331	0.1496	3.206	1.528	>0.05
		Forest	0.839	0.7586	2.5234	10.43	>0.05
		Generalist	0.4953	0.2429	2.570	1.963	>0.05
		Savanna	0.7278	0.5916	-1.8879	5.346	>0.05
	Basal area (m^2 ha^{-1})	Total	0.9761	0.9642	0.13705	81.77	<0.01
		Forest	0.9885	0.9827	0.096	171.7	<0.01
		Generalist	0.9619	0.9428	0.05574	50.49	<0.01
		Savanna	0.5723	0.3585	-0.0147	2.676	>0.05
	Aboveground biomass (Mg ha^{-1})	Total	0.9072	0.8608	51.62	19.55	<0.05
		Forest	0.9484	0.9227	30.866	36.79	<0.05
		Generalist	0.8217	0.7325	23.008	9.216	>0.05
		Savanna	0.289	-0.0665	-2.256	0.8129	>0.05
DW-2	Density (ind ha^{-1})	Total	0.7699	0.6549	-4.935	6.693	>0.05
		Forest	0.146	-0.281	0.6355	0.3419	>0.05
		Generalist	0.908	0.862	-4.3364	19.74	<0.05
		Savanna	0.9693	0.9539	-1.2336	63.13	<0.01
	Basal area (m^2 ha^{-1})	Total	0.8592	0.7888	0.3596	12.21	>0.05
		Forest	0.93	0.8949	0.25505	26.56	<0.05

		Generalist	0.7045	0.5568	0.13204	4.769	>0.05
		Savanna	0.5059	0.2588	-0.02745	2.048	>0.05
	Aboveground biomass (Mg ha^{-1})	Total	0.9984	0.9976	15.38	1257	<0.01
		Forest	0.9965	0.9947	8.772	563.9	<0.01
		Generalist	0.9855	0.9782	6.415	135.7	<0.01
		Savanna	0.289	-0.06653	-2.256	0.8129	>0.05
TC-1	Density (ind ha^{-1})	Total	0.9941	0.9911	15.79	334.8	<0.01
		Forest	0.9742	0.9613	2.5514	75.43	<0.01
		Generalist	0.982	0.973	4.7477	109.2	<0.01
		Savanna	0.9989	0.9983	8.495	1766	<0.01
	Basal area (m^2 ha^{-1})	Total	0.9975	0.9962	0.2464	791.5	<0.01
		Forest	0.9831	0.9746	0.05316	116.2	<0.01
		Generalist	0.9932	0.9898	0.08272	291.9	<0.01
		Savanna	0.9912	0.9868	0.1106	225.6	<0.01
TC-2	Aboveground biomass (Mg ha^{-1})	Total	0.9886	0.9829	24.446	173.8	<0.01
		Forest	0.9761	0.9641	5.896	81.65	<0.01
		Generalist	0.9816	0.9724	8.301	106.6	<0.01
		Savanna	0.9932	0.9898	10.25	292.3	<0.01
	Density (ind ha^{-1})	Total	0.9744	0.9615	5.804	75.97	<0.01
		Forest	0.9695	0.9543	5.140	63.6	<0.01
		Generalist	0.4494	0.1742	0.4299	1.633	>0.05
		Savanna	0.07788	-0.3832	0.2336	0.1689	>0.05
	Basal area (m^2 ha^{-1})	Total	0.9897	0.9846	0.1013	192.4	<0.01
		Forest	0.9866	0.9799	0.09589	146.9	<0.01

		Generalist	0.9537	0.9305	0.018692	41.15	<0.05
		Savanna	0.2763	-0.0856	-0.01374	0.7635	>0.05
	Aboveground biomass (Mg ha^{-1})	Total	0.9574	0.9361	10.521	44.95	<0.05
		Forest	0.9954	0.9931	10.32	431.7	<0.01
		Generalist	0.8264	0.7395	1.4990	9.518	>0.05
		Savanna	0.2431	-0.1353	-1.294	0.6424	>0.05
OC-1	Density (ind ha^{-1})	Total	0.9693	0.9539	11.103	63.13	<0.01
		Forest	0.957	0.9355	1.7944	44.52	<0.05
		Generalist	0.9962	0.8842	4.4206	517.9	<0.01
		Savanna	0.877	0.8157	4.888	14.26	>0.05
	Basal area (m^2 ha^{-1})	Total	0.9977	0.9966	0.2063	879	<0.01
		Forest	0.9755	0.9632	0.04448	79.6	<0.01
		Generalist	0.9902	0.9853	0.07901	201.6	<0.01
		Savanna	0.9557	0.9335	0.08283	43.11	<0.05
	Aboveground biomass (Mg ha^{-1})	Total	0.9869	0.9803	21.250	150.1	<0.01
		Forest	0.9558	0.9336	6.244	43.21	<0.05
		Generalist	0.9795	0.9693	8.024	95.64	<0.01
		Savanna	0.9733	0.96	6.982	73.03	<0.01