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Patterns of tree species composition at watershed-scale in the Amazon 'Arc of Deforestation': implications for conservation

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SUMMARY

The loss of biodiversity in transitional forests between the Cerrado and Amazonia, the two largest neotropical phytogeographic domains, is an issue of great concern. This extensive region is located within the zone of the 'arc of deforestation' where tropical forests are being lost at the fastest rate on the planet, but floristic diversity and variation among forests here is still poorly understood. We aimed to characterize the floristic composition of forests in this zone and explore the degree and drivers of differentiation within and across Araguaia and Xingu watersheds. In ten sites we identified all trees with diameter ≥ 10 cm; these totaled 4,944 individuals in 257 species, 107 genera and 52 families. We evaluated the data for multivariate variation using TWINSPAN and DCA to understand the species distribution among sites. There was a larger contribution from the Amazonian flora (169 species) than that of the Cerrado (109) to the transitional forests. Remarkably, 142 species (55%) were restricted to only one sampling site, while 29 species (> 16%) are endemic to Brazil, suggesting a high risk for biological conservation, and the disappearance of species and forests with unique floristic composition with loss and fragmentation of large areas. Watersheds may be a critical factor driving species distribution among forests in the Amazonian-Cerrado transition zone, and quantifying their role can provide powerful insight into devising better conservation strategies of the remaining forests.

Keywords: endemic species; floristic connections; Araguaia; Xingu; watersheds; species distribution.

INTRODUCTION

Between the two major tropical domains of the South America, Amazonia and Cerrado, there are transitional zones (Ackerly et al. 1989) where a mosaic of various forest and savanna communities exists (Staver et al. 2011; Murphy and Bowman 2012). The transition forests have lower density, height, basal area, biomass and species richness than the forests located in the core region of Amazonia (Ivanauskas et al. 2004a; Balch et al. 2008) and represent the Amazonia advancing front on the Cerrado (Marimon et al. 2006).

Different environmental factors may determine transitions between phytogeographic domains, depending on the scale being considered. Tropical forests generally occur in regions with wetter climate (Schwartz and Namri 2002) and lower precipitation seasonality in comparison with savannas (Staver et al. 2011). The climate variation acts at broad scales, determining the differentiation of vegetation patterns, as one can see in both Amazonia and Cerrado domains (Ab'Saber 2003; Staver et al. 2011; Lehmann et al. 2011).

The rainfall seasonality also shapes forest and savanna distribution patterns, but this factor is most evident in Africa than in Australia and South America (Lehmann et al. 2011). In regions with intermediate rainfall (1,000 to 2,500 mm) and average seasonality (<7 months), forest and savanna coexist as alternative stable states, depending on fire frequency (Staver et al. 2011; Murphy and Bowman 2012). At smaller scales, edaphic factors play a greater role in determining the species composition of plant communities (Askew et al. 1970; Veenendaal et al. 2015). Additionally, fire, resource availability and species traits can influence the occurrence of certain vegetation types (Hoffmann et al. 2012). Topographic features, such as the groundwater level, also determine the occurrence of forest or savanna (Murphy and Bowman 2012; Silva 2015). Here, we investigate floristic diversity and variations in a transition zone at a large scale, between phytogeographic domains.

In the large contact region between Cerrado and Amazonia there are different tree-dominated vegetation types, including semideciduous forests (Araujo et al. 2009; Mews et al. 2011), monodominant forests of Brosimum rubescens Taub. (Marimon et al. 2001a), evergreen seasonal forests (Ivanauskas et al. 2008), deciduous forests (Pereira et al. 2011), cerrado sensu stricto and cerradão (Marimon et al. 2014). This transition zone hundreds of kilometres wide with a sinuous total length of more than 6,000 km following the complex inter digitation of Amazonia and the entire Cerrado domain around the southern Brazilian Amazon Basin (Ackerly et al. 1989; Marimon et al. 2014; Ratter et al. 1973), has high biodiversity, forming a vegetation mosaic (Ratter et al. 2003; Marimon et al. 2006; Torello-Raventos et al. 2013), which contributes to the fauna diversity (Sick 1955; Lacher and Alho 2001; Oliveira et al. 2010; Rocha et al. 2014).

The loss of biodiversity of the Amazonia-Cerrado transition forests is of great concern, mainly because it is located within the region known as the ‘arc of deforestation’. Here land-use change is progressively removing most of the natural forest vegetation (Fearnside 2005), and deforestation for agriculture is the main threat (Araujo et al. 2009; Ivanauskas et al. 2004a, 2004b). Furthermore, anthropogenic fires (Fearnside 2005) and the severe drought events of the last decade in this region (e.g., Lewis et al. 2011; Marengo et al. 2011) have also been linked to floristic and structural changes (Marimon et al. 2014; Phillips et al. 2009), and to the rate of deforestation itself (Davidson et al. 2012). Stronger seasonal droughts may also be linked to anthropogenic climate change and most global climate model simulations for the 21st century show a markedly increase drought risk for southern Amazonia (e.g., Fu et al. 2013). Wherever species are restricted to only one area or region they are vulnerable to extinction as a result of human disturbance (Peterson and Watson 1998; Werneck et al. 2011) and large-scale environmental changes such as drought and fire.

The vegetation of the Amazonia-Cerrado transition region is gradually being revealed, but not enough is known yet to evaluate the threat to biodiversity posed by the elimination of the transition forests. For example, in an evergreen seasonal forest of the Xingu River Basin, there are many species (94%) with Amazonian distribution (Ivanauskas et al. 2004b; Lista de Espécies da Flora do Brasil 2012). One explanation for the high contribution of Amazonian flora to these transitional forests could be the high number of streams distributed across a general flat relief, which reduces water stress compared to that encountered in other seasonal forests of the Central Highlands of Brazil in similar climate (Ivanauskas et al. 2008; Oliveira-Filho and Ratter 1995).

Phytogeographic studies should consider the varied causes and mechanisms potentially involved in species turnover across space. One ‘null’ explanation for species turnover is simply that it is influenced by geographic distance (Hubbell 2001). Space will be an important factor influencing the separation of communities if all individuals of the same trophic guild are equivalent competitors and have limited dispersal ability - this scenario results in a decreased similarity between communities with increasing geographic distance (Hubbell 2001). However, other mechanisms, such as physical barriers (e.g., watersheds), also act to control species distribution (Francis and Currie 1998) and may determine the variation in floristic composition between communities (Bell 2001; Condit et al. 2002). Thus, species migration may be favored by corridors shaped by the forests accompanying streams and rivers, constituted into networks of dendritic connections between waterways in a basin (Oliveira-Filho and Ratter

1995). Based on this hypothesis, watersheds should form links between major forested biomes (here, Atlantic and Amazonian forests), acting as routes of species dispersal and hence genetic linkages connecting floras (Oliveira-Filho and Ratter 1995) and faunas (Costa 2003; Ribas et al. 2011).

In addition to the above mentioned factors that can influence the distribution of taxa, environmental condition also affects the occurrence of the species. Thus, the presence of a particular species at a site is favored by adaptations of this species to a range of environmental conditions and resources available there, in which the species has a range of tolerances and requirements, that is, the ecological niche (Hutchinson 1957). Thus, we expected that areas under similar environmental conditions would share more species than areas under different environmental conditions (Gurevitch et al. 2009).

This work was intended to inform conservation decisions by quantifying the contributions made by species endemic to Brazil and, more specifically, endemic to Cerrado and Amazonia domains. We addressed two questions. 1) Does the Amazon and/or the Cerrado flora dominate the composition of the sampling site? We expected a greater contribution of Amazonian flora because, despite the region having a markedly seasonal climate, locally enhanced water availability favors the occurrence of Amazonian species (Ivanauskas et al. 2008). 2) How do the forests vary in distribution and floristic composition? We expected to find signatures of both ‘neutral’ and habitat-driven phytogeographic variation. Thus, closer sites, independent of the watershed in which they happen to be located (Xingu River or Araguaia River), should have higher floristic similarity than more distant areas because species turnover typically increases with geographic distance (Hubbell 2001) and among different habitat types (e.g., Condit et al. 2002).

METHODS

Study sites

In the transition zone between the Cerrado and Amazonian domains in Brazil we sampled 10 sites, five located in the Xingu River Basin and five in the Araguaia River Basin. These sampling sites were distributed over a distance of up to 606.4 km (Table S1, see supplementary material as Journals.cambridge.org/ENC) and all within the central part of the 'arc of deforestation' (Fig.1). The climate, according to the Köppen classification, is Aw (tropical with a dry winter) (Alvares et al. 2013), with highly seasonal annual average rainfall between 1,500 and 1,740 mm (Table 1). We selected primary forests with no obvious sign of human actions. According to IBGE (2012), all studied forests were Evergreen Seasonal, the five located in the Araguaia River Basin being Evergreen Seasonal of the Lowlands (Floresta Estacional Sempre-Verde das Terras Baixas), and the five of the Xingu River Evergreen Seasonal Submontane (Floresta Estacional Sempre-Verde Submontana).

Table 1

The data were curated within the ForestPlots database (Lopez-Gonzalez et al. 2009, 2011), where each forest has a unique site code. In this study, we applied new codes to reflect the vegetation differences (viz, XIN= Xingu River Basin forest and ARA= Araguaia River Basin forest) (Table 1, Fig. 1).

Figure 1

Data collection

We sampled 1 ha in each sampling site, and identified all tree individuals with diameter at breast height (DBH at 1.30 m above the ground) ≥ 10 cm. We identified the species in the field by comparisons with herbarium (NX, UFMT, UnB and IAN) material of known specific identity, and with the help of specialists. After identification, the material was incorporated into the Herbarium NX, Mato Grosso, Nova Xavantina (Coleção Zoobotânica James Alexander Ratter). We determined the classification of families based on APG III (2009), and assigned species names using the 'Flora of Brazil' database (Lista de Espécies da Flora do Brasil 2012). We used this same database to determine the occurrence of species in different Brazilian phytogeographic domains and Brazilian endemic species.

Data analysis

We evaluated species distribution among forests based on a 'compound' graph from the function of Landeiro et al. (2010) in R version 3.0.3 (R Development Core Team 2014), where species and their abundances are represented on the y axis, ordered according to the weighted average, with the ecological gradient represented on the x axis. We analyzed the 48 most abundant species (> 13 individuals) to help ensure confidence that results are not affected by sampling issues of rarest taxa (see also Landeiro et al. 2010).

We also investigated the spatial patterns of species distribution by means of Mantel tests in PASSaGE 2.0 (Rosenberg and Anderson 2011), using the abundance species matrix. The distance coefficient used in this step was the Czekanowski index (McCune and Grace 2002). The decision on the presence of spatial autocorrelation was made after 999 permutations.

To classify the forests based on species composition and their respective abundances, we used TWINSPAN (Two-Way Indicator Species Analysis), using the default option of the software PC-ORD 5.0 (McCune and Mefford 2006) to define the cut off level of the 'pseudo species' (see McCune and Grace 2002).

We ordinated the plots based on a DCA (Detrended Correspondence Analysis) in PC-ORD 5.0. We obtained the standardized length of the gradient, assuming that a value greater than four standard deviations (SD) would indicate complete replacement of species (Hill and Gauch 1980). Since the DCA is based on chi-square distance, which is sensitive to rare species (McCune and Grace 2002), we removed these species, here understood as the singletons (species with only one individual). The DCA, however, still showed excessive residuals in the first axis, and therefore, we also eliminated species with only two individuals. We submitted the reduced matrix (with 146 species) to a new DCA; here the residuals were better distributed.

RESULTS

We sampled 4,944 trees, distributed in 257 species, 107 genera and 52 families in the 10 sampling sites (Table S2). Species diversity was concentrated in a few families: 20% of the families contained 60% of the species, while on the other hand 35% (18 families) were represented only by a single species (Table S2, Table 2). In almost every sampling site, more than 50% of families were represented by a single species, with the marginal exceptions of XIN-02 and ARA-03 (48 and 45%) (Table 2). The richest families were Chrysobalanaceae (24 species), Fabaceae (22), Annonaceae (21), Melastomataceae (17), Moraceae (14), Sapotaceae (13), Apocynaceae (11), Burseraceae and Myrtaceae (10 each) and Lauraceae (9) (Table S2). The richest genera were Licania (13 species), Miconia (12), Aspidosperma, Hirtella and Xylopia (10 each), Pouteria (9), Inga (8), Ficus and Ocotea (7 each), Casearia, Cecropia, and Trichilia (5 each) (Table S2). The proportion of genera with only one local species was also high ranging from 68 to 100% in each forest (Table 2).

Table 2.

Contribution of Amazonian and Cerrado floras to transitional forests

The species recorded in this transitional region also occur in four Brazilian phytogeographic domains, with 169 species in the Amazonian domain, 109 in the Cerrado, 88 in the Atlantic Forest and 49 in the Caatinga domain. All ten of our sampling sites had more species from the Amazonian (from 71 to 100%) than the Cerrado domain (42 to 85%). Still, the two forests (ARA-01 and ARA-02) located further south, most distant from the Amazonian domain, showed the smallest difference between the occurrence of the Amazonia and Cerrado species, while the forests ARA-03 and ARA-04 located further north, closer to Amazonia, were dominated by typical Amazonian species (Table 2). Twenty-nine of the sampled species were endemic to Brazil, representing 16% of taxa identified to the species level. Of these, seven occur only in the Amazonian and in the Cerrado domains and seven in Amazonia (Table S2). Every sampling site plot included at least two species that are endemic to Brazil (Table 2).

Spatial distribution, watersheds, and floristic composition

Considering the amplitude of species occurrence among sampling sites, 43 (17%) occurred in five or more sites, while 143 (55%) were restricted to just one forest, especially ARA-02 (19 unique species), XIN-04 and ARA-04 (20 unique species each) and ARA-05 (21 unique species) (Table S2, Table 2). The highest degree of species sharing was observed in the plots close to the Araguaia River Basin in Mato Grosso state (ARA-01 and ARA-02) (Table S2). However, the progressive substitution of species across space is evident throughout the study areas (Fig.2). Only 11 species were recorded with high abundance (> 70 individuals) in the forests of both Xingu and Araguaia watersheds: Tapirira guianensis Aubl., Pseudolmedia macrophylla Trécul, Trattinnickia glaziovii Swart, Jacaranda copaia (Aubl.) D. Don, Sacoglottis guianensis Benth., Sloanea eichleri K.Schum., Protium pilossissimum Engl., Miconia pyrifolia Naudin, Amaioua guianensis Aubl., Chaetocarpus echinocarpus (Baill.) Ducke and Cheiloclinium cognatum (Miers) A.C.Sm. (Fig.2). Overall, the most abundant species were preferentially found in particular watersheds (i.e., abundant in either Rio Xingu or Rio Araguaia watersheds, but rarely in both).

Figure 2

Two floristic groups emerge from TWINSPAN (Fig.3), the first composed of seasonal forests of the Xingu River Basin (XIN-01, XIN-02, XIN-03, XIN-04 and XIN-05), and the second of seasonal forests (ARA-01, ARA-02, ARA-03, ARA-04 and ARA-05) of the Araguaia River Basin (Fig.3). The first division (eigenvalue= 0.56) separated the Araguaia from the Xingu forests, while in the second division (eigenvalue= 0.42) two new groups were revealed: one with XIN-01 and XIN-03 and the other by XIN-02, XIN-04 and XIN-05 (Fig.3). Only in the third division (eigenvalue= 0.61), were the southern Araguaia forests (ARA-01 and ARA-02) separated from the other Araguaia forests far to the north.

Figure 3

In the DCA (Eigenvalues: Axis 1= 0.59032; Axis 2= 0.33288) we captured similar trends as recorded in TWINSPAN. Here, ARA-01 and ARA-02 were floristically disconnected from ARA-03, ARA-04 and ARA-05 on the second axis (Fig.4), but these geographically distant plot groups still scored closer to one another than did either to the Xingu Basin forests which geographically lie between the southernmost and northernmost Araguaia forests. The DCA also confirmed the high species replacement indicated by the 'compound' graph, because both the length of the gradient (> 4 SD) and the eigenvalues for the first two axes were high. Geographic distance had no effect on species replacement, since there was no significant correlation between floristic composition and geographical distances (Mantel test, $r = -0.0633$; $p = 0.5360$).

Figure 4

DISCUSSION

Our results reveal the influence of both, the Amazonia and the Cerrado domains on the composition of transitional forests, but confirmed our expectation that the contribution of the Amazonian flora is greater, which probably is related to the fact that the environmental conditions are more favorable to Amazonian species. We also detected an apparent large-scale role that watersheds play in structuring regional forest composition. Thus, while there was a signature of potentially neutrally-driven phytogeographic variation, because closer forests tended to be more similar, very distant pairs of forests in the Araguaia watershed were actually more similar to one another than were either to geographically-intermediate Xingu sites.

Influence of phytogeographic domain on floristic composition

The families Chrysobalanaceae, Fabaceae, Annonaceae and Sapotaceae, the species-richest in this study, are common in Amazonia (Oliveira-Filho and Ratter 1995). These are among the pan-Amazon dominant groups (ter Steege et al. 2006), being also among the most speciose in Amazonian upland 'Terra Firme' forests 1,000 km to the north of our sites and more than 2,000 km to the west (Lima-Filho et al. 2004; Oliveira and Amaral 2004; Oliveira et al. 2008; Phillips et al. 2003), as well as in seasonal forests (Ivanauskas et al. 2004a; Kunz et al. 2008; Marimon et al. 2006), and savanna woodland (Marimon-Junior and Haridasan 2005; Marimon et al. 2006) at the southern edge of the Amazonian domain. Fabaceae, in particular, though, also have high richness in the Cerrado domain (Sano et al. 2008). Sapotaceae, Burseraceae and Moraceae are typical of the Amazonian domain, and Melastomataceae, Myrtaceae and Lauraceae, are more speciose in Atlantic moist forests, with Annonaceae featuring strongly in both domains (Pinto and Oliveira-Filho 1999). The occurrence of the humid tropical forest flora in seasonally-dry Central Brazil, as in this study, would be favored by a dendritic network of rivers that acting as bridges, allowing species from Amazonian and Atlantic domains to migrate deep into areas that would otherwise be climatically challenging for such taxa (Oliveira-Filho and Ratter 1995). These findings therefore reinforce the transitional aspect of the study sites, and confirm the ecological importance of these key families in the composition and characterization of the transitional zone flora.

The finding that families with most species also have the highest abundance of individuals is not unexpected (e.g., Campbell et al. 1986; Ivanauskas et al. 2004a). Families richer in species and/or more abundant than others are capable of better exploit the environment, because they have adaptive characteristics (Tello et al. 2008). The large number of families and genera represented by only one species in each community on the other hand highlights the great taxonomic diversity of the studied forests.

Licania, Miconia, Pouteria, Inga and Ocotea, among the richest genera in this study, are well represented in different vegetation types of the transition zone (Araujo et al. 2009; Kunz et al. 2008; Marimon et al. 2006) and also in the distant, terra firme forests of central Amazonia growing in much wetter climates (Oliveira et al. 2008). This overlapping of genera from different vegetation sources further confirms the transitional aspect of southern Amazonia (Oliveira-Filho and Ratter 1995). The fact that most species belong to the Amazonian domain confirms our expectation that transitional forest tree floristics are more strongly influenced by the Amazon than by the Cerrado domain, especially for forests that occur in the northern portion of the studied area.

This information is not new to ecology, but it is new for the vegetation of the study sites and has an important consequence for conservation measures. An approach on genera is important because this taxa level helped reinforce which biome has greater contribution in species composition, and also confirmed the change in species diversity between areas, as in other studies (Condit et al. 2005; Qian 1999).

Spatial separation and watersheds

The third division of TWINSPAN and the second axis of DCA show that there may be a spatial effect in the dissimilarity between the communities, especially in the Araguaia Basin. However, this effect was not a clear pattern; if it had been we expected that ARA-01 and ARA-02 would be more similar to the forests of the Xingu Basin, because they are closer to each other, but this was not the case. Thus, we emphasize on the results of the first division of TWINSPAN and the first DCA axis.

The Mantel test showed further that geographic distance does not drive the spatial turnover of species and the floristic dissimilarity between these sites, suggesting that factors associated with habitat type appear to be involved (Condit et al. 2002; Gurevitch et al. 2009). Why though should the abundant species in the forests of Mato Grosso State also be shared with those of the forests of southern Pará, given the great geographic distance among the sites? These data suggest that other geographical processes have allowed these taxa to overcome dispersal limitation. Thus, and in support of Oliveira-Filho and Ratter (1995) in discussing the origin of the forests of Central Brazil, it appears that it is the north-south hydrological network associated with the Araguaia River Basin that provides the ultimate explanation for the greater floristic similarity between these distant forests than that which exists between any of them and much geographically-closer vegetation in the Xingu River Basin.

Conservation

Conservation of the transition zone vegetation is of paramount importance for three reasons. First, on-going land-use processes have already destroyed most natural vegetation here (Marimon et al. 2014). Second, both Amazonian and

Cerrado vegetation are highly diverse (Castro et al. 1999; Fiaschi and Pirani 2009; Gentry 1988). And third, this transitional region connects the floras of the Cerrado, the Atlantic Forest, and Amazon Rainforest (Méio et al. 2003; Oliveira-Filho and Ratter 1995; see also study on fauna: e.g. Costa 2003), and thus can potentially provide critical habitat space and corridors for the migration that could help to partly mitigate the great biological challenge that global climate change poses for communities of the neotropics (Loarie et al. 2009).

To emphasize the relevance of conserving the communities and ecosystems of the transition zone, it is important also to take into account the high faunal diversity of the region. On the banks of the tributaries of the Mortes River (Araguaia Basin) 81 species of birds living in forests and cerrado (Sick 1955), 238 species of birds and 57 species of non-flying mammals were recorded in some forests of the Xingu Basin (Oliveira et al. 2010). Forests of the Araguaia basin have been considered as shelters and food source for several species of small mammals (Rocha et al. 2014), and the mosaic of habitats generated by the Amazonia-Cerrado contact may determine species diversity in this region (Lacher and Alho 2001; Oliveira et al. 2010; Rocha et al. 2014). Thus, conservation of the vegetation becomes more urgent and necessary as it will also benefit the rich fauna of this important transitional area (Sick 1955; Lacher and Alho 2001; Oliveira et al. 2010; Rocha et al. 2014).

Our eco-floristic results reinforce the need for serious conservation action here. We found that one in six of the species identified in these forests are endemic to Brazil, and that most of these endemic species are also endemic to the two phytogeographic domains (Cerrado and Amazonian). We also conclude that most of the species must be either very rare, have restricted distribution, or both, as almost three-fifths of the tree taxa were only found in one of the 10 studied sites, suggesting the existence of a large and heterogeneous mosaic of plant communities in the Amazonia-Cerrado transition. The removal and fragmentation of large areas due to agricultural activities may therefore already be leading to the disappearance of species and unique assemblages, before they can even be adequately documented.

Furthermore, our finding that the taxonomic coherence within watersheds trumps effects of geographic proximity highlights the importance of considering whole watersheds in conservation efforts. As a simple but important example, establishing a single large reserve around the Xingu watershed may be less effective in conserving maximal tree diversity than would ensuring that the same size of area captures vegetation lying within both the Xingu and Araguaia watersheds.

Tree composition in this complex transition zone appears to be partly driven by subtle environmental patterns at the watershed scale, suggesting that the biogeography of the major neotropical domains has still to be well understood. Further investigations should focus on better understanding of how environmental factors determine the species composition and distribution across the transitional regions. This information will help improve the ability of conservation efforts to protect floristic and structural diversities in the communities of the vast Amazonia-Cerrado contact zone. This is especially important in light of the intense threat facing this region due to its close alignment with the ‘arc of deforestation’.

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REFERENCES

Ab’Sáber, A. (2003) Os Domínios de natureza no Brasil: potencialidades paisagísticas. São Paulo, SP, Brasil: Ateliê.

Ackerly, D.D., Thomas, W.W., Ferreira, C.A.C. & Pirani, J.R. (1989) The forest-cerrado transition zone in southern Amazonia: results of the 1985 Projeto Flora Amazonica Expedition to Mato Grosso. Brittonia **41**: 113-128.

Alvares, C.A., Stape, J.L., Sentelhas, P.C., Moraes, J.L.M. & Sparovek, G. (2013) Köppen’s climate classification map for Brazil. Meteorologische Zeitschrift **22**: 711-728.

APGIII - ANGIOSPERM PHYLOGENY GROUP. (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Botanical journal of the Linnean Society of London **161**: 105-121.

Araujo, R.A., Costa, R.B., Felfili, J.M., Kuntz, I., Sousa, R.A.T.M. & Dorval, A. (2009) Florística e estrutura de fragmento florestal em área de transição na Amazônia Matogrossense no município de Sinop. Acta Amazonica **39**: 865-878.

Askew, G.P., Moffatt, D.J., Montgomery, R.F. & Searl, P.L. (1970) Soil landscapes in northeastern Mato Grosso. The Geographical Journal **136**: 211-227.

Balch, J.K., Nepstad, D.C., Brando, P.M., Curran, L.M., Portela, O., Carvalho-Jr., O. & Lefebvre, P. (2008) Negative fire feedback in a transitional forest of southeastern Amazonia. Global Changes Biology **14**: 1-12.

Bell, G., 2001. Neutral macroecology. Science **293**: 2413.

Campbell, D.G., Daly, D.C., Prance, G.T. & Maciel, U.N. (1986) Quantitative ecological inventory of terra firme and varzea tropical forest on the Rio Xingu, Brazilian Amazon. Brittonia **38**: 369-393.

Castro, A.A.J.F, Martins, F.R., Tamashiro, J.Y. & Shepherd, G.J. (1999) How rich is the flora of Brazilian Cerrados? Annals of the Missouri Botanical Garden **86**: 192-224.

Condit, R., Pitman, N., Leigh Jr., E.G., Chave, J., Terborgh, J. Foster, R.B., Núñez V., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H.C., Losos, E. & Hubbell, S.P. (2002) Beta-diversity in tropical forest trees. Science **295**: 666-669.

Condit, R., Ashton, P., Balslev, H., Brokaw, N., Bunyavejchewin, S., Chuyong, G., Co, L., Dattaraja, H., Davies, S., Esufali, S., Ewango, C., Foster, R., Gunatilleke, S., Gunatilleke, N., Hernandez, C., Hubbell, S. P., John, R., Kenfack, D., Kiratiprayoon, S., Hall, P., Hart, T., Itoh, A., LaFrankie, J., Liengola, I., Lagunzad, D., Lao, S., Losos, E., Magard, E., Makana, J., Manokaran, N., Navarrete, H., Mohammed Nur, S., Okhubo, T., Pérez, R., Samper, C., Seng, L. H., Sukumar, R., Svenning, J., Tan, S., Thomas, D., Thomspon, J., Vallejo, M., Villa Muñoz, G., Valencia, R., Yamakura, T. & Zimmerman, J. (2005)

Tropical tree α-diversity: results from a worldwide network of large plots. Biologiske Skrifter **55**: 565–582.

Costa, L.P. (2003) The historical bridge between the Amazon and the Atlantic Forest of Brazil: a study of molecular phylogeography with small mammals. Journal of Biogeography **30**: 71-86.

Davidson, E.A., Araújo, A.C., Artaxo, P., Balch, J.K., Brown, I.F., Bustamante, M.M.C., Coe, M.T., DeFries, R.S., Keller, M., Longo, M., Munger, J.W., Schroeder, W., Soares-Filho, B.S., Sousa-Jr, C.M. & Wofsy, S.C. (2012) The Amazon basin in transition. Nature **481**: 321-328.

FAO (2006) Guidelines for Soil Descriptions, 5th ed. Food and Agricultural Organization of United Nations, Rome, Italy.

Fearnside, P.M. (2005) Deforestation in Brazilian Amazonia: History, Rates, and Consequences. Conservation Biology **19**: 680-688.

Fiaschi, P. & Pirani, J.R. (2009) Review of plant biogeographic studies in Brazil. Journal of Systematics and Evolution **47**: 477-496.

Francis, A.P. & Currie, D.J. (1998) Global patterns of tree species richness in moist forests: another look. Oikos **81**: 598-602.

Fu, R., Yin, L., Li, W., Arias, P.A., Dickinson, R.E., Huang, L., Chakraborty, S., Fernandes, K., Liebmann, B., Fisher, R. & Myneni, R.B. (2013) Increased dry-season length over southern Amazonia in recent decades and its implication for future climate projection. Proceedings of the National Academy of Sciences **110**: 18110-18115.

Gentry, A.H. (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. Annals of the Missouri Botanical Garden **75**: 1-34.

Gurevitch, J., Scheiner, S.M. & Fox, G.A. (2009) Ecologia vegetal. 2. ed., Porto Alegre, RS, Brasil: Artmed.

Hill, M.O. & Gauch, H.G. (1980) Detrended correspondence analysis: an improved ordination technique. Vegetatio **42**: 47-58.

Hoffmann, W.A., Geiger, E.L., Gotsch, S.G., Rossatto, D.R., Silva, L.C.R., LAU, O.L., Haridasan, M. & Franco, A. (2012) Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. Ecology Letters **15**: 759-768.

Hubbell, S.P. (2001) The Unified Neutral Theory of biodiversity and biogeography. Princeton, New Jersey, USA: Princeton University Press.

Hutchinson, G.E. (1957) Concluding remarks. Cold Spring Harbor Symp, **22**: 415-427.

IBGE - Instituto Brasileiro de Geografia e Estatística. (2012). Manual Técnico da Vegetação Brasileira. 2. ed., Rio de Janeiro, RJ, Brasil: Editora IBGE.

IBGE – Instituto Brasileiro de Geografia e Estatística (2015) Mapa Geomorfológico. IBGE-Brasília. In <ftp://geoftp.ibge.gov.br/mapas_tematicos/geomorfologia/unidades_federacao/mt_geomorfologia.pdf> (Accessed: 23 november 2015).

Ivanauskas, N.M., Monteiro, R. & Rodrigues, R.R. (2004a) Estrutura de um trecho de Floresta Amazônica na Bacia do Alto Rio Xingu. Acta Amazonica **34**: 275-299.

Ivanauskas, M.M., Monteiro, R. & Rodrigues, R.R. (2004b) Composição florística de trechos florestais na borda sul-amazônica. Acta Amazonica **34**: 399-413.

Ivanauskas, N.M., Monteiro, R. & Rodrigues, R.R. (2008) Classificação fitogeográfica das florestas do Alto Rio Xingu. Acta Amazonica **38**: 387-402.

Gurevitch, J., Scheiner, S.M. & Fox, G.A. (2009) Ecologia vegetal. 2. ed., Porto Alegre, RS, Brasil: Editora Artmed.

Kunz, S.H., Ivanauskas, N.M., Martins, S.V., Silva, E. & Stefanello, D. (2008) Aspectos florísticos e fitossociológicos de um trecho de Floresta Estacional Perenifólia na Fazenda Trairão, Bacia do Rio das Pacas, Querência-MT. Acta Amazonica **38**: 245-254.

Lacher, T.E., Alho, C.J.R. (2001) Terrestrial small mammal richness and habitat associations in an Amazon forest-Cerrado contact zone. Biotropica **33**: 171-181.

Landeiro, V.L., Hamada, N., Godoy, B.S. & Melo, A.S. (2010) Effects of litter patch area on macroinvertebrate assemblage structure and leaf breakdown in Central Amazonian streams. Hydrobiologia **649**: 355-363.

Lehmann, C.E.R., Archibald, S.A., Hoffmann, W.A. & Bond, W.J. (2011) Deciphering the distribution of the savanna biome. New Phytologist **191**: 197-209.

Lewis, S.L., Brando, P.M., Phillips, O.L., Heijden, G.M.F. & Nepstad, D. (2011) The 2010 Amazon drought. Science **331**: 554.

Lima-Filho, D.A., Rivilha, J., Amaral, I.L., Matos, F.D.A., Coelho, L.S., Ramos, J.F., Silva, G.B. & Guedes, J.O. (2004) Aspectos florísticos de 13 hectares da área de Cachoeira Porteira-PA. Acta Amazonica **34**: 415-423.

Lista de espécies da Flora do Brasil. (2012) Jardim Botânico do Rio de Janeiro. In <http://floradobrasil.jbrj.gov.br/2012/> (Acessed: 20 mar 2014).

Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009) The velocity of climate change. Nature **462**: 1052-1055.

Lopez-Gonzalez, G., Lewis, S.L., Burkitt, M., Baker T.R. & Phillips, O.L. (2009) ForestPlots.net Database. www.forestplots.net.

Lopez-Gonzalez, G., Lewis, S.L., Burkitt, M. & Phillips, O.L. (2011) ForestPlots.net: a web application and research tool to manage and analyse tropical forest plot data. Journal of Vegetation Science **22**: 610-613.

Marengo, J.A., Tomasella, J., Alves, L.M., Soares, W.R. & Rodriguez, D.A. (2011) The drought of 2010 in the context of historical droughts in the Amazon region. Geophysical Research Letters **38**: 1-5.

Marimon, B.S., Felfili, J.M. & Haridasan, M. (2001a) Studies in monodominant forests in eastern Mato Grosso, Brazil: I. A forest of Brosimum rubescens Taub. Edinburgh Journal of Botany **58**: 123-137.

Marimon, B.S., Lima, E.S., Duarte, T.G., Chieregatto, L.C. & Ratter, J.A. (2006) Observations on the vegetation of northeastern Mato Grosso, Brazil. IV. An analysis of the Cerrado-Amazonian Forest ecotone. Edinburgh Journal of Botany **63**: 323-341.

Marimon-Junior, B.H. & Haridasan, M. (2005) Comparação da vegetação arbórea e características edáficas de um cerradão e um cerrado sensu stricto em áreas adjacentes sobre solo distrófico no leste de Mato Grosso, Brasil. Acta Botanica Brasilica **19**: 913-926.

Marimon, B.S., Marimon-Junior, B.H., Feldpausch, T.R., Oliveira-Santos, C., Mews, H.A., Lopez-Gonzalez, G., Franczak, D.D., Oliveira, E.A., Maracahipes, L., Miguel, A., Lenza, E. & Phillips, O.L. (2014) Disequilibrium and hyperdynamic tree turnover at the forest-savanna transition zone in southern Amazonia. Plant Ecology & Diversity **7**: 281-292.

McCune, B. & Grace, J.B. (2002) Analysis of Ecological Communities. Gleneden Beach, Oregon, USA: MjM Software Design.

McCune, B. & Mefford, M.J. (2006) PC-ORD – multivariate analysis of ecological data, version 5.0. Gleneden Beach, Oregon, USA: MjM Software Design.

Méio, B.B., Freitas, C.V., Jatobá, L., Silva, M.E.F., Ribeiro, J.F. & Henriques, R.P.B. (2003) Influência da flora das florestas amazônica e atlântica na vegetação do cerrado sensu stricto. Revista Brasileira de Botânica **26**: 437-444.

Mews, H.A., Marimon, B.S., Pinto, J.R.R. & Silvério, D.V. (2011) Dinâmica estrutural da comunidade lenhosa em Floresta Estacional Semidecidual na transição Cerrado-Floresta Amazônica, Mato Grosso, Brasil. Acta Botanica Brasilica **25**: 845-857.

Murphy, B.P. & Bowman, D.M.J.S. (2012) What controls the distribution of tropical forest and savanna? Ecology Letters **15**: 748-758.

Oliveira, A.N. & Amaral, I.L. (2004) Florística e fitossociologia de uma floresta de vertente na Amazônia Central, Amazonas, Brasil. Acta Amazonica **34**: 21-34.

Oliveira, A.N., Amaral, I.L., Ramos, M.B.P., Nobre, A.D., Couto, L.B. & Sahdo, R.M. (2008) Composição e diversidade florístico-estrutural de um hectare de floresta densa de terra firme na Amazônia Central, Amazonas, Brasil. Acta Amazonica **38**: 627-642.

Oliveira, C.M., Santos, J.B. & Santos-Costa, M.C. (2010) Os animais da Tanguro, Mato Grosso: diversidade na zona de transição entre a Floresta Amazônica e o Cerrado. Ed UFPA, Belém, PA.

Oliveira-Filho, A.T. & Ratter, J.A. (1995) A study of the origin of central Brazilian forests by the analysis of plant species distribution patterns. Edinburgh Journal of Botany **52**: 141-194.

Pereira, B.A.S., Venturoli, F. & Carvalho, F.A. (2011) Florestas estacionais no cerrado: uma visão geral. Pesquisa Agropecuária Tropical **41**: 446-455.

Peterson, A.T. & Watson, D.M. (1998) Problems with areal definitions of endemism: the effects of spatial scaling. Diversity and Distribuitions **4**: 189-194.

Phillips, O.L., Martinez, R.V., Vargas, P.N., Monteagudo, A.L., Zans, M.C., Sánchez, W.G. & Rose, S. (2003) Efficient plot-based floristic assessment of tropical forests. Journal of Tropical Ecology **19**: 629-645.

Phillips, O.L., Aragão, L.E.O.C., Lewis, S.L., Fisher, J.B., López-González, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C.A., Van Der Heijden, G., Almeida, S., Amaral, I., Arroyo, L., Aymard, G., Baker, T.R., Bánki, O., Blanc, L., Bonal, D., Brando, P.M., Chave, J., Oliveira, A.C.A., Cardozo, N.D., Czimczik, C.I., Feldpausch, T.R., Freitas, M.A., Gloor, E., Higuchi, N., Jiménez, E., Lloyd, G., Meir, P., Mendoza, C., Morel, A., Neill, D.A., Nepstad, D., Patiño, S., Peñuela, M.C., Prieto, A., Ramirez, F., Schwartz, M., Silva, J., Silveira, M., Thomas, A.S., Ter Steege, H., Stropp, J., Vásques, R., Zelazowski, P., Dávila, E.A., Andelman, S., Andrade, A., Chao, K.J., Erwin, T., Di Fiore, A., Homorio, E., Keeling, H., Killeen, T.J., Laurance, W.F., Cruz, A.P., Pitman, N.C.A., Vargas, P.N., Ramírez-Angulo, H., Rudas, A., Salamão, R., Silva, N., Terborgh, J. & Torres-Lezama, A. (2009) Drought sensitivity of the Amazon rainforest. Science **323**: 1344-1347.

Pinto, J.R.R. & Oliveira-Filho, A.T. (1999) Perfil florístico e estrutura da comunidade arbórea de uma floresta de vale no Parque Nacional da Chapada dos Guimarães, Mato Grosso, Brasil. Revista Brasileira de Botanica **22**: 53-67.

Qian, H. (1999) Spatial Pattern of Vascular Plant Diversity in North America North of Mexico and its Floristic Relationship with Eurasia. Annals of Botany **83:** 271-283.

R Development Core Team. (2014) A language and environment for statistical computing. http://www.R-project.org [ver. 2.13.0]. R Foundation for Statistical Computing. Vienna, Austria.

Ratter, J.A., Richards, P.W., Argent, G. & Gifford, D.R. (1973) Observations on the vegetation of northeastern Mato Grosso: I. The woody vegetation types of the Xavantina-Cachimbo Expedition area. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences **266**: 449-492.

Ratter, J.A., Bridgewater, S. & Ribeiro, J.F. (2003) Analysis of the floristic composition of the Brazilian cerrado vegetation III: comparison of the woody vegetation of 376 areas. Edinburgh Journal of Botany **60**: 57-109.

Ribas, C.C., Aleixo, A., Nogueira, A.C.R., Miyaki, C.Y., Cracraft, J. (2011) A palaeobiogeographic model for biotic diversification within Amazonia over the past three million years. Proceedings of the Royal Society B **279**: 681-689.

Rosenberg, M.S. & C.D. Anderson, C.D. (2011) PASSaGE: Pattern Analysis, Spatial Statistics, and Geographic Exegesis. Version 2. Methods in Ecology and Evolution **2**: 229-232.

Rocha, R.G., Ferreira, E., Martins, I.C.M., Costa, L.P., Fonseca, C. (2014) Seasonally flooded stepping stones: emerging diversity of small mammal assemblage in the Amazonia-Cerrado ecotone, central Brazil. Zoological Studies **53**: 2-10.

Sano, S.M., Almeida, S.P. & Ribeiro, J.F. (2008) Cerrado: ecologia e flora. Brasília, DF, Brasil: Embrapa Cerrados.

Schwartz, D. & Namri, M. (2002) Mapping the total organic carbon in the soils of the Congo. Global and Planetary Change **33**: 77-93.

Sick, H. (1955) O aspecto fitofisionômico da paisagem do médio Rio das Mortes, Mato Grosso, e a avifauna da região. Arquivos do Museu Nacional **42**: 541-576.

Silva, L.C.R. (2015) Seasonal variation in groundwater depth does not explain structure and diversity of tropical savannas. Journal of Vegetation Science **26**: 404-406.

Staver, A.C., Archibald, S. & Levin, S.A. (2011) The global extent and determinants of savanna and forest as alternative biome states. Science **334**: 230-232.

Tello, J.C.R., Irmão, M.N., Viana, A.L., Bezerra, S.A.S. & Castro, J.P. (2008) Composição florística e estrutura fitossociológica da floresta ombrófila densa sub montana (Platô) face à elaboração do plano de gestão ambiental da área verde do Campus da Universidade Federal do Amazonas. Revista Forestal Venezolana **52**: 149-158.

ter Steege, H., Pitman, N.C., Phillips, O.L., Chave, J., Sabatier, D., Duque, A. Molino, J.F., Prévost, M.F., Spichiger, R., Castellanos, H., von Hildebrand, P. & Vásquez, R. (2006) Continental-scale patterns of canopy tree composition and function across Amazonia. Nature **443**: 444-447.

Torello-Raventos, M., Feldpausch, T.R., Veenendaal, E., Schrodt F., Saiz, G., Domingues, T.F., Djagbletey, G., Ford, A., Kemp, J., Marimon, B.S., Marimon-Junior, B.H., Lenza, E., Ratter, J.A., Maracahipes, L., Sasaki, D., Sonke, B., Zapfack, L., Taedoumg, H., Villarroel, D., Schwarz, M., Quesada, C.A., Ishida, F.Y., Nardoto, G.B., Affum-Baffoe, K., Arroyo, L., Bowman, D.M.J.S., Compaore, H., Davies, K., Diallo, A., Fyllas, N.M., Gilpin, M., Hien, F., Johnson, M., Killeen, T.J., Metcalfe, D., Miranda, H.S., Steininger, M., Thomson, J., Sykora, K., Mougin, E., Hiernaux, P., Bird, M.I., Grace, J., Lewis, S.L., Phillips, O.L. & Lloyd, J. (2013) On the delineation of tropical vegetation types with an emphasis on forest/savanna transitions. Plant Ecology & Diversity **6**: 101-137.

Veenendaal, E.M., Torello-Raventos, M., Feldpausch, T.R., Domingues, T.F., Gerard, F., Schrodt, F., Saiz, G., Quesada, C.A., Djagbletey, G., Ford, A., Kemp, J., Marimon, B.S., Marimon-Junior, B.H., Lenza, E., Ratter, J.A., Maracahipes, L., Sasaki, D., Sonké, B., Zapfack, L., Villarroel, D., Schwarz, M., Ishida, F.Y., Gilpin, M., Nardoto, G.B., Affum-Baffoe, K., Arroyo, L., Bloomfield, K., Ceca, G., Compaore, H., Davies, K., Diallo, A., Fyllas, N.M., Gignoux, J., Hien, F., Johnson, M., Mougin, E., Hiernaux, P., Killeen, T., Metcalfe, D., Miranda, H.S., Steininger, M., Sykora, K., Bird, M.I., Grace, J., Lewis, S., Phillips, O.L. & Lloyd, J. (2015) Structural, physiognomic and above-ground biomass variation in savanna-forest transition zones on three continents - how different are co-occurring savanna and forest formations? Biogeosciences **12**: 2927-2951.

Werneck, M.S., Sobral, M.E.G., Rocha, C.T.V., Landau, E.C. & Stehmann, J.R. (2011) Distribution and endemism of Angiosperms in the Atlantic Forest. Natureza & Conservação **9**: 188-193.

FIGURE LEGENDS

Figure 1 Amazonia-Cerrado transition zone and the ‘arc of deforestation’ in Brazil. The right box indicates the study area and dashed line indicates the boundary between the watersheds of the Xingu River and the Araguaia River. ARA= Araguaia River Basin forest, states of Mato Grosso and Pará and XIN= Xingu River Basin forest, states of Mato Grosso.

Figure 2 ‘Compound’ graph of species distribution (relative abundance) based on the weighted average according to the site in the Amazonia-Cerrado transition zone, Brazil. At the top of the graph, from left to right, the first two and last three bars are Araguaia River Basin forest (ARA); other bars are Xingu River Basin forest (XIN). Sites plotted in a latitudinal gradient (from left: southern forests, nearest the Cerrado domain, to right: northern forests, near the Amazonian domain).

Figure 3 Floristic classification of the 10 studied forests in the Amazonia-Cerrado transition zone, based on the TWINSPAN method. ARA= Araguaia River Basin forest and XIN= Xingu River Basin forest.

Figure 4 Ordination by DCA summarizing the floristic patterns of 10 forests in the Amazonia-Cerrado transition zone, Brazil. ▲ARA-01, ▼ARA-02, ◆ARA-03, ●ARA-04 and ■ARA-05: Araguaia River Basin forests; ○XIN-01, ◇XIN-02, □XIN-03, △XIN-04 and ▽XIN-05: Xingu River Basin forests.