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 'arc of deforestation' zone 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 explored the degree and drivers of differentiation within and across Araguaia and Xingu watersheds. In 10 sites we identified all trees with diameter ≥10 cm; these totaled 4944 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 potentially large loss of species and unique forest communities with the loss and fragmentation of large areas. Our results also suggest that 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 for the remaining forests.

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INTRODUCTION

Between the two major tropical domains of South America, Amazonia and Cerrado, there are transitional zones (Ackerly *et al.* 1989) where mosaics of various forest and savanna communities predominate (Staver *et al.* 2011; Murphy & Bowman 2012). The transition forests have lower density, height, basal area, biomass and species richness than forests located in the core region of Amazonia (Ivanauskas *et al.* 2004 *a*; Balch *et al.* 2008) and represent the advancing front of Amazonia into 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 & Namri 2002) and lower precipitation seasonality than savannas (Staver *et al.* 2011). Climatic variation acts at broad scales, with rainfall seasonality in particular determining large-scale differentiation of vegetation patterns, such as the Amazonian and Cerrado domains (Ab'Saber 2003; Lehmann *et al.* 2011; Staver *et al.* 2011).

In regions with intermediate rainfall (1000–2500 mm) and average seasonality (<7 months), forest and savanna may coexist as alternative stable states, depending on fire frequency (Staver *et al.* 2011; Murphy & Bowman 2012). At smaller scales, edaphic factors play a greater role in determining the species composition of plant communities (Askew *et al.* 1970). 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 & Bowman 2012; Silva 2015).

Here, our primary aim was to investigate large-scale floristic diversity and variation in a transition zone between phytogeographic domains of the Cerrado and Amazonia, where different tree-dominated vegetation types predominate.

These include semideciduous forests (Araujo *et al.* 2009; Mews *et al.* 2011), monodominant forests of *Brosimum rubescens* Taub. (Marimon *et al.* 2001), evergreen seasonal forests (Ivanauskas *et al.* 2008), deciduous forests (Pereira *et al.* 2011) and *cerrado sensu stricto* and *cerradão* (Marimon *et al.* 2014). This complex transition zone is hundreds of kilometres wide, with a sinuous total length of more than 6000 km following the complex inter-digitation of Amazonia with the Cerrado domain in the southern Brazilian Amazon Basin (Ratter *et al.* 1973; Ackerly *et al.* 1989; Marimon *et al.* 2014). It has high phytodiversity, with the vegetation mosaic (Ratter *et al.* 2003; Marimon *et al.* 2006; Torello-Raventos *et al.* 2013) also contributing to faunal diversity (Sick 1955; Lacher & Alho 2001; Oliveira *et al.* 2010; Rocha *et al.* 2014).

The loss of biodiversity of the Amazonia–Cerrado transition forests is of great concern. Located within the region known as the arc of deforestation, land-use change is progressively removing most of the natural forest vegetation (Fearnside 2005), with deforestation for agriculture the principal threat (Araujo *et al.* 2009; Ivanauskas *et al.* 2004 *a*, 2004 *b*). Furthermore, anthropogenic fires (Fearnside 2005) and the severe drought events of the last decade in this region (Lewis *et al.* 2011; Marengo *et al.* 2011) are also driving floristic and structural changes (Phillips *et al.* 2009; Marimon *et al.* 2014), and contributing to deforestation itself (Davidson *et al.* 2012). Stronger seasonal droughts may be linked to anthropogenic climate change, with most global climate model simulations for the 21st century showing a markedly increased drought risk for southern Amazonia (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 & Watson 1998; Werneck *et al.* 2011) and large-scale environmental changes such as drought and fire.

While the threats are clear, knowledge of the biogeography of the Amazonia–Cerrado transition region is still insufficient to evaluate the threat to biodiversity posed by the elimination of the transition forests. For example, in a single evergreen seasonal forest site of the Xingu River Basin, almost all species (94%) have an Amazonian distribution (Ivanauskas *et al.* 2004 *b*; Lista de Espécies da Flora do Brasil 2012), but it is not clear if such a pattern is typical, and if so, why. One explanation for a high contribution of Amazonian flora to these transitional forests could be the frequent streams distributed across a general flat relief, so reducing water stress compared to that encountered in seasonal forests of the central highlands of Brazil in a similar climate (Oliveira-Filho & Ratter 1995; Ivanauskas *et al.* 2008).

While phytogeographic studies should consider the varied causes and mechanisms potentially involved in geographic variation of biodiversity, one 'null' explanation for species turnover may be simply that it is controlled 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 & Currie 1998) and may determine the variation in floristic composition between communities (Bell 2001; Condit *et al.* 2002). Thus, species migration may be favoured by corridors shaped by the forests accompanying streams and rivers, constituted into networks of dendritic connections between waterways in a basin (Oliveira-Filho & Ratter 1995). According to this hypothesis, watersheds provide vital links between major forested biomes (here, Atlantic and Amazonian forests), acting as routes of species dispersal and hence genetic linkages connecting floras (Oliveira-Filho & Ratter 1995) and faunas (Costa 2003; Ribas *et al.* 2011).

Alternatively or additionally to such historical explanations, environmental conditions also frequently affect the occurrence of species. Thus, the presence of a particular species at a site may be favoured by adaptations to the environmental conditions and resources available there, for which the species has a range of tolerances and requirements ('the ecological niche' of Hutchinson [1957]). If so, areas sharing similar environmental conditions should share more species than areas with differing environments (Gurevitch *et al.* 2009).

This study is intended to help inform conservation decisions by quantifying the contributions to transitional forests made by species endemic to Brazil and, more specifically, endemic to the 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 favours the occurrence of Amazonian species (Ivanauskas *et al.* 2008); and 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 or Araguaia rivers), should have higher floristic similarity than more distant areas because species turnover typically increases with geographic distance (Hubbell 2001) and among different habitat types (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 sites were distributed over a distance of up to 606 km (Table S1) and all lie 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 1500 and 1740 mm (Table 1). We selected primary forests with no obvious sign of human actions. According to IBGE (2012), all studied forests
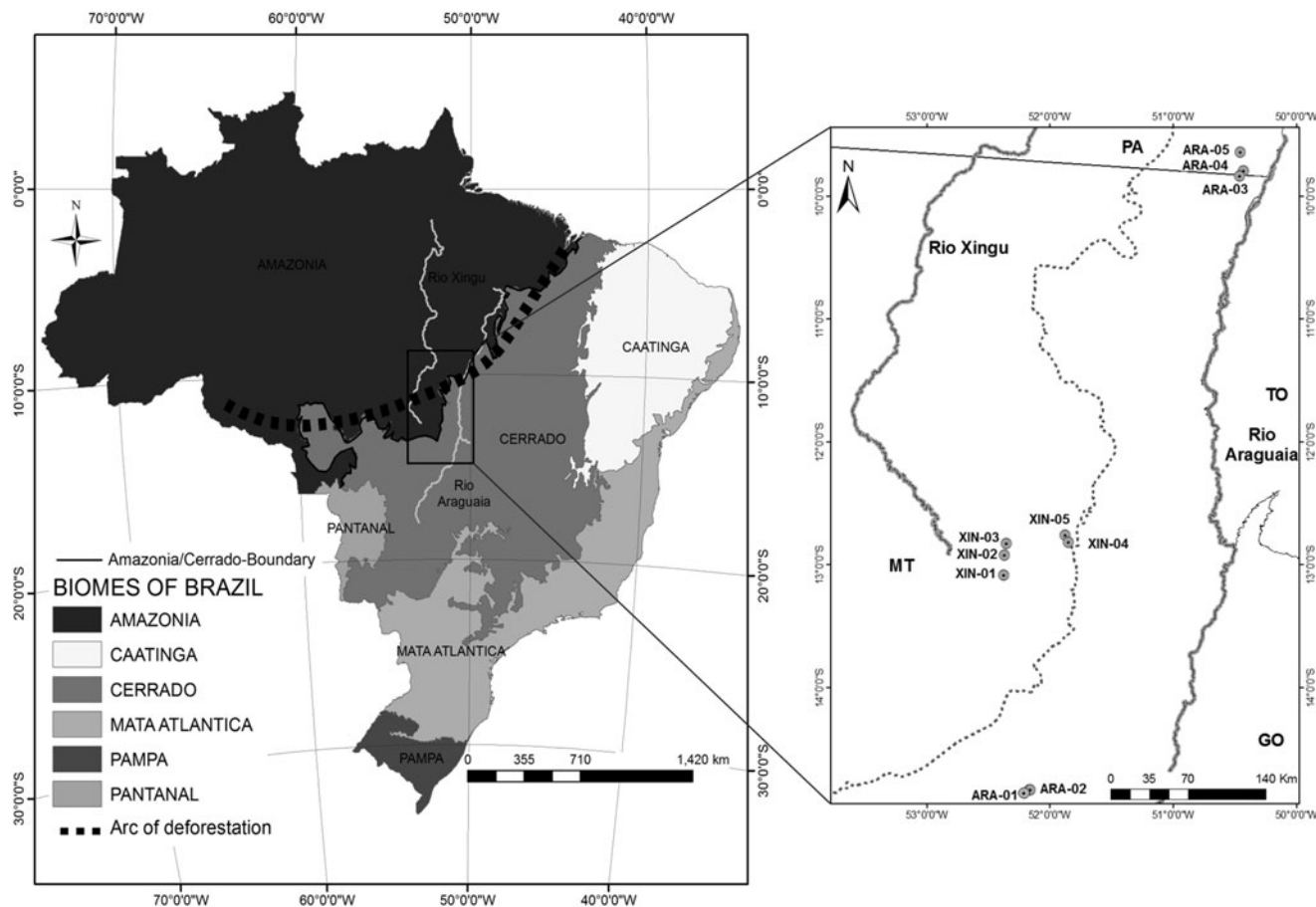
Figure 1 Amazonia–Cerrado transition zone and the arc of deforestation in Brazil. The right box indicates the study area and dashed line indicates the boundary between the watersheds of the Xingu River and the Araguaia River.

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 being Evergreen Seasonal Submontane (Floresta Estacional Sempre-Verde Submontana).

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

Data collection

We sampled 1 ha in each site, and identified all trees 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, UB and IAN) material of known identity, and with the help of specialists. After identification, the material was incorporated into Herbarium NX, Mato Grosso and Nova Xavantina (Coleção Zoobotânica James Alexander Ratter). We determined the classification of families based on APG III (Angiosperm Phylogeny Group

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 analysed 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 & Anderson 2011), using the abundance species matrix. The distance coefficient used in this step was the Czekanowski index (McCune & Grace 2002). Decisions on

Table 1 Geographic location, forest types, geomorphological units (GU), morphostructural domains (MD) and precipitation data of the 10 studied forests in the Cerrado–Amazonia transition zone, Brazil. Precipitation data from: [a]Marimon *et al.* (2010), [b]Moraes *et al.* (2005) and [c]Balch *et al.* (2008). MT = Mato Grosso; P = Precipitation; PA = Pará.

| Codes of sites (ForestPlots code) | Location | | | P (mm) | Soil types (FAO 2006) | GU/MD (IBGE 2015) |
	County	Lat (S)	Long (W)			
ARA-01 (VCR-01)	Nova Xavantina-MT	14°49′	52°09′	~1500[a]	Plinthosol	Alto Araguaia depression/quaternary sedimentary deposits
ARA-02 (VCR-02)	Nova Xavantina-MT	14°49′	52°10′	~1500[a]	Plinthosol	Alto Araguaia depression/quaternary sedimentary deposits
ARA-03 (SAT-01)	Santana do Araguaia-PA	09°47′	50°25′	~1600[b]	Ferralsol	Santana do Araguaia depression/neoproterozoic cratons
ARA-04 (SAA-01)	Santana do Araguaia-PA	09°38′	50°27′	~1600[b]	Ferralsol	Santana do Araguaia depression/neoproterozoic cratos
ARA-05 (SAA-02)	Santa Terezinha-MT	09°50′	50°27′	~1600[b]	Ferralsol	Santana do Araguaia depression/neoproterozoic cratons
XIN-01 (TAN-02)	Querência-MT	13°05′	52°22′	~1740[c]	Ferralsol	Plateau of Xingu headwaters/quaternary sedimentary deposits
XIN-02 (TAN-04)	Querência-MT	12°55′	52°22′	~1740[c]	Ferralsol	Plateau of Xingu headwaters/quaternary sedimentary deposits
XIN-03 (TAN-03)	Querência-MT	12°49′	52°21′	~1740[c]	Ferralsol	Plateau of Xingu headwaters/quaternary sedimentary deposits
XIN-04 (FLO-01)	Ribeirão Cascalheira-MT	12°48′	51°51′	~1740[c]	Ferralsol	Plateau of Xingu headwaters/quaternary sedimentary deposits
XIN-05 (FLO-02)	Ribeirão Cascalheira-MT	12°45′	51°52′	~1740[c]	Ferralsol	Plateau of Xingu headwaters/quaternary sedimentary deposits

the presence of spatial autocorrelation were made after 999 permutations.

To classify the forests based on species composition and their respective abundances, we used TWINSPAN (Two-Way Indicator Species Analysis), with the default option of the software PC-ORD 5.0 (McCune & Mefford 2006) to define cut-off levels for 'pseudo-species' (McCune & 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 & Gauch 1980). Since the DCA is based on chi-square distance, which is sensitive to rare species (McCune & 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 4944 trees, distributed among 257 species, 107 genera and 52 families in the 10 sampling sites (Table S2). Species diversity was concentrated in a few families: 20% of families contained 60% of the species, while on the other hand 35% (18 families) were represented by a single species (Table S2 and 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).

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 10 of our sampling sites had more species from the Amazonian (from 71 to 100%) than the Cerrado domain (42 to 85%). The two most southerly forests (ARA-01 and ARA-02), most distant from the Amazonian domain, showed the smallest difference between the occurrence of the Amazonia and Cerrado species, while the most northerly forests (ARA-03 and ARA-04) were dominated by typical Amazonian species (Table 2). A total of

Table 2 Floristic parameters of 10 studied forests in the Cerrado–Amazonia transition zone, Brazil. NI = Number of individuals; SPAM and SPCE = Number of species occurring in the Amazonian and Cerrado domains, respectively, considering those identified at the species level; SPED = Brazilian endemic species; SPEX = Number of unique species to the respective site. Percentage values between parenthesis.

Sites	SPAM	SPCE	SPEX	SPED	Total of families	Total of genera	Families with only one species	Genera with only one species	NI
ARA-01	13 (100)	11 (85)	∼	2	10	13	8 (80)	13 (100)	247
ARA-02	43 (81)	39 (74)	19	8	29	42	18 (62)	35 (83)	359
ARA-03	70 (88)	41 (51)	14	10	35	63	16 (45)	54 (86)	518
ARA-04	75 (86)	46 (53)	20	14	37	64	19 (51)	53 (83)	505
ARA-05	64 (80)	43 (54)	21	10	33	58	20 (61)	49 (85)	546
XIN-01	40 (77)	22 (42)	11	5	31	40	22 (71)	32 (80)	485
XIN-02	44 (80)	28 (50)	12	8	27	40	13 (48)	29 (72)	551
XIN-03	40 (71)	24 (43)	14	5	24	37	13 (54)	28 (76)	591
XIN-04	66 (84)	48 (61)	20	10	34	53	18 (53)	36 (68)	602
XIN-05	55 (89)	34 (55)	11	8	30	44	20 (67)	36 (82)	540
Total	169 (95)	109 (61)	142	29	52	107	18 (35)	63 (59)	4944

29 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 alone (Table S2). Every sampling site plot included at least two species 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 and Table 2). The greatest degree of species sharing was observed in the plots close to the Araguaia River Basin (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 pilosissimum* 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).

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
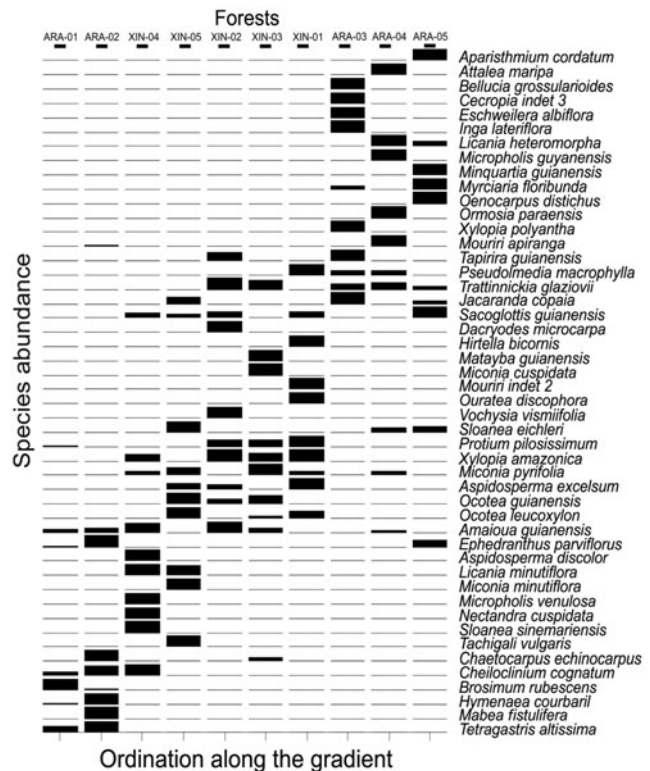

Figure 2 'Compound' graph of species distribution (relative abundance) based on the weighted average according to the site in the Amazonia–Cerrado transition zone, Brazil. At the top of the graph, from left to right, the first two and last three bars are ARA; other bars are XIN. Sites plotted in a latitudinal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

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
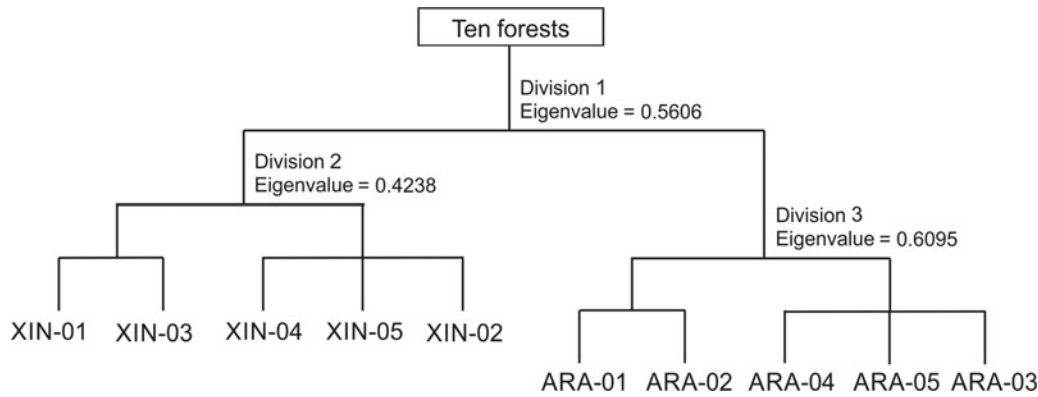
Figure 3 Floristic classification of the 10 studied forests in the Amazonia–Cerrado transition zone, based on the TWINSPAN method.

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.

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).

DISCUSSION

Our results reveal the influence of both the Amazonian and the Cerrado domains on the composition of transitional forests, but confirmed our expectation that the contribution of the Amazonian flora is greater. 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 & Ratter 1995). These are among
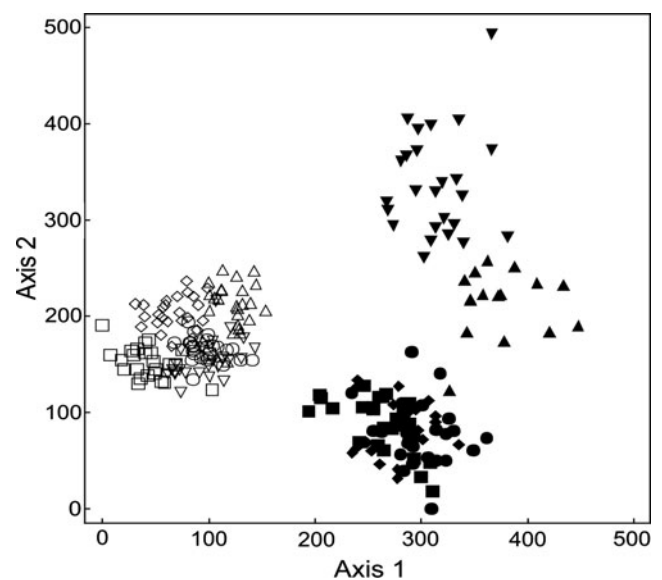

Figure 4 Ordination by DCA summarizing the floristic patterns of 10 forests in the Amazonia–Cerrado transition zone, Brazil. ▲ ARA-01, ▼ ARA-02, ♦ ARA-03, ● ARA-04 and ■ ARA-05: Araguaia River Basin forests; ○ XIN-01, ◇ XIN-02, □ XIN-03, △ XIN-04 and ▽ XIN-05: Xingu River Basin forests.

the pan-Amazon dominant groups (ter Steege *et al.* 2006), being also among the most speciose in Amazonian upland *Terra Firme* forests 1000 km to the north of our sites and more than 2000 km to the west (Phillips *et al.* 2003; Lima-Filho *et al.* 2004; Oliveira & Amaral 2004; Oliveira *et al.* 2008), as well as in seasonal forests (Ivanauskas *et al.* 2004 *a*; Marimon *et al.* 2006; Kunz *et al.* 2008) and savanna woodland (Marimon-Junior & 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 & Oliveira-Filho 1999). The occurrence of the humid tropical

forest flora in seasonally dry central Brazil, as in this study, would be favoured by a dendritic network of rivers that act 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 & 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 (Campbell *et al*. 1986; Ivanauskas *et al*. 2004 *a*). Families richer in species and/or more abundant than others are capable of better exploiting 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*, which are among the richest genera in this study, are well represented in different vegetation types of the transition zone (Marimon *et al*. 2006; Kunz *et al*. 2008; Araujo *et al*. 2009) and also in the distant, terra firme forests of central Amazonia (Oliveira *et al*. 2008). This overlapping of genera from different vegetation sources further confirms the transitional aspect of southern Amazonia (Oliveira-Filho & 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. The genus-level approach of this study helped reinforce which biome has greater contribution to floristic composition, and also confirmed that differences in species diversity are reflected at the genus level, as seen elsewhere (Qian 1999; Condit *et al*. 2005).

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 the results of the first division of TWINSPAN and the first DCA axis.

The Mantel test further showed 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 why these distant forests are floristically more similar to each other than they are to the much geographically closer vegetation in the Xingu River Basin.

Conservation

Conservation of the transition zone vegetation is of paramount importance for three reasons. First, ongoing land-use processes have already destroyed most natural vegetation here (Marimon *et al*. 2014). Second, both Amazonian and Cerrado vegetation are highly diverse (Gentry 1988; Castro *et al*. 1999; Fiaschi & Pirani 2009). And third, this transitional region connects the floras of the Cerrado, the Atlantic Forest and Amazon Rainforest (Oliveira-Filho & Ratter 1995; Méio *et al*. 2003; see also study on fauna: 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 to also 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 a food source for several species of small mammals, and the mosaic of habitats generated by the Amazonia–Cerrado contact may determine species diversity in this region (Lacher & 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 & Alho 2001; 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 and 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 is 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.

Supplementary material

To view supplementary material for this article, please visit http://dx.doi.org/10.1017/S0376892916000278

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