1 **Patterns of tree species composition at watershed-scale in the Amazon 'Arc**

2 **of Deforestation': implications for conservation**

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27 **SUMMARY**

28 The loss of biodiversity in transitional forests between the Cerrado and Amazonia,

29 the two largest neotropical phytogeographic domains, is an issue of great concern.

30 This extensive region is located within the 'arc of deforestation' zone where

31 tropical forests are being lost at the fastest rate on the planet, but floristic diversity

32 and variation among forests here is still poorly understood. We aimed to

33 characterize the floristic composition of forests in this zone and explore the degree

34 and drivers of differentiation within and across Araguaia and Xingu watersheds. In

35 10 sites we identified all trees with diameter ≥ 10 cm; these totaled 4944

36 individuals in 257 species, 107 genera and 52 families. We evaluated the data for

37 multivariate variation using TWINSPAN and DCA to understand the species

38 distribution among sites. There was a larger contribution from the Amazonian flora

39 (169 species) than that of the Cerrado (109) to the transitional forests.

40 Remarkably, 142 species (55%) were restricted to only one sampling site, while 29

41 species (> 16%) are endemic to Brazil, suggesting potentially large loss of species

42 and unique forest communities with the loss and fragmentation of large areas. Our

43 results also suggest that watersheds may be a critical factor driving species

44 distribution among forests in the Amazonian-Cerrado transition zone, and

45 quantifying their role can provide powerful insight into devising better conservation

46 strategies for the remaining forests.

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48 Keywords: Araguaia, biodiversity, endemic species, floristic connections, species

49 distribution, Xingu

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INTRODUCTION

Between the two major tropical domains of the 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 and 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 and 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 (1,000 to 2,500 mm) and average seasonality (<7 months), forest and savanna may 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). 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, our primary aim was to investigate large-scale floristic diversity and variation in a transition zone between phytogeographic domains of the Cerrado

78 and Amazonia, where different tree-dominated vegetation types predominate.

79 These include semideciduous forests (Araujo *et al*. 2009; Mews *et al*. 2011),

80 monodominant forests of *Brosimum rubescens* Taub. (Marimon *et al*. 2001),

81 evergreen seasonal forests (Ivanauskas *et al*. 2008), deciduous forests (Pereira *et*

82 *al*. 2011) and *cerrado sensu stricto* and *cerradão* (Marimon *et al*. 2014). This

83 complex transition zone is hundreds of kilometres wide, with a sinuous total length

84 of more than 6,000 km following the complex inter-digitation of Amazonia with the

85 Cerrado domain in the southern Brazilian Amazon Basin (Ratter *et al*. 1973;

86 Ackerly *et al*. 1989; Marimon *et al*. 2014). It has high phytodiversity, with the

87 vegetation mosaic (Ratter *et al*. 2003; Marimon *et al*. 2006; Torello-Raventos *et al*.

88 2013) also contributing to faunal diversity (Sick 1955; Lacher and Alho 2001;

89 Oliveira *et al*. 2010; Rocha *et al*. 2014).

90   The loss of biodiversity of the Amazonia-Cerrado transition forests is of

91 great concern. Located within the region known as the arc of deforestation, land-

92 use change is progressively removing most of the natural forest vegetation

93 (Fearnside 2005), with deforestation for agriculture the principal threat (Araujo *et*

94 *al*. 2009; Ivanauskas *et al*. 2004a, 2004b). Furthermore, anthropogenic fires

95 (Fearnside 2005) and the severe drought events of the last decade in this region

96 (Lewis *et al*. 2011; Marengo *et al*. 2011) are also driving floristic and structural

97 changes (Phillips *et al*. 2009; Marimon *et al*. 2014), and contributing to

98 deforestation itself (Davidson *et al*. 2012). Stronger seasonal droughts may be

99 linked to anthropogenic climate change, with most global climate model

100 simulations for the 21st century show a markedly increased drought risk for

101 southern Amazonia (Fu *et al*. 2013). Wherever species are restricted to only one

102 area or region they are vulnerable to extinction as a result of human disturbance

103 (Peterson and Watson 1998; Werneck *et al.* 2011) and large-scale environmental

104 changes such as drought and fire.

105   While the threats are clear, knowledge of the biogeography of the

106 Amazonia-Cerrado transition region is still insufficient to evaluate the threat to

107 biodiversity posed by the elimination of the transition forests. For example, in a

108 single evergreen seasonal forest site of the Xingu River Basin, almost all species

109 (94%) have an Amazonian distribution (Ivanauskas *et al.* 2004b; Lista de Espécies

110 da Flora do Brasil 2012), but it is not clear such a pattern is typical, and if so, why.

111 One explanation for a high contribution of Amazonian flora to these transitional

112 forests could be the frequent streams distributed across a general flat relief, so

113 reducing water stress compared to that encountered in seasonal forests of the

114 central highlands of Brazil in similar climate (Oliveira-Filho and Ratter 1995;

115 Ivanauskas *et al.* 2008).

116   While phytogeographic studies should consider the varied causes and

117 mechanisms potentially involved in geographic variation of biodiversity, one 'null'

118 explanation for species turnover may be simply that it is controlled by geographic

119 distance (Hubbell 2001). Space will be an important factor influencing the

120 separation of communities if all individuals of the same trophic guild are equivalent

121 competitors and have limited dispersal ability - this scenario results in a decreased

122 similarity between communities with increasing geographic distance (Hubbell

123 2001). However, other mechanisms, such as physical barriers (e.g., watersheds),

124 also act to control species distribution (Francis and Currie 1998) and may

125 determine the variation in floristic composition between communities (Bell 2001;

126 Condit *et al.* 2002). Thus, species migration may be favored by corridors shaped

127 by the forests accompanying streams and rivers, constituted into networks of

128 dendritic connections between waterways in a basin (Oliveira-Filho and Ratter

129   1995). According to this hypothesis, watersheds provide vital links between major

130   forested biomes (here, Atlantic and Amazonian forests), acting as routes of

131   species dispersal and hence genetic linkages connecting floras (Oliveira-Filho and

132   Ratter 1995) and faunas (Costa 2003; Ribas *et al*. 2011).

133   Alternatively or additionally to such historical explanations, environmental

134   conditions also frequently affect the occurrence of species. Thus, the presence of

135   a particular species at a site may be favoured by adaptations to the environmental

136   conditions and resources available there, for which the species has a range of

137   tolerances and requirements ('the ecological niche' of Hutchinson [1957]). If so,

138   areas sharing similar environmental conditions should share more species than

139   areas with differing environments (Gurevitch et al. 2009).

140   This study is intended to help inform conservation decisions by quantifying

141   the contributions to transitional forests made by species endemic to Brazil and,

142   more specifically, endemic to Cerrado and Amazonia domains. We addressed two

143   questions. 1) Does the Amazon and/or the Cerrado flora dominate the composition

144   of the sampling site? We expected a greater contribution of Amazonian flora

145   because, despite the region having a markedly seasonal climate, locally enhanced

146   water availability favours the occurrence of Amazonian species (Ivanauskas *et al*.

147   2008). 2) How do the forests vary in distribution and floristic composition? We

148   expected to find signatures of both 'neutral' and habitat-driven phytogeographic

149   variation. Thus, closer sites, independent of the watershed in which they happen

150   to be located (Xingu or Araguaia rivers), should have higher floristic similarity than

151   more distant areas because species turnover typically increases with geographic

152   distance (Hubbell 2001) and among different habitat types (e.g., Condit *et al*.

153   2002).

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METHODS

Study sites

158   In the transition zone between the Cerrado and Amazonian domains in

159 Brazil we sampled 10 sites, five located in the Xingu River Basin and five in the

160 Araguaia River Basin. These sites were distributed over a distance of up to 606

161 km (Table S1) and all lie within the central part of the arc of deforestation (Fig.1).

162 The climate, according to the Köppen classification, is Aw (tropical with a dry

163 winter) (Alvares *et al.* 2013), with highly seasonal annual average rainfall between

164 1500 and 1740 mm (Table 1). We selected primary forests with no obvious sign of

165 human actions. According to IBGE (2012), all studied forests were Evergreen

166 Seasonal, the five located in the Araguaia River Basin being Evergreen Seasonal

167 of the Lowlands (Floresta Estacional Sempre-Verde das Terras Baixas), and the

168 five of the Xingu River Evergreen Seasonal Submontane (Floresta Estacional

169 Sempre-Verde Submontana).

170   Data are curated within the ForestPlots database (Lopez-Gonzalez *et al.*

171 2011), where each forest has a unique site code. In this study, we applied new

172 codes to reflect the vegetation differences (ARA= Araguaia River Basin forest;

173 XIN= Xingu River Basin forest) (Table 1, Fig. 1).

174

Data collection

176   We sampled 1 ha in each site, and identified all trees with diameter at

177 breast height (DBH at 1.30 m above the ground) ≥ 10 cm. We identified the

178 species in the field by comparisons with herbarium (NX, UFMT, UB and IAN)

179 material of known identity, and with the help of specialists. After identification, the

180 material was incorporated into the Herbarium NX, Mato Grosso and Nova

181   Xavantina (Coleção Zoobotânica James Alexander Ratter). We determined the

182   classification of families based on APG III (Angiosperm Phylogeny Group 2009),

183   and assigned species names using the 'Flora of Brazil' database (Lista de

184   Espécies da Flora do Brasil 2012). We used this same database to determine the

185   occurrence of species in different Brazilian phytogeographic domains and Brazilian

186   endemic species.

187

188   **Data analysis**

189   We evaluated species distribution among forests based on a 'compound'

190   graph from the function of Landeiro *et al.* (2010) in *R* version 3.0.3 (R

191   Development Core Team 2014), where species and their abundances are

192   represented on the y-axis, ordered according to the weighted average, with the

193   ecological gradient represented on the x-axis. We analyzed the 48 most abundant

194   species (> 13 individuals) to help ensure confidence that results are not affected

195   by sampling issues of rarest taxa (see also Landeiro *et al.* 2010).

196   We also investigated the spatial patterns of species distribution by means of

197   Mantel tests in PASSaGE 2.0 (Rosenberg and Anderson 2011), using the

198   abundance species matrix. The distance coefficient used in this step was the

199   Czekanowski index (McCune and Grace 2002). Decisions on the presence of

200   spatial autocorrelation were made after 999 permutations.

201   To classify the forests based on species composition and their respective

202   abundances, we used TWINSPAN (Two-Way Indicator Species Analysis), with the

203   default option of the software PC-ORD 5.0 (McCune and Mefford 2006) to define

204   cut-off levels for 'pseudo-species' (McCune and Grace 2002).

205   We ordinated the plots based on a DCA (Detrended Correspondence

206   Analysis) in PC-ORD 5.0. We obtained the standardized length of the gradient,

207 assuming that a value greater than four standard deviations (SD) would indicate

208 complete replacement of species (Hill and Gauch 1980). Since the DCA is based

209 on chi-square distance, which is sensitive to rare species (McCune and Grace

210 2002), we removed these species, here understood as the singletons (species

211 with only one individual). The DCA, however, still showed excessive residuals in

212 the first axis, and therefore, we also eliminated species with only two individuals.

213 We submitted the reduced matrix (with 146 species) to a new DCA; here the

214 residuals were better distributed.

215

216 **RESULTS**

217 We sampled 4,944 trees, distributed among 257 species, 107 genera and

218 52 families in the 10 sampling sites (Table S2). Species diversity was

219 concentrated in a few families: 20% of families contained 60% of the species,

220 while on the other hand 35% (18 families) were represented by a single species

221 (Table S2, Table 2). In almost every sampling site, more than 50% of families were

222 represented by a single species, with the marginal exceptions of XIN-02 and ARA-

223 03 (48 and 45%) (Table 2). The richest families were Chrysobalanaceae (24

224 species), Fabaceae (22), Annonaceae (21), Melastomataceae (17), Moraceae

225 (14), Sapotaceae (13), Apocynaceae (11), Burseraceae and Myrtaceae (10 each)

226 and Lauraceae (9) (Table S2). The richest genera were *Licania* (13 species),

227 *Miconia* (12), *Aspidosperma*, *Hirtella* and *Xylopia* (10 each), *Pouteria* (9), *Inga* (8),

228 *Ficus* and *Ocotea* (7 each), *Casearia*, *Cecropia*, and *Trichilia* (5 each) (Table S2).

229 The proportion of genera with only one local species was also high, ranging from

230 68 to 100% in each forest (Table 2).

231 **Contribution of Amazonian and Cerrado floras to transitional forests**

232   The species recorded in this transitional region also occur in four Brazilian

233   phytogeographic domains, with 169 species in the Amazonian domain, 109 in the

234   Cerrado, 88 in the Atlantic Forest and 49 in the Caatinga domain. All 10 of our

235   sampling sites had more species from the Amazonian (from 71 to 100%) than the

236   Cerrado domain (42 to 85%). The two most southerly forests (ARA-01 and ARA-

237   02), most distant from the Amazonian domain, showed the smallest difference

238   between the occurrence of the Amazonia and Cerrado species, while the most

239   northerly forests (ARA-03 and ARA-04) were dominated by typical Amazonian

240   species (Table 2). A total of 29 of the sampled species were endemic to Brazil,

241   representing 16% of taxa identified to the species level. Of these, seven occur only

242   in the Amazonian and in the Cerrado domains and seven in Amazonia alone

243   (Table S2). Every sampling site plot included at least two species endemic to

244   Brazil (Table 2).

245

246   **Spatial distribution, watersheds and floristic composition**

247   Considering the amplitude of species occurrence among sampling sites, 43

248   (17%) occurred in five or more sites, while 143 (55%) were restricted to just one

249   forest, especially ARA-02 (19 unique species), XIN-04 and ARA-04 (20 unique

250   species each) and ARA-05 (21 unique species) (Table S2, Table 2). The greatest

251   degree of species sharing was observed in the plots close to the Araguaia River

252   Basin (ARA-01 and ARA-02) (Table S2). However, the progressive substitution of

253   species across space is evident throughout the study areas (Fig. 2). Only 11

254   species were recorded with high abundance (> 70 individuals) in the forests of

255   both Xingu and Araguaia watersheds: *Tapirira guianensis* Aubl., *Pseudolmedia*

256   *macrophylla* Trécul, *Trattinnickia glaziovii* Swart, *Jacaranda copaia* (Aubl.) D. Don,

257   *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 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.

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 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 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 and Amaral 2004; Oliveira *et al.* 2008), as well as in seasonal forests (Ivanauskas *et al.* 2004a; Marimon *et al.* 2006; Kunz *et al.* 2008), 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

310 dendritic network of rivers that act as bridges, allowing species from Amazonian

311 and Atlantic domains to migrate deep into areas that would otherwise be

312 climatically challenging for such taxa (Oliveira-Filho and Ratter 1995). These

313 findings therefore reinforce the transitional aspect of the study sites, and confirm

314 the ecological importance of these key families in the composition and

315 characterization of the transitional zone flora.

316 The finding that families with most species also have the highest

317 abundance of individuals is not unexpected (Campbell *et al*. 1986; Ivanauskas *et*

318 *al*. 2004a). Families richer in species and/or more abundant than others are

319 capable of better exploiting the environment, because they have adaptive

320 characteristics (Tello *et al*. 2008). The large number of families and genera

321 represented by only one species in each community on the other hand highlights

322 the great taxonomic diversity of the studied forests.

323 *Licania*, *Miconia*, *Pouteria*, *Inga* and *Ocotea*, which are among the richest

324 genera in this study, are well represented in different vegetation types of the

325 transition zone (Marimon *et al*. 2006; Kunz *et al*. 2008; Araujo *et al*. 2009) and also

326 in the distant, terra firme forests of central Amazonia (Oliveira *et al*. 2008). This

327 overlapping of genera from different vegetation sources further confirms the

328 transitional aspect of southern Amazonia (Oliveira-Filho and Ratter 1995). The fact

329 that most species belong to the Amazonian domain confirms our expectation that

330 transitional forest tree floristics are more strongly influenced by the Amazon than

331 by the Cerrado domain, especially for forests that occur in the northern portion of

332 the studied area.

333 This information is not new to ecology, but it is new for the vegetation of the

334 study sites and has an important consequence for conservation measures. The

335 genus-level approach of this study helped reinforce which biome has greater

336 contribution to floristic composition, and also confirmed that differences in species

337 diversity are reflected at the genus level, as seen elsewhere (Qian 1999; Condit *et*

338 *al.* 2005).

339

340 **Spatial separation and watersheds**

341 The third division of TWINSPAN and the second axis of DCA show that

342 there may be a spatial effect in the dissimilarity between the communities,

343 especially in the Araguaia Basin. However, this effect was not a clear pattern; if it

344 had been, we expected that ARA-01 and ARA-02 would be more similar to the

345 forests of the Xingu Basin, because they are closer to each other, but this was not

346 the case. Thus, we emphasize on the results of the first division of TWINSPAN

347 and the first DCA axis.

348 The Mantel test further showed that geographic distance does not drive the

349 spatial turnover of species and the floristic dissimilarity between these sites,

350 suggesting that factors associated with habitat type appear to be involved (Condit

351 *et al.* 2002; Gurevitch *et al.* 2009). Why though should the abundant species in the

352 forests of Mato Grosso State also be shared with those of the forests of southern

353 Pará, given the great geographic distance among the sites? These data suggest

354 that other geographical processes have allowed these taxa to overcome dispersal

355 limitation. Thus, and in support of Oliveira-Filho and Ratter (1995) in discussing

356 the origin of the forests of Central Brazil, it appears that it is the north-south

357 hydrological network associated with the Araguaia River Basin that provides the

358 ultimate explanation for why these distant forests are floristically more similar to

359 each other than they are to the much geographically closer vegetation in the Xingu

360 River Basin.

361

362 **Conservation**

363   Conservation of the transition zone vegetation is of paramount importance

364 for three reasons. First, ongoing land-use processes have already destroyed most

365 natural vegetation here (Marimon *et al.* 2014). Second, both Amazonian and

366 Cerrado vegetation are highly diverse (Castro *et al.* 1999; Fiaschi and Pirani 2009;

367 Gentry 1988). And third, this transitional region connects the floras of the Cerrado,

368 the Atlantic Forest, and Amazon Rainforest (Méio *et al.* 2003; Oliveira-Filho and

369 Ratter 1995; see also study on fauna: Costa 2003), and thus can potentially

370 provide critical habitat space and corridors for the migration that could help to

371 partly mitigate the great biological challenge that global climate change poses for

372 communities of the neotropics (Loarie *et al.* 2009).

373   To emphasize the relevance of conserving the communities and

374 ecosystems of the transition zone, it is important to also take into account the high

375 faunal diversity of the region. On the banks of the tributaries of the Mortes River

376 (Araguaia Basin) 81 species of birds living in forests and *cerrado* (Sick 1955), 238

377 species of birds and 57 species of non-flying mammals were recorded in some

378 forests of the Xingu Basin (Oliveira *et al.* 2010). Forests of the Araguaia basin

379 have been considered as shelters and food source for several species of small

380 mammals, and the mosaic of habitats generated by the Amazonia-Cerrado contact

381 may determine species diversity in this region (Lacher and Alho 2001; Oliveira *et*

382 *al.* 2010; Rocha *et al.* 2014). Thus, conservation of the vegetation becomes more

383 urgent and necessary as it will also benefit the rich fauna of this important

384 transitional area (Sick 1955; Lacher and Alho 2001; Rocha *et al.* 2014).

385   Our eco-floristic results reinforce the need for serious conservation action

386 here. We found that one in six of the species identified in these forests are

387 endemic to Brazil, and that most of these endemic species are also endemic to the

388 two phytogeographic domains (Cerrado and Amazonian). We also conclude that

389 most of the species must be either very rare and have restricted distribution, or

390 both, as almost three-fifths of the tree taxa were only found in one of the 10

391 studied sites, suggesting the existence of a large and heterogeneous mosaic of

392 plant communities in the Amazonia-Cerrado transition. The removal and

393 fragmentation of large areas due to agricultural activities may therefore already be

394 leading to the disappearance of species and unique assemblages, before they can

395 even be adequately documented.

396   Furthermore, our finding that the taxonomic coherence within watersheds

397 trumps effects of geographic proximity highlights the importance of considering

398 whole watersheds in conservation efforts. As a simple but important example,

399 establishing a single large reserve around the Xingu watershed may be less

400 effective in conserving maximal tree diversity than would ensuring that the same

401 size of area captures vegetation lying within both the Xingu and Araguaia

402 watersheds.

403   Tree composition in this complex transition zone appears to be partly driven

404 by subtle environmental patterns at the watershed scale, suggesting that the

405 biogeography of the major neotropical domains is still to be well understood.

406 Further investigations should focus on better understanding of how environmental

407 factors determine the species composition and distribution across the transitional

408 regions. This information will help improve the ability of conservation efforts to

409 protect floristic and structural diversities in the communities of the vast Amazonia-

410 Cerrado contact zone. This is especially important in light of the intense threat

411 facing this region due to its close alignment with the arc of deforestation.

412

Supplementary material

To view supplementary material for this article, please visit

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678

679

680 **TABLE AND FIGURE**

681

682 **Table 1** Geographic location, forest types, geomorphological units (GU),

683 morphostructural domains (MD) and precipitation data of the 10 studied forests in

684 the Cerrado-Amazonia transition zone, Brazil. Precipitation data from: [a]Marimon *et*

685 *al.* (2010), [b]Moraes *et al.* (2005) and [c]Balch *et al.* (2008). States: MT= Mato

686 Grosso; P= precipitation; PA= Pará.

| Codes of sites (ForestPlots code) | Location | | | | Soil types (FAO 2006) | GU/MD (IBGE 2015) |
	County	Lat (S)	Long (W)	P (mm)		
ARA-01 (VCR-01)	Nova Xavantina-MT	14°49'	52°09'	~1,500[a]	Plinthosol	Alto Araguaia depression/ quaternary sedimentary deposits
ARA-02 (VCR-02)	Nova Xavantina-MT	14°49'	52°10'	~1,500[a]	Plinthosol	Alto Araguaia depression/ quaternary sedimentary deposits
ARA-03 (SAT-01)	Santana do Araguaia-PA	09°47'	50°25'	~1,600[b]	Ferralsol	Santana do Araguaia depression/ neoproterozoic cratons
ARA-04 (SAA-01)	Santana do Araguaia-PA	09°38'	50°27'	~1,600[b]	Ferralsol	Santana do Araguaia depression/ neoproterozoic cratons
ARA-05 (SAA-02)	Santa Terezinha-MT	09°50'	50°27'	~1,600[b]	Ferralsol	Santana do Araguaia depression/ neoproterozoic cratons
XIN-01 (TAN-02)	Querência-MT	13°05'	52°22'	~1,740[c]	Ferralsol	Plateau of Xingu headwaters/ quaternary sedimentary deposits
XIN-02 (TAN-04)	Querência-MT	12°55'	52°22'	~1,740[c]	Ferralsol	Plateau of Xingu headwaters/

|						
						quaternary sedimentary deposits
XIN-03 (TAN-03)	Querência-MT	12°49'	52°21'	~1,740[c]	Ferralsol	Plateau of Xingu headwaters/ quaternary sedimentary deposits
XIN-04 (FLO-01)	Ribeirão Cascalheira-MT	12°48'	51°51'	~1,740[c]	Ferralsol	Plateau of Xingu headwaters/ quaternary sedimentary deposits
XIN-05 (FLO-02)	Ribeirão Cascalheira-MT	12°45'	51°52'	~1,740[c]	Ferralsol	Plateau of Xingu headwaters/ quaternary sedimentary deposits

687

688

689 **Table 2.** Floristic parameters of 10 studied forests in the Cerrado-Amazonia

690 transition zone, Brazil. NI = Number of individuals; SPAM and SPCE = number of

691 species occurring in the Amazonian and Cerrado domains, respectively,

692 considering those identified at the species level; SPED = Brazilian endemic

693 species; SPEX = number of unique species to the respective site. Percentage

694 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-	40	22	11	5	31	40	22 (71)	32 (80)	485

01	(77)	(42)							
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
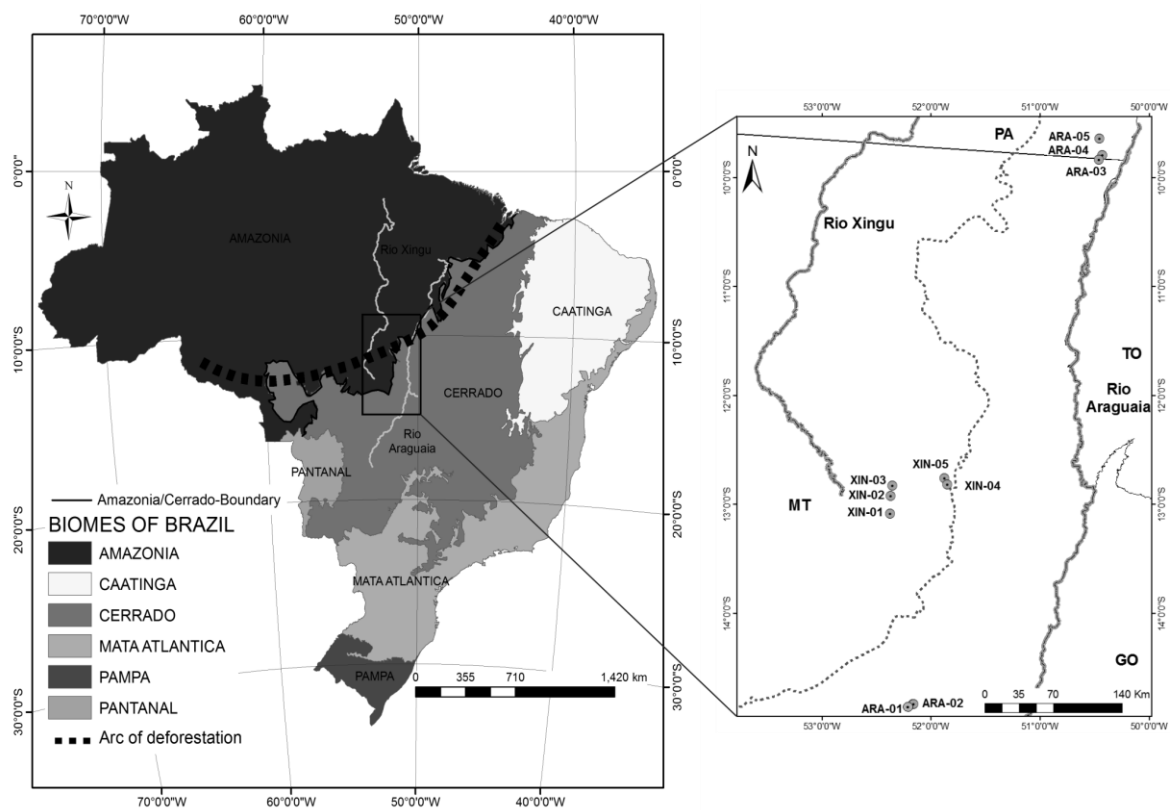
Figure 1 Amazonia-Cerrado transition zone and the arc of deforestation in Brazil. The right box indicates the study area and dashed line indicates the boundary between the watersheds of the Xingu River and the Araguaia River.
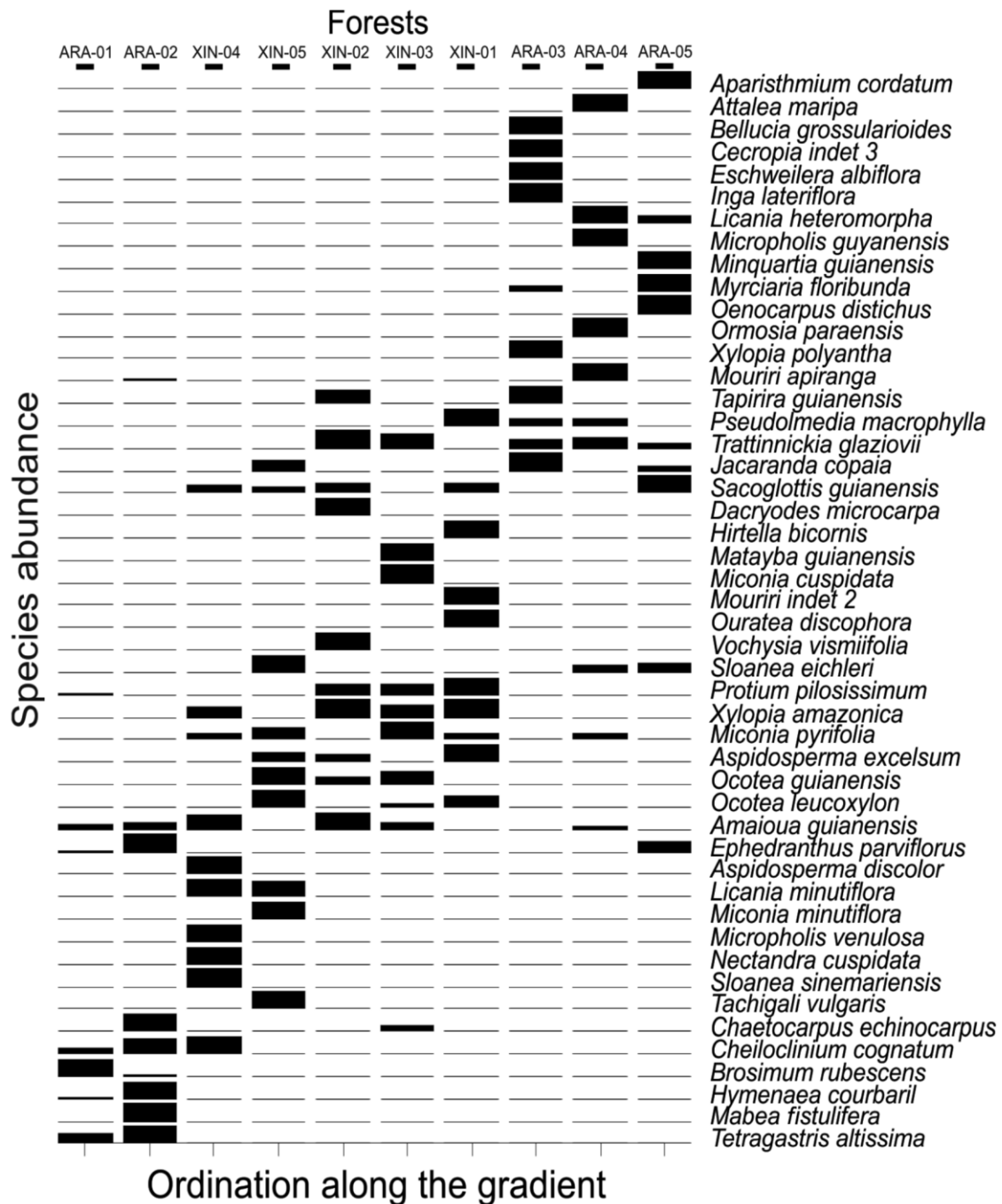
Figure 2 'Compound' graph of species distribution (relative abundance) based on the weighted average according to the site in the Amazonia-Cerrado transition zon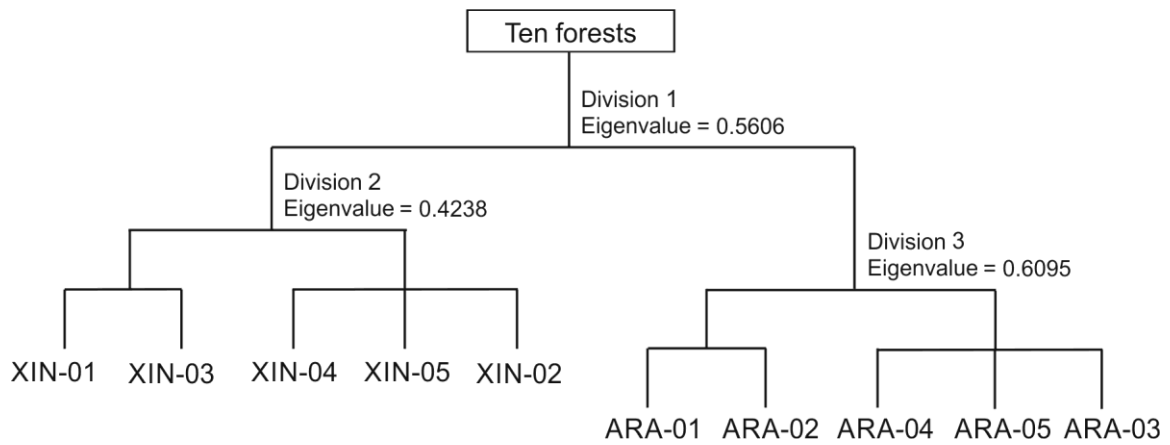e, Brazil. At the top of the graph, from left to right, the first two and last three bars are ARA; other bars are XIN. Sites plotted in a latitudinal gradient (from left: southern forests, nearest the Cerrado domain, to right: northern forests, near the Amazonian domain).
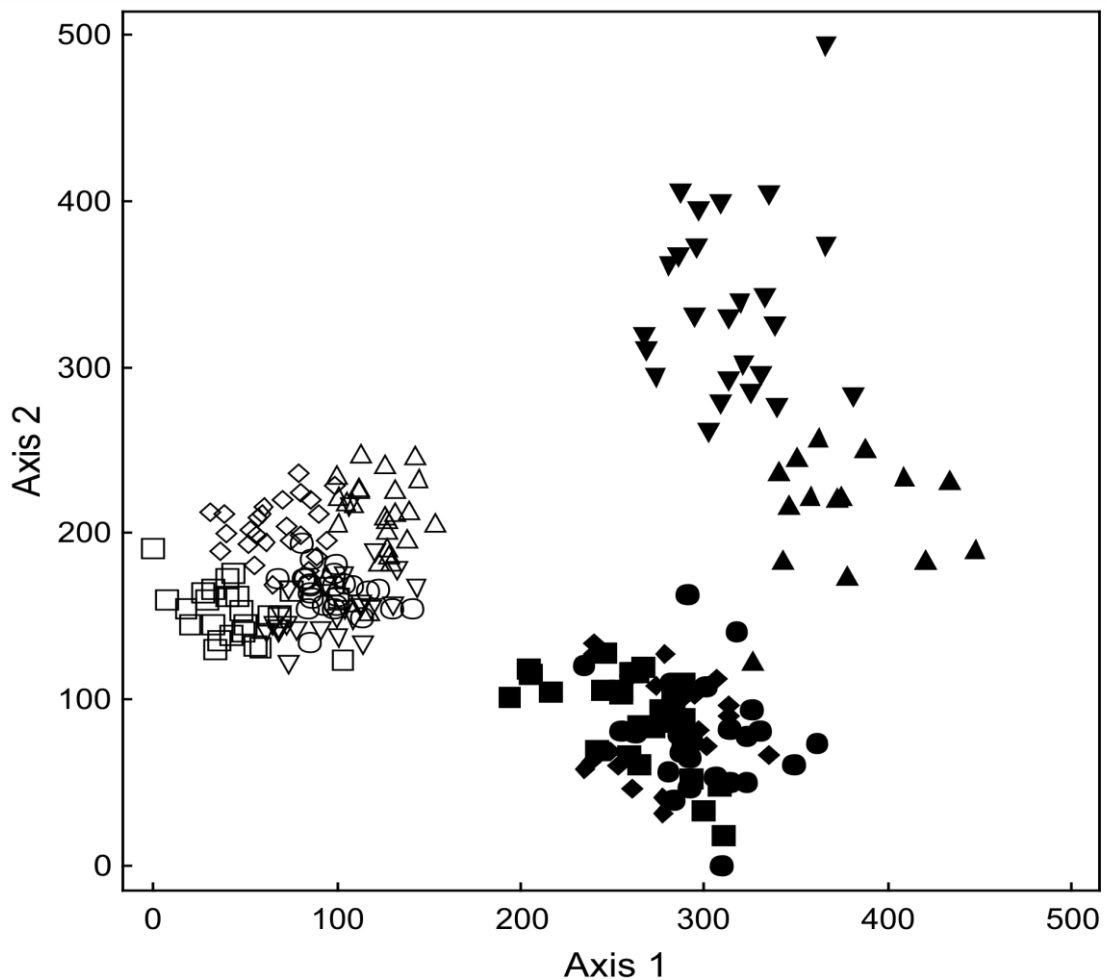
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Figure 3 Floristic classification of the 10 studied forests in the Amazonia-Cerrado transition zone, based on the TWINSPAN method.

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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,

717 ●ARA-04 and ■ARA-05: Araguaia River Basin forests; ○XIN-01, ◇XIN-02,

718 □XIN-03, △XIN-04 and ▽XIN-05: Xingu River Basin forests.

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