

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 TWINSPLAN 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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52 INTRODUCTION

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

60 Different environmental factors may determine transitions between
61 phytogeographic domains, depending on the scale being considered. Tropical
62 forests generally occur in regions with wetter climate (Schwartz and Namri 2002)
63 and lower precipitation seasonality than savannas (Staver *et al.* 2011). Climatic
64 variation acts at broad scales, with rainfall seasonality in particular determining
65 large-scale differentiation of vegetation patterns, such as the Amazonian and
66 Cerrado domains (Ab'Saber 2003; Lehmann *et al.* 2011; Staver *et al.* 2011).

67 In regions with intermediate rainfall (1,000 to 2,500 mm) and average
68 seasonality (<7 months), forest and savanna may coexist as alternative stable
69 states, depending on fire frequency (Staver *et al.* 2011; Murphy and Bowman
70 2012). At smaller scales, edaphic factors play a greater role in determining the
71 species composition of plant communities (Askew *et al.* 1970). Additionally, fire,
72 resource availability and species traits can influence the occurrence of certain
73 vegetation types (Hoffmann *et al.* 2012). Topographic features, such as the
74 groundwater level, also determine the occurrence of forest or savanna (Murphy
75 and Bowman 2012; Silva 2015).

76 Here, our primary aim was to investigate large-scale floristic diversity and
77 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 phylogeographic
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).

154

155

156 METHODS**157 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

175 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) \geq 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*

258 Engl., *Miconia pyrifolia* Naudin, *Amaioua guianensis* Aubl., *Chaetocarpus*
259 *echinocarpus* (Baill.) Ducke and *Cheilochlinium cognatum* (Miers) A.C.Sm. (Fig.2).
260 Overall, the most abundant species were preferentially found in particular
261 watersheds (i.e., abundant in either Rio Xingu or Rio Araguaia watersheds, but
262 rarely in both).

263 Two floristic groups emerge from TWINSPAN (Fig. 3), the first composed of
264 seasonal forests of the Xingu River Basin (XIN-01, XIN-02, XIN-03, XIN-04 and
265 XIN-05), and the second of seasonal forests (ARA-01, ARA-02, ARA-03, ARA-04
266 and ARA-05) of the Araguaia River Basin (Fig. 3). The first division (eigenvalue =
267 0.56) separated the Araguaia from the Xingu forests, while in the second division
268 (eigenvalue = 0.42) two new groups were revealed: one with XIN-01 and XIN-03
269 and the other by XIN-02, XIN-04 and XIN-05 (Fig.3). Only in the third division
270 (eigenvalue = 0.61), were the southern Araguaia forests (ARA-01 and ARA-02)
271 separated from the other Araguaia forests far to the north.

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

283

284 **DISCUSSION**

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

293

294 **Influence of phytogeographic domain on floristic composition**

295 The families Chrysobalanaceae, Fabaceae, Annonaceae and Sapotaceae,
296 the species-richest in this study, are common in Amazonia (Oliveira-Filho and
297 Ratter 1995). These are among the pan-Amazon dominant groups (ter Steege *et al.*
298 *et al.* 2006), being also among the most speciose in Amazonian upland *Terra Firme*
299 forests 1000 km to the north of our sites and more than 2000 km to the west
300 (Phillips *et al.* 2003; Lima-Filho *et al.* 2004; Oliveira and Amaral 2004; Oliveira *et al.*
301 *et al.* 2008), as well as in seasonal forests (Ivanauskas *et al.* 2004a; Marimon *et al.*
302 2006; Kunz *et al.* 2008), and savanna woodland (Marimon-Junior and Haridasan
303 2005; Marimon *et al.* 2006) at the southern edge of the Amazonian domain.
304 Fabaceae, in particular, though, also have high richness in the Cerrado domain
305 (Sano *et al.* 2008). Sapotaceae, Burseraceae and Moraceae are typical of the
306 Amazonian domain, and Melastomataceae, Myrtaceae and Lauraceae, are more
307 speciose in Atlantic moist forests, with Annonaceae featuring strongly in both
308 domains (Pinto and Oliveira-Filho 1999). The occurrence of the humid tropical
309 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 (Méo *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 phylogeographic 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

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426

427 **Supplementary material**

428 To view supplementary material for this article, please visit

429 <https://www.cambridge.org/core/journals/environmental-conservation>

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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: ^aMarimon *et al.*
 685 *et al.* (2010), ^bMoraes *et al.* (2005) and ^cBalch *et al.* (2008). States: MT= Mato
 686 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'	~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/

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

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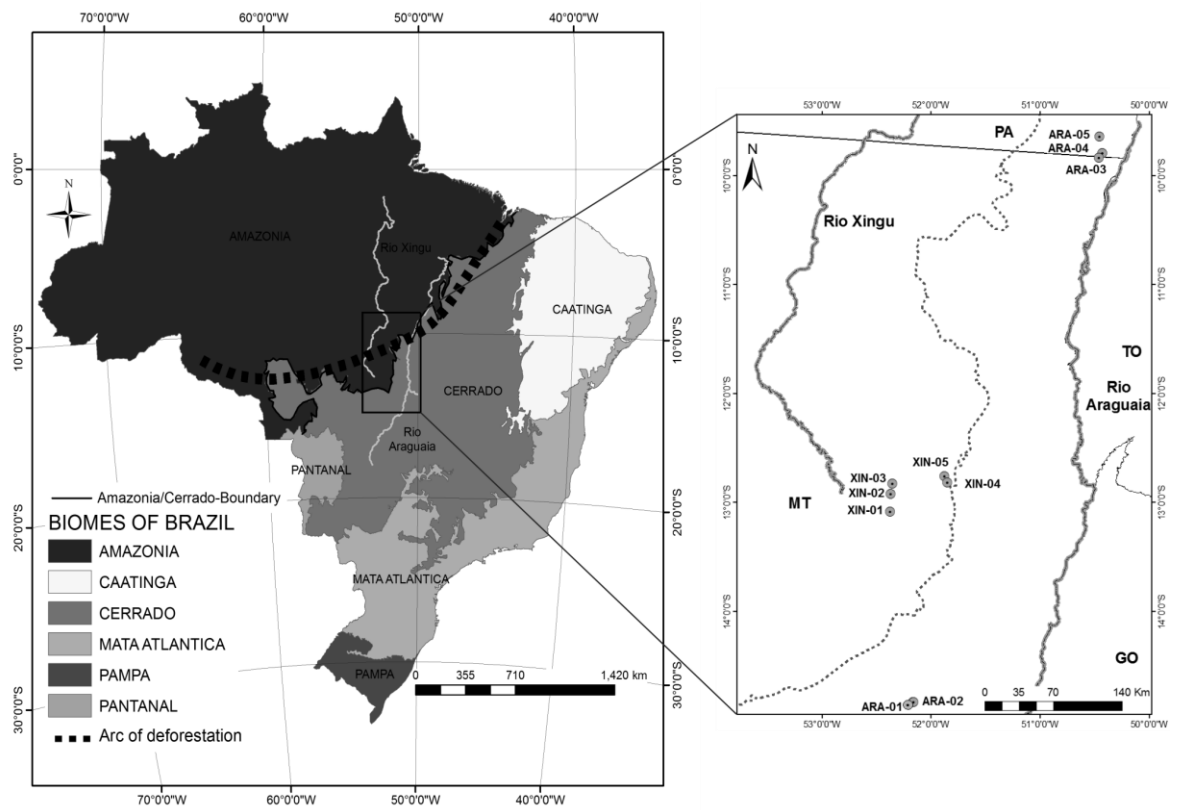
689 **Table 2.** Floristic parameters of 10 studied forests in the Cerrado-Amazonia
690 transition zone, Brazil. NI = Number of individuals; SPAM and SPCE = number of
691 species occurring in the Amazonian and Cerrado domains, respectively,
692 considering those identified at the species level; SPED = 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

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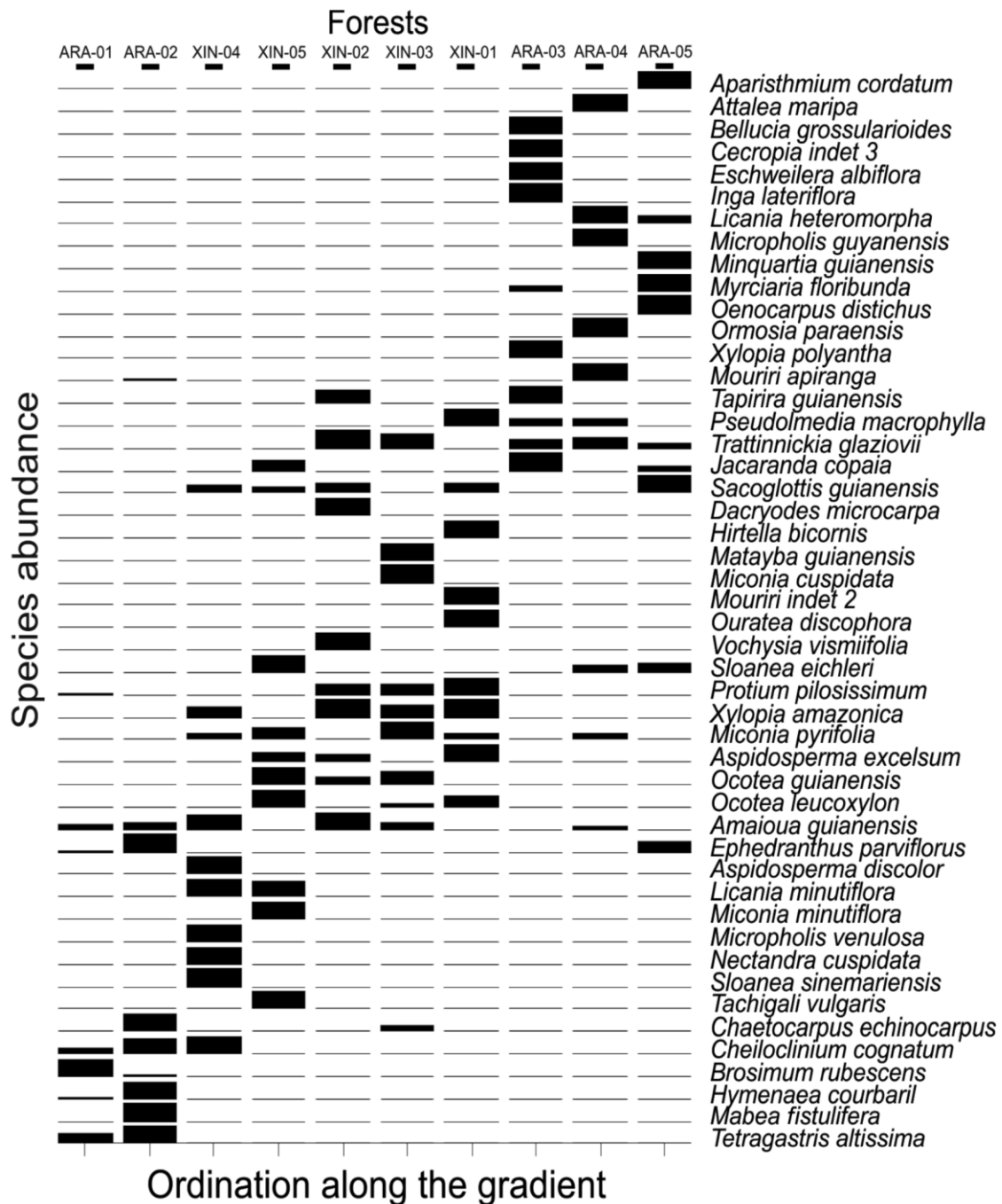
697

698 **Figure 1** Amazonia-Cerrado transition zone and the arc of deforestation in Brazil.

699 The right box indicates the study area and dashed line indicates the boundary

700 between the watersheds of the Xingu River and the Araguaia River.

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702

703 **Figure 2** 'Compound' graph of species distribution (relative abundance) based on

704 the weighted average according to the site in the Amazonia-Cerrado transition

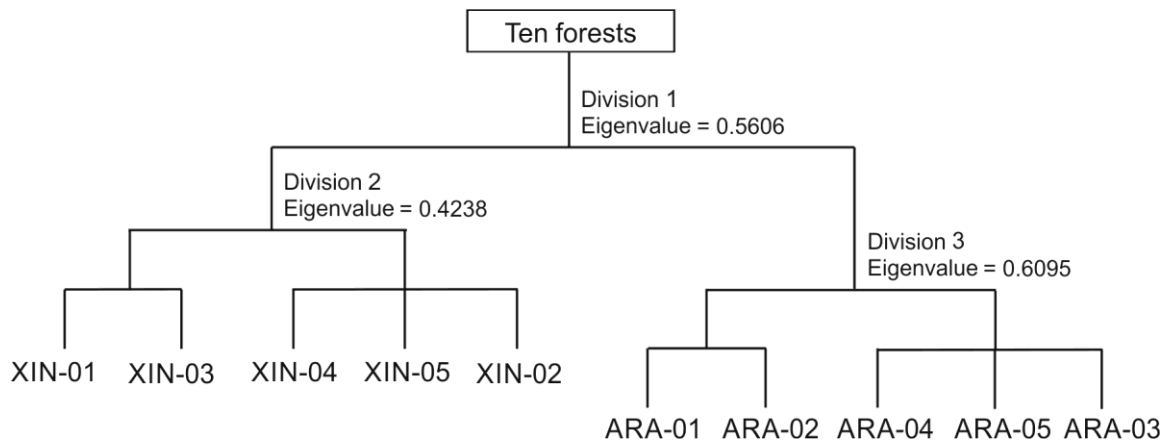
705 zone, Brazil. At the top of the graph, from left to right, the first two and last three

706 bars are ARA; other bars are XIN. Sites plotted in a latitudinal gradient (from left:

707 southern forests, nearest the Cerrado domain, to right: northern forests, near the

708 Amazonian domain).

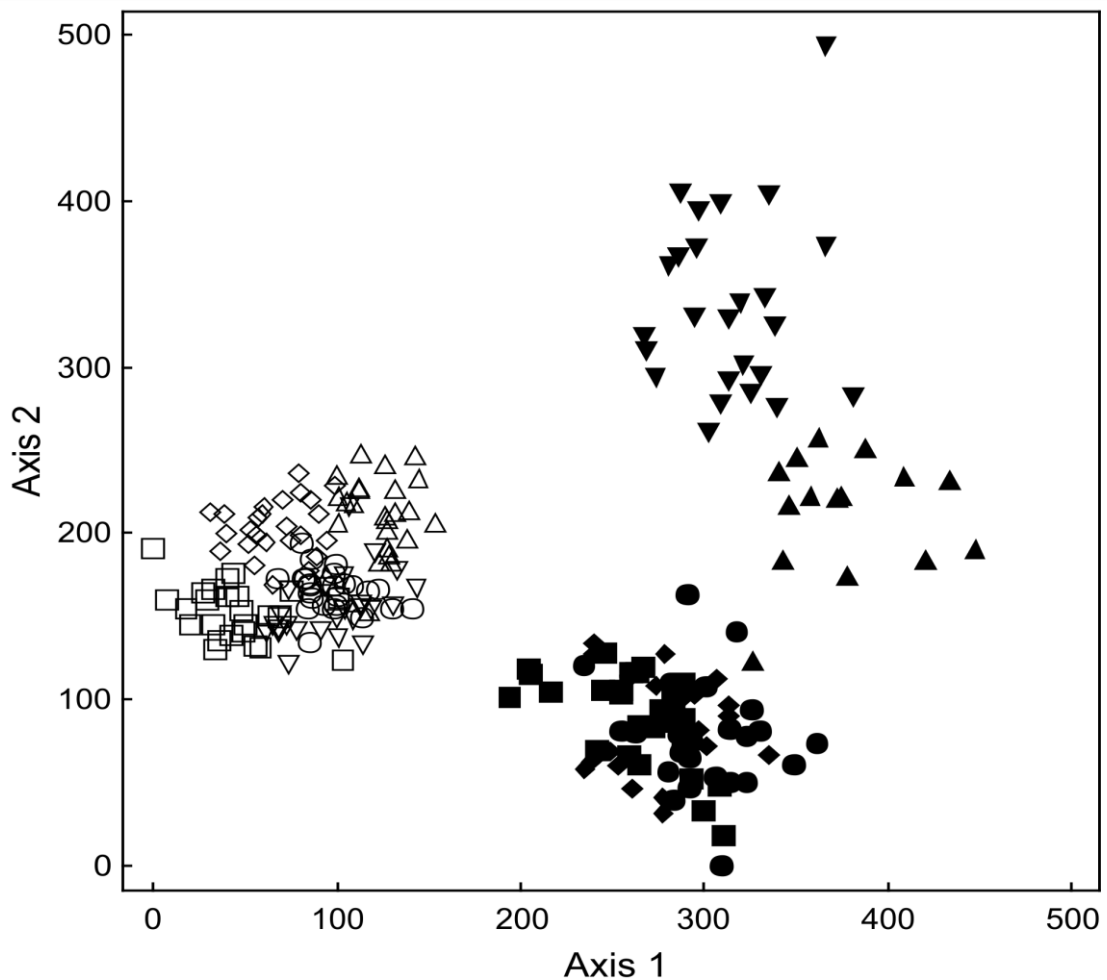
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710

711 **Figure 3** Floristic classification of the 10 studied forests in the Amazonia-Cerrado
 712 transition zone, based on the TWINSpan method.

713



714

715 **Figure 4** Ordination by DCA summarizing the floristic patterns of 10 forests in the
 716 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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