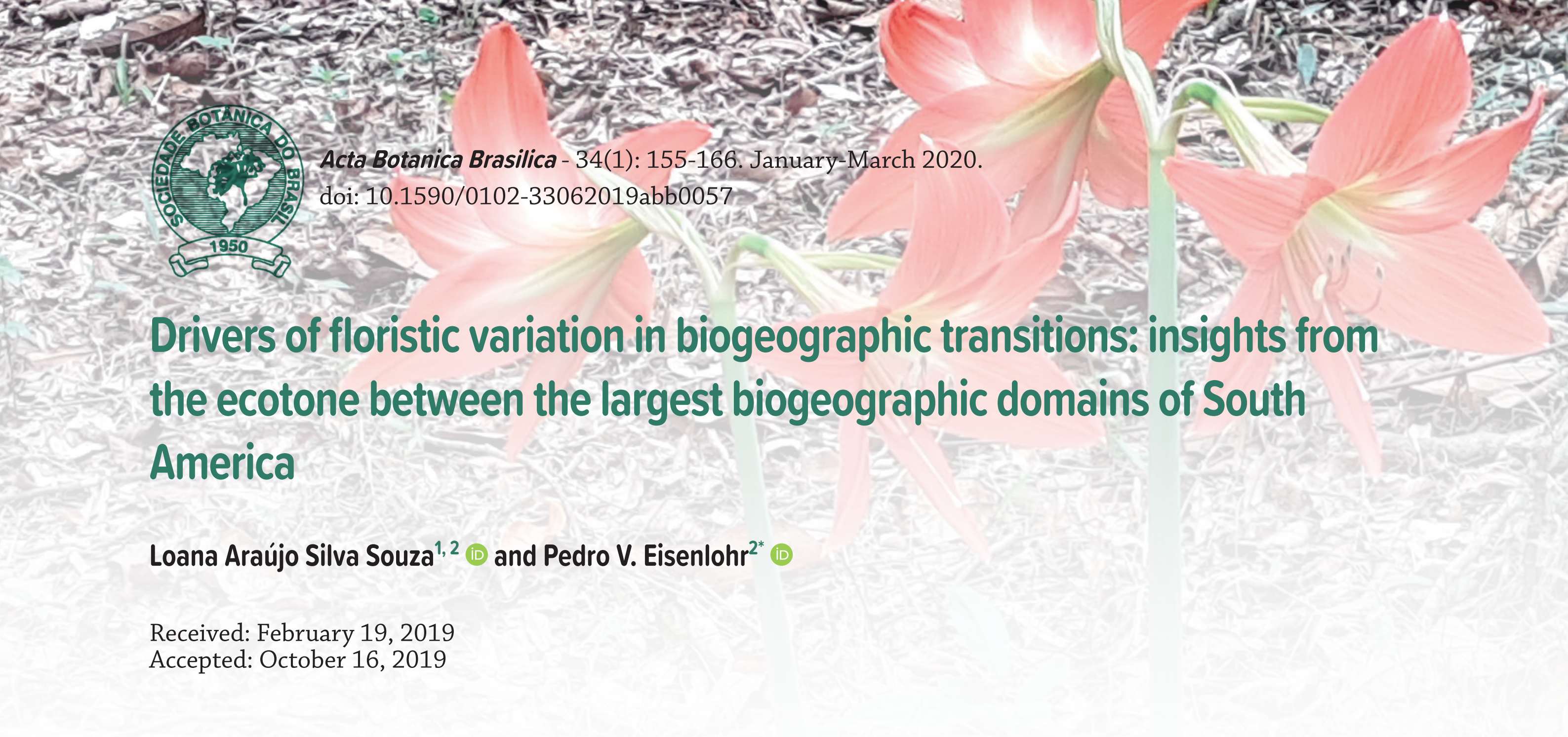

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Drivers of floristic variation in biogeographic transitions: insights from the ecotone between the largest biogeographic domains of South America

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ABSTRACT

Ecological transitions usually represent vulnerable ecosystems and high biodiversity. Investigating their drivers is important from both biogeographic and conservationist perspectives. One of these transitions is situated between the two largest biogeographic domains of South America — the Amazon and the Cerrado. We evaluated variation in tree floristic composition throughout this transition and assessed which factors explain this variation. We used 17,240 records of occurrences of 2,530 tree species from the NeotropTree database. We investigated variation in floristic composition using UPGMA cluster analysis with bootstrap resampling and NMDS ordination, and modeled the distribution of species in relation to environmental and spatial predictors by means of transformation-based Redundancy Canonical Analysis (tb-RDA) and variance partitioning. We found four general floristic groups: 1) flooded forests; 2) white sand dwarf-forests; 3) savannic and dwarf forests; and 4) non-flooded forest types. Floristic variation along the transition was influenced by the environment, especially variables related to fire and soil moisture, and by space, especially variables acting on broader scales. Correspondence between the environmental heterogeneity found throughout the transition and our results demonstrates once again the importance of conserving biogeographical transition zones in general, and the most comprehensive of South America in particular.

Keywords: biogeographical patterns, ecological transitions, ecotone, floristic variation, tb-RDA, variance partitioning, vegetation types

Introduction

Transition zones among ecological communities, ecosystems and ecoregions, also known as ecotones (*sensu lato* Risser 1995), may occur at multiple spatial scales, from vegetation types to biogeographic regions (Longman & Jeník 1992; Risser 1995; Hufkens *et al.* 2009; Kark 2013). Regardless of the scale, transition zones usually cover vulnerable ecosystems that are relevant to the organisms flow (Yarrow & Marín 2007), with high biodiversity and presence of rare species (Smith *et al.* 2001; Araújo 2002). Transitions between forests and savannas, for example, show a high variety of vegetation types, which have different characteristics, floristic composition and ecosystem functions (Bueno *et al.* 2018; Dexter *et al.* 2018). It is precisely in such transitions that changes in the species distribution range have been increasingly observed, being associated not only to historical and isolation factors, but also to environmental heterogeneity as global changes intensify (Poloczanska *et al.*

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2013; Neves *et al.* 2015). In fact, more robust predictions about the impacts of climate change in biogeographical transitions require approaches that shed light on important ecological aspects (Sommer *et al.* 2018).

An extensive transitional region (> 6,000 km) is located between the two largest biogeographic domains of South America – Amazon, predominantly occupied by forests, and Cerrado, predominantly occupied by savannas –, presenting a complex mosaic of vegetation landscapes composed of different vegetation types, such as dense or open forests, deciduous, semideciduous or evergreen upland forests, riparian forests, savannas and rupestrian environments (Oliveira-Filho & Ratter 1995; 2002; IBGE 2004; Marimon *et al.* 2006; Torello-Raventos *et al.* 2013). Floristically, the Cerrado-Amazon transition presents high complexity, because there are species that are widespread throughout the Cerrado (such as *Qualea grandiflora*; Marimon *et al.* 2006), typical Amazon species (such as *Tetragastris altissima* and *Xylopia amazonica*; Marimon *et al.* 2006), and there are also contributions of Atlantic species (Méio *et al.* 2003). This is a transition encompassing more than 1,500 tree and tree-like species (*i.e.,* plants that are able to grow taller than 3 m in stature without climbing or leaning against other plants; Oliveira-Filho 2017), being 89 of them considered as priority for conservation due to a combination of regional responsibility, habitat vulnerability and local rarity (Maciel *et al.* 2016). These characteristics, coupled with the lack of geographical barriers, such as large mountain ranges, indicate that patterns associated with habitat type appear to be involved in floristic similarity (*e.g.*, Morandi *et al.* 2016).

Variations of vegetation patterns are usually linked, but not exclusively, to deterministic environmental predictors (Kunz *et al.* 2009; Lippok *et al.* 2013), such as climate (Costa & Pires 2010; Hirota *et al.* 2010; Vourlitis *et al.* 2014), in special the different precipitation patterns (Hutyra *et al.* 2005; Staver *et al.* 2011; Marimon *et al.* 2014). In more local scales, the influence of soil properties (Murphy & Bowman 2012; Pontara *et al.* 2016) and the role of fire (Hoffmann *et al.* 2012) should be considered as important drivers of floristic variations. Together, these predictors are considered as modulators of niche-based processes in metacommunities (*e.g.*, Tilman 1982; Chase & Leibold 2003; Shipley *et al.* 2012). For the Amazon-Cerrado transition, evidences show a significant correlation between precipitation patterns and their forest cover (Debortoli *et al.* 2016) and the influence of different soil attributes on vegetation structure, including species diversity (Rodrigues *et al.* 2016). In stable and alternative states of climate, soil and natural fire, this transition undergoes a progressive replacement of its savanna vegetation by forest formations (Maracahipes-Santos *et al.* 2018), but the existence of various types of substrates and the greater presence of fire caused by anthropogenic processes tends to promote changes in the vegetation because their effects cause a decrease in density, basal area and, consequently, in biomass (Marimon *et al.* 2006; Bueno *et al.* 2018; Maracahipes-Santos *et al.* 2018). Thus, these three components (climate, soil and fire) seem to be important drivers of vegetation changes in the Cerrado-Amazon transition.

Spatial processes may also be important drivers of vegetation patterns. Spatial predictive component is often associated (at least in part) to neutral factors, such as dispersion limitation (Gilbert & Lechowicz 2004; see, however, Diniz-Filho *et al.* 2012; Neves *et al.* 2015), and can act on various scales (Borcard *et al.* 2011; Dray *et al.* 2012), allowing species to be sorted along environmental gradients (Leibold *et al.* 2004). The similarity distance-decay of species occurrence, however, can be explained by two different components of variation: the "pure" spatial processes and the shared fraction between space and environment, sometimes referred to as "spatially structured environment" (Diniz-Filho *et al.* 2012 and references therein). Dissociating these two components is essential to ensure an accurate assessment of community patterns and their rules (Diniz-Filho *et al.* 2012; Clappe *et al.* 2018). In the Cerrado-Amazon transition, besides evidence on environmental processes acting on vegetation patterns as pointed out above, we have also evidence regarding the influence of spatial processes. For example, the floristic composition and structure of three vegetation types (forested savanna, dense savanna and typical savanna) of the Cerrado-Amazon transition would be determined by the space interacting with the environment (Maracahipes-Santos *et al.* 2017). Forests closer to water bodies were demonstrated to be more similar to each other than the more distant ones, with dominance by Amazon species due to the greater presence of soil moisture (Morandi *et al.* 2016). In both cases, space seems to act more decisively on vegetation patterns when coupled with environmental variables.

Thus, there are clues pointing to the predictive capacity of the environmental and spatial components on the tree vegetation patterns of the Cerrado-Amazon transition, but little is known about the magnitude of the influences of different environmental determinants and different scales of spatial processes. Moreover, the Amazon-Cerrado transition coincides with the "Deforestation Arc", a region known for its high environmental degradation. Most of the natural forest vegetation has already been removed (Fearnside 2005), which resulted from deforestation for agriculture (Ivanauskas *et al.* 2004; Araujo *et al.* 2009). Anthropogenic fires (Fearnside 2005) and severe drought events (Lewis *et al.* 2011; Marengo *et al.* 2011) can cause losses of carbon storage, changes in regional precipitation patterns and river discharge, resulting in the death of species that are not resistant to this type of drastic change (Davidson *et al.* 2012). Such issues, in addition to the floristic relevance of the region, make it important to generate theoretical and empirical support that could be capable of facilitating conservation decisions in these environments (Gaston 2000; Cestaro & Soares 2004;

Machado *et al.* 2004). Recognizing species that characterize each vegetation landscape and investigating the drivers of floristic patterns for the whole extension of this transition are of utmost importance for conservation and will bring fundamental knowledge to better understand it, thereby favoring public policies and restoration programs that could act to reduce the impact of human pressure.

We took advantage of a comprehensive database (NeotropTree; Oliveira-Filho 2017) to investigate floristic similarities, to assess indicator species of different habitats and to model the influence of environmental and spatial variables on patterns of floristic variations along this transition. Our hypotheses and predictions were two-fold: i) the floristic composition of most typical forest types of the Amazon Domain would be notably distinct to the floristic composition of savanna types, which are more typical of the Cerrado Domain, thereby confirming the influence of habitat type suggested by Morandi *et al.* (2016). If this would be true, and if this would be the predominant pattern along this transition, we can predict that soil and fire variables are powerful drivers of phytogeographic patterns along this transition, because they are widely recognized as decisive actors in such scales (*e.g.*, Hoffmann *et al.* 2012; Murphy & Bowman 2012); ii) since there are no large geographic barriers throughout the transition investigated, we expected to find no severe dispersion constraints over large distances. If this would be true, we can predict to find a reduced role of the "pure" spatial component acting on broader scales. In this case, since dispersal occurs over restricted spatial scales, similarity in community composition declines with increasing distance (Condit *et al.* 2002; Soininen *et al.* 2007; Page & Shanker 2018), and spatial variables representing finer scales (Borcard *et al.* 2011; Dray *et al.* 2012) would be significant predictors of floristic variations.

Materials and methods

Database

We used the database NeotropTree (NTT) (Oliveira-Filho 2017) to obtain biotic and abiotic data. The NTT consists of checklists of tree species, which are defined as stem plants larger than 3 meters high, capable of sustaining themselves without relying on other plants (Eisenlohr & Oliveira-Filho 2015), and geo-climatic information for the entire Neotropical region. Each site of NTT consists of a circular area with a radius of 5 km determining a single type of vegetation, characterized according to the system proposed by Oliveira-Filho (2015). All vegetation types were listed according to this system, and we defined nine major groups of vegetation types (Tab. 1).

We examined the 92 NTT sites for the Cerrado-Amazon transition zone (hereafter also referred to as Transition), delimited according to Ab'Saber (2003) (Fig. 1). Our choice for the classification of Ab'Saber (2003) relies on the fact that this is a holistic way of seeing and analyzing biogeographic regions; such mapping considers vegetation types as well as environmental characteristics, including relief, soil and climatic-hydrological conditions. We worked with 17,240 occurrence records distributed in 11 families, 569 genera and 2,530 species occurring throughout the Transition.

The environmental data consisted of 30 variables obtained for the center of each NTT site (see details in Oliveira-Filho 2017). The 11 bioclimatic descriptors related to temperature and precipitation patterns were obtained from WorldClim, a set of global high resolution layers created by Hijmans *et al.* (2005). The aridity index was generated according to Zomer *et al.* (2006). The mean duration and severity of the periods of deficit and excess water were extracted according to the Walter Diagram (Walter 1985). Soil variables were obtained using satellite imagery from Google Earth and the Harmonized World Soil Database v. 1.2 (Fischer *et al.* 2008). The spatial data consisted of geographical coordinates (latitude and longitude) obtained from the center of each NTT site.

Data analysis

We performed all analyzes in the R statistical environment, version 3.4.1 (R Development Core Team 2017). We used the following matrices: floristic data (with occurrence records of families, genera and species from each NTT site), environmental data (with 30 environmental variables from each site) and geographic coordinate's data (latitude and longitude) from each site. In all statistical tests, we used a significance level of 5 %.

Table 1. Groups of vegetation types used in this study, followed by their respective vegetation types.

Vegetation type groups	Specific vegetation types (Phytophysiognomies)
forested savannas	dystrophic forested savanna, mesotrophic forested savanna
shrub/woodland savannas	shrub/woodland savannas
rocky savanna	rocky savanna
seasonal forest	non-flooded seasonal forest, non-flooded seasonal sub-mountain forest
floodplain forest	flooded seasonal forest, tidal flooded forest
fluvial-sandstone	coastal fluvial-sandstone mosaic
dwarf-forest	sandy dwarf-forest, sandy-rocky dwarf-forest, white water dwarf-forest, rocky dwarf-forest
rain forest	non-flooded rain forest, mountain rain forest, sub-mountain rain forest
riparian forest	riparian forest

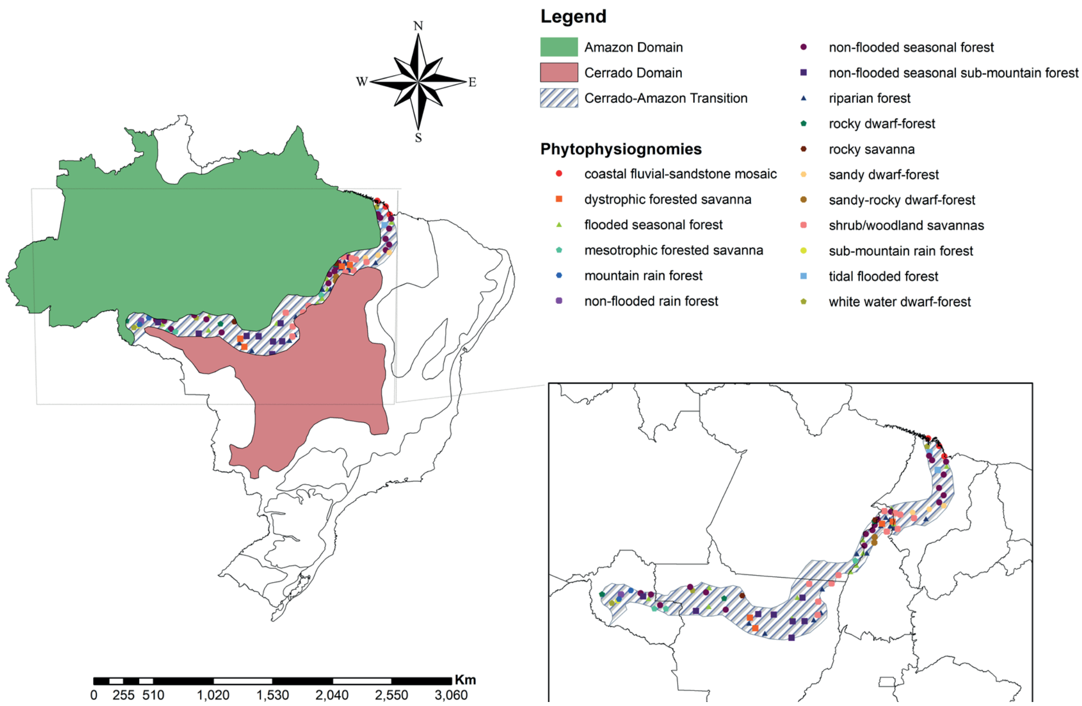

Figure 1. Transition area between the Amazon and Cerrado Domains with the 92 sites of the 'NeotropTree' database used in this study. Each point is highlighted with different symbols and colors according to its vegetation type.

Identity and floristic connections

Using the floristic matrices, we examined the unique and shared number of families, genera and species for the Transition in relation to Amazon and Cerrado using Venn Diagrams. We performed an Indicator Species Analysis for the Transition in relation to both domains, and also for the vegetation types of the Transition (Tab. 1). The specificity (A) and sensitivity (B) metrics are considered to the calculation of the indicator value – (A) is the mean of species occurrence of the target group (Transition, in a first moment, and each vegetation type of the Transition, in a second moment), divided by the sum of the mean abundance values in all groups, and (B) is the relative frequency of occurrence (presence-absence) of species within the target group (Cáceres & Legendre 2009). These two measures are combined to produce 'Stat' values (Stat = A + B / 2), which is an indicator metric for each species. The 'Stat' significance for each species was obtained by randomization test (999 permutations) (Borcard *et al.* 2011).

We here used the 'venn.diagram' function of the 'VennDiagram' package (Hanbo 2018) and the 'multipatt' function of the 'indicspecies' package (Cáceres & Legendre 2009).

Floristic groups and gradients

We examined possible floristic groups (species-level) involving the Transition sites by means of cluster analysis, using the UPGMA (Unweighted Pair Group Method with Arithmetic Mean) algorithm. We used Simpson distance because this coefficient is less affected by variation in species richness between sites (Baselga *et al.* 2007). We performed this analysis using the floristic matrix of species without uniques (22 %). Uniques generally cause noise and do not contribute to the most important floristic patterns (Lepš & Smilauer 2003).

We calculated the possible number of groups through a cut-off threshold in the dendrogram that accounted for 90 % of floristic dissimilarity (Dapporto *et al.* 2013; Holt *et al.* 2013). We retained a total of 16 statistically consistent groups, which were reduced to 11 after the discard of groups without phytogeographic cohesion (groups composed of only one site). Each of these 11 groups had their sites grouped to build a single list per group (see DRYFLOR 2016). Based on these 11 groups, we obtained an AU (Approximately Unbiased) value, highlighting in the dendrogram the groups that are strongly supported by the data, *i.e.*, that present AU greater than 95 % (Suzuki & Shimodaira 2006).

We examined the unconstrained floristic gradients throughout the Transition by means of NMDS (Non-Metric Multidimensional Scaling) ordination performed on the floristic matrix of species, using the Simpson index (200 iterations). We calculated the stress as a measure of fit and interpreted it according to Clarke (1993). Lower stress indicates a better adjustment between original dissimilarity and the result displayed by ordination diagrams.

Performing both cluster and ordination analyses is important to obtain complementary results on vegetation patterns (Kent 2011). For cluster analyses, we used different functions available at the 'recluster' (Dapporto *et al.* 2013) and 'pvclust' (Suzuki & Shimodaira 2006) packages. Specifically for NMDS, we used the 'metaMDS' function of the 'vegan' package (Oksanen *et al.* 2018).

Environmental and spatial predictive power on floristic patterns

We modeled the floristic variations in relation to environmental and spatial variables by means of the Redundancy Analysis based on transformation (tb-RDA) (Borcard *et al.* 2011). Tb-RDA has been demonstrated to be a powerful method to model ecological community data (Legendre & Gallagher 2001; Borcard *et al.* 2011).

First, the species matrix, without uniques, was submitted to Hellinger's transformation, which is well suited for ecological community data (Legendre & Gallagher 2001). The environmental matrix was subjected to a hierarchical clustering of variables (Chavent *et al.* 2012) in order to reduce dimensionality, which is useful to remove collinearities. We retained eight clusters (Tab. 2) with bootstrap curve assistance ('stability' function of 'ClustOfVar' package). Each cluster was submitted to a Mixed PCA (Principal Components Analysis for a mixture of quantitative and qualitative variables; Chavent *et al.* 2012 and references therein), being retained its first component as a proxy of the correspondent subset of variables (Chavent *et al.* 2012). We therefore obtained an environmental matrix with eight PCA components, each one being considered a synthetic variable of each cluster (Tab. 2).

We obtained spatial variables from Moran's Eigenvector Maps (MEMs; Dray *et al.* 2006), which are orthogonal variables derived from latitude and longitude obtained from a spatial weighting matrix (SWM) whose corresponding eigenvalues are linearly related to Moran's index of spatial autocorrelation (Dray *et al.* 2006; Bauman *et al.* 2018). MEMs are usually referred to as "spatial filters" (*e.g.*, Diniz-Filho & Bini 2005 and references therein). Since there are several SWMs available by selecting a set of predefined connectivity and weighting matrices (a total of 21 SWMs, if one applies the 'listw.candidates' function of 'adespatial' package of R; Dray *et al.* 2018), each one generating different spatial filters (Dray *et al.* 2006; Bauman *et al.* 2018), we selected the SWM that generated the most adjusted selected model (higher adjusted R^2 to explain the floristic variations; Bauman *et al.* 2018).

We selected the environmental and spatial variables that influenced the floristic variations at the species level

Table 2. Environmental variables retained in each cluster according to the method of hierarchical clustering of variables.

Clusters	Environmental variables	Within-cluster Sum of squares	Squared loadings
1	Minimum temperature of the coldest month	4.8073	0.9830
	Annual Temperature Range		0.9089
	Mean Temperature Range		0.8532
	Isothermality		0.8005
	Annual Mean Temperature		0.6888
	Altitude		0.5729
2	Precipitation in the driest period	1.9575	0.7009
	Temperature Seasonality		0.6671
	Maximum Temperature of the Warmest Month		0.5895
3	Severity of water excess	2.7599	0.9741
	Annual Precipitation		0.9380
	Precipitation in the wettest period		0.8478
4	Duration of the water deficit	3.3097	0.9424
	Precipitation seasonality		0.8577
	Severity of water deficit		0.8086
	Duration of the water excess		0.7010
5	Soil Drainage Class	3.6294	0.9945
	Ranked drainage		0.9945
	Hyperseasonality		0.8460
	Soil Water Storage		0.7945
6	Flammability index	1.9883	0.9942
	Grassy Cover		0.9942
7	Ranked Sand	3.0471	0.8163
	Soil Texture Class		0.7990
	Surface Rockiness		0.7387
	Ranked Rockiness		0.6932
8	Soil Fertility Class	2.8763	0.7191
	Ranked Total Base Saturation		0.7191
	Salinity Class		0.7191
	Ranked salinity		0.7191

by means of forward selections, after making sure that each global model was significant (ANOVA p<0.05; Blanchet *et al.* 2008). Both forward-selection procedures followed the double-stop criterion of Blanchet *et al.* (2008). With the selected variables, we partitioned the tb-RDA variance among the components that explain the floristic patterns: [a] environmental variables; [b] environmental variables and spatial filters indistinguishably; [c] spatial filters; [d] undetermined fraction (residuals). We applied the corrections proposed by Clappe *et al.* (2018) by performing a Moran Spectral Randomization for variation partitioning. This procedure ensures corrected estimates of each fraction by adjusting the test for spurious contributions due to spatial autocorrelation from the environmental fraction (Clappe *et al.* 2018).

We used the following packages in the above-mentioned analyses: 'ClustOfVar' (Chavent *et al.* 2012), to perform hierarchical clustering of variables and, thus, to obtain PCA axes that summarize each subset of environmental variables; 'spdep' (Bivand *et al.* 2019), 'ade4' (Dray & Dufour 2007) and 'adespatial' (Dray *et al.* 2018), to generate and select SWMs, and to perform forward selections; 'vegan' (Oksanen *et al.* 2018) and 'ade4', to perform tb-RDA models and variance partitioning; 'adespatial', to calculate Moran Spectral Randomization for variation partitioning; and 'ggplot2' (Wickham *et al.* 2018), to generate and edit the tb-RDA graphs.

Results

Identity and floristic connections

The Transition shared 110 families, 545 genera and 2,322 species with the Amazon and 106 families, 567 genera and 1,533 species with the Cerrado (Fig. 2). The main indicator species for the Transition in relation to the Amazon and the Cerrado was *Senna silvestris* (Stat = 0.541, p<0.01). We show the main indicator species for each vegetation type (Tab. 3). Riparian forests did not present indicator species.

Floristic groups and gradients

The cluster analysis revealed four floristic groups (Fig. 3). The first group (highlighted in blue, Fig. 3) was formed by flooded forests; the second group, solely by white sand dwarf-forests; the third group, by savannas and dwarf-forests (highlighted in green, Fig. 3); the fourth group (highlighted in purple, Fig. 3), by the majority of forest types as well as by the coastal fluvial-sandstone mosaic.

The NMDS produced a two-dimensional solution with a stress of 0.162, indicating a good representation of general patterns (Clarke 1993). The first axis of the diagram (Fig. 4) indicated a gradient opposing, as a general rule, savannic physiognomies (shrub/woodland savannas and rocky savannas), to the left, to forest physiognomies (seasonal, rain and riparian forests), to the right, passing through dwarf-forests. The second axis indicated a gradient that started from the rain forests and contrasted with the fluvial-sandstone areas and other forest types. We also detected a greater discrimination for the flooded areas in relation to all other vegetation types of the Transition.

Environmental and spatial predictive power on floristic patterns

The model retained seven of the eight PCA clusters that summarized the environmental variables (Table S1 in supplementary material). Eleven spatial filters from SWM coded by 'Dnear 1.79_Down_5', a distance-based connectivity matrix obtained by concave-down weighting function (see Bauman *et al.* 2018; Dray *et al.* 2018), were selected to account for spatial structures.

The variance partition and the tests performed on partial tb-RDAs showed a significant contribution of both environmental (p = 0.001) and spatial variables (p =

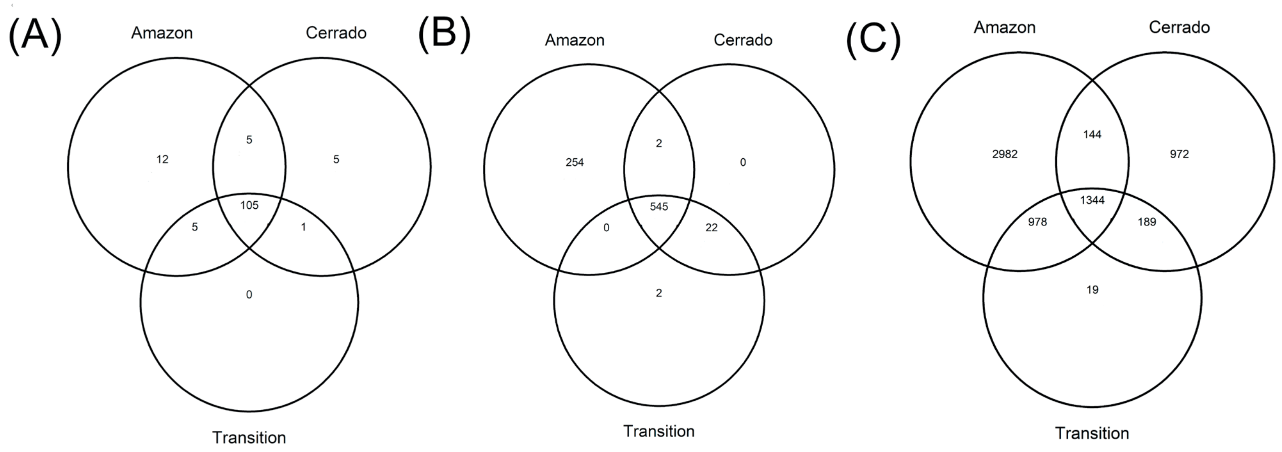

Figure 2. Venn diagram showing the number of families (**A**), genera (**B**) and species (**C**) exclusive and shared for the Amazon, Cerrado and the transition area between these two phytogeographic domains.

0.001). The floristic variance (adjusted R²) due to [a] only environmental variables totaled 6.49 %, [b] the shared fraction between environmental and spatial variables totaled 2.07 %, [c] only spatial variables totaled 8.57 % and [d] the undetermined fraction (residuals) totaled 82.87 %.

The final tb-RDA diagram (Fig. 5) captured, for the first axis, an explanation of 29.02 % of the canonical variation in the species distribution (F = 14.95; p = 0.001) and, for the second axis, 16.74 % of this variation (F = 8.62, p = 0.001) - 12 % and 6.9 % of the total variation, respectively. For both axes, 'Cluster 6' (fire-related variables, Tab. 2) and 'Cluster 5' (variables related to soil moisture, Tab. 2) were the most important environmental predictors (Fig. 5). However, in the axis 2, one of the spatial filters ('MEM 9') presented greater contribution than 'Cluster 6' (Fig. 5).

Discussion

Despite the consistent identity of each group, our results strongly reinforce the floristic connections of the Cerrado-Amazon transition with its adjacent domains. This makes this a region with its own floristic characteristics, but also a floristic subset of the Amazon and Cerrado domains. Such floristic features, when influenced significantly by environmental and spatial variables, as is the case with the Transition's flora, may point to consistent responses to environmental changes and neutral dynamics, including limitation to dispersal processes, making this region an area of great relevance for biological conservation (Soininen *et al.* 2007; Castillo-Campos *et al.* 2008).

Table 3. Main indicator species for each vegetation type group, followed by their respective statistics (see Materials and methods).

Vegetation type groups	Main indicator species	stat	p
forested savannas	*Plenckia populnea* (Reissek)	0.756	<0.01
shrub/woodland savannas	*Tachigali aurea* Tul.	0.832	<0.01
rocky savanna	*Chamaecrista multiseta* (Benth.) H.S.Irwin & Barneby.	0.957	<0.01
seasonal forest	*Parkia pendula* (Willd.) Benth. ex Walp.	0.711	<0.01
floodplain forest	*Astrocaryum jauari* Mart.	0.839	<0.01
fluvial-sandstone	*Miconia lepidota* DC.	0.807	<0.01
dwarf-forest	*Eugenia stictopetala* Mart. ex DC.	0.886	<0.01
rain forest	*Miconia dolichorhyncha* Mart. ex DC.	0.935	<0.01
riparian forest	-	-	-

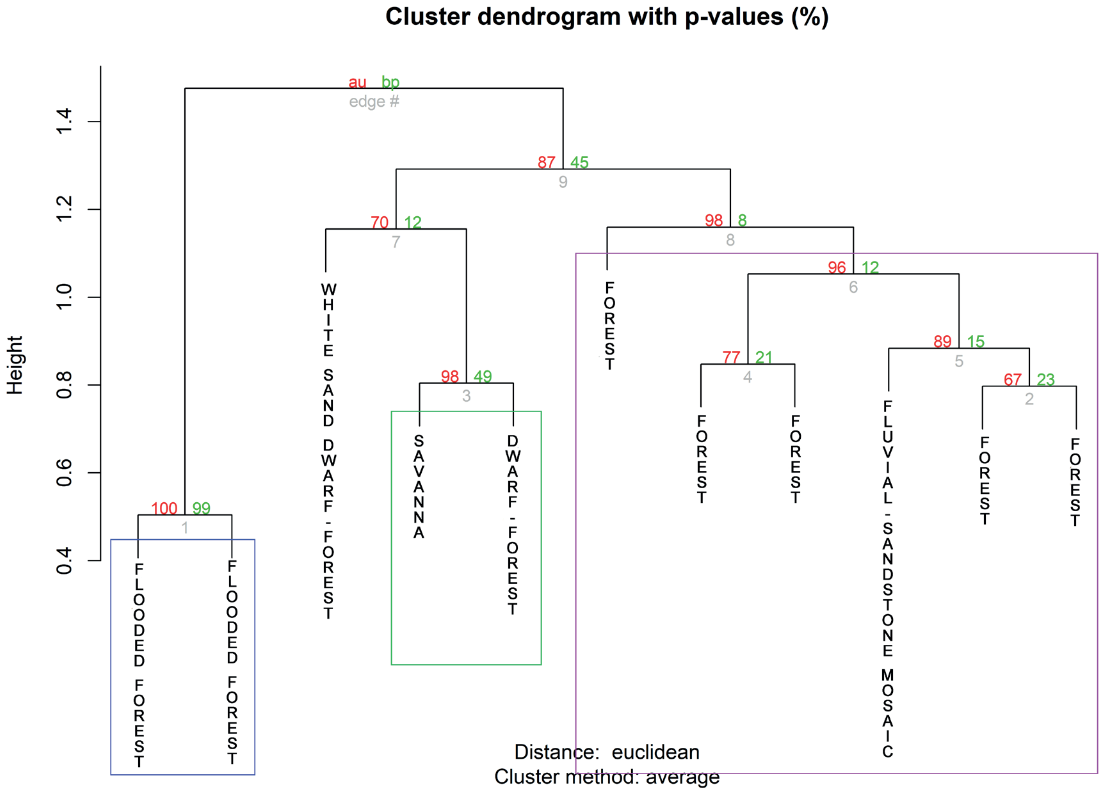

Figure 3. Dendrogram obtained by the 'pvclust' method, highlighting the groups (rectangles with different colors) with high values of support (numbers in red), *i.e.*, those which presented values of AU (Approximately Unbiased) higher than 95 %.

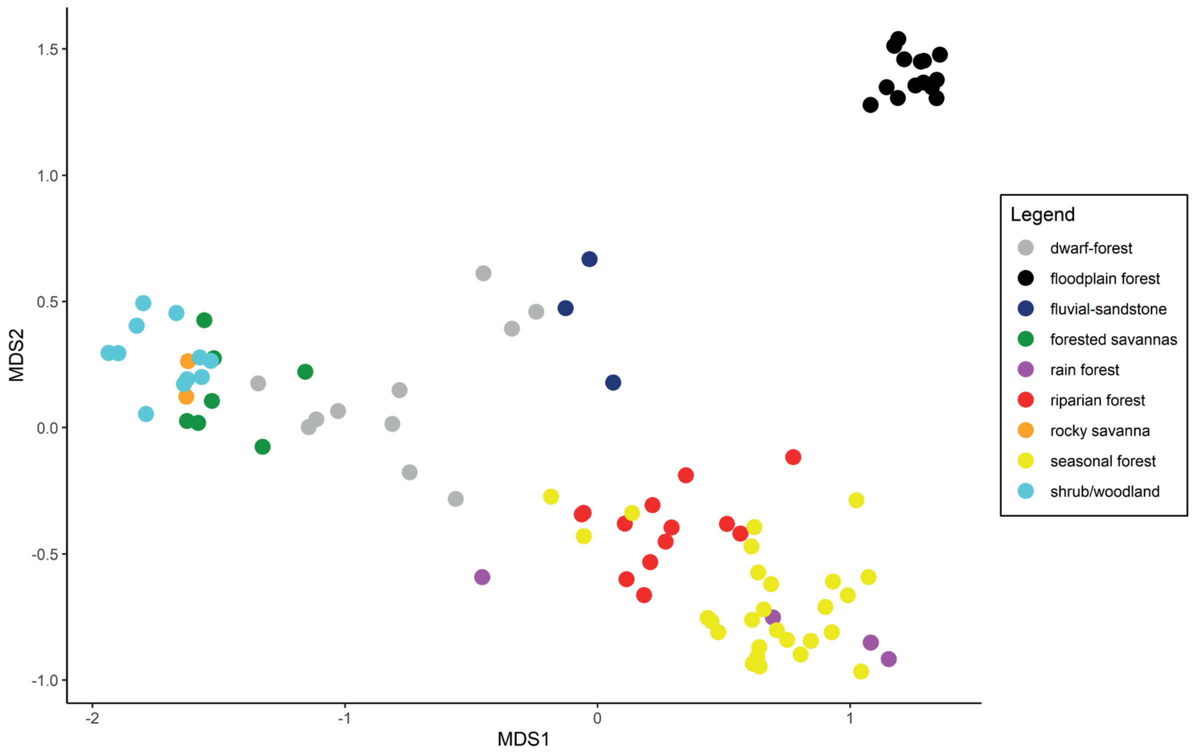

Figure 4. Non-metric multidimensional scaling (NMDS - Simpson index) of Cerrado-Amazon transition sites in a two-dimensional space (stress = 0.162). Points represent each group of vegetation type (see Tab. 1).

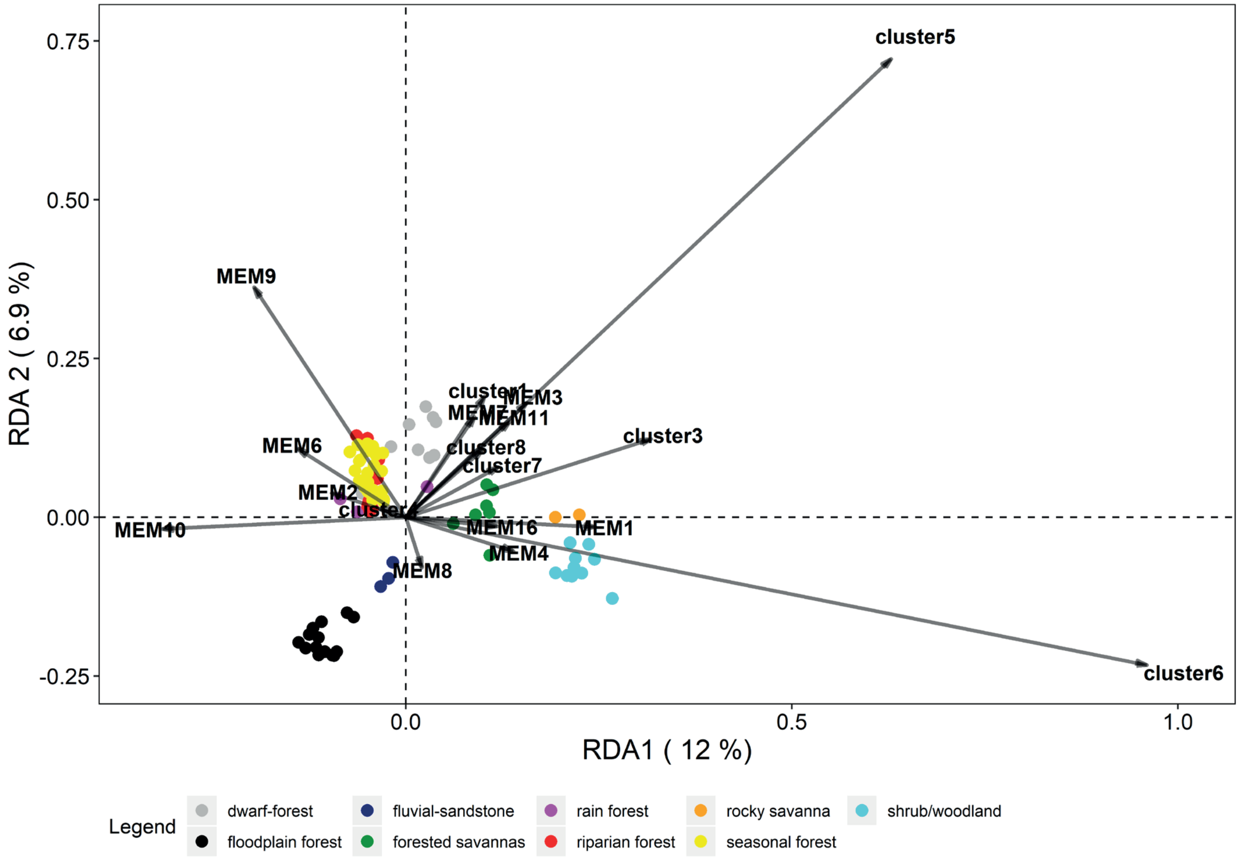

Figure 5. Diagram yielded by tb-RDA for the complete selected model, *i.e.*, with environmental and spatial filters (MEMs). Each 'Cluster' represents a group of environmental variables (see Table 2).

The strongest indicator species of the Transition, *Senna silvestris,* is widely distributed and shown to be adapted to different habitats. As the Transition has several habitats that offer conditions for the occurrence of this species, this result was attributed to a preferential occurrence in the region in relation to the Amazon and Cerrado domains. This means that although *S. silvestris a*lso occurs in the Amazon and the Cerrado, its distribution in these regions is not as frequent as along the Transition, in which the species can be found in 52 of the 92 sites present in NeotropTree database.

Regarding the indicator species of each vegetation type of the Transition, these may have physiological and ecological characteristics that make them have a preference for a certain habitat. These characteristics help in the differentiation of the vegetation types presented here. For example, *Astrocaryum jauari,* the main indicator species of flooded forests, has different characteristics that allow it to survive in flooded areas (Schluter *et al.* 1993). Furthermore, because they have associations that are consistent with a single habitat type, the indicator species of each vegetation type can be used as diagnostic species, which are useful in the identification of a particular habitat. In this sense, examining their physiological characteristics can inform responses related to impacts or disturbances in different habitats (Cáceres & Legendre 2009; Kanagaraj *et al.* 2011).

The differences in floristic composition between savanna and forest are widely reported (Borchet 1988; Rocha *et al.* 2009; Staver *et al.* 2011; Davidson *et al.* 2012; Hoffmann *et al.* 2012; Dantas *et al.* 2013; Oliveira *et al.* 2014; Bueno *et al.* 2018; Dexter *et al.* 2018). We here confirmed this distinction, which is in accordance with our first hypothesis. This was evidenced by the grouping of the most typical forest physiognomies of the Amazon Domain (such as seasonal and rain forests) as opposed to the savannic physiognomies, which are more typical of the Cerrado Domain. However, rather than confirming patterns already reported in the literature, our work was the first to present such an approach to the transition between the major phytogeographic domains of South America, and the first to elucidate some of the processes responsible for these patterns.

Our analyzes also showed that the floodplains differ from the others in both cluster analysis and ordination. The influence of soil and river basin moisture is evident, showing that the floristic variation of the Transition is strongly related to local variations, and closer areas tend to be more similar to each other than to areas geographically close to river basins (Lenza *et al.* 2015; Morandi *et al.* 2016). Another remarkable pattern was the fact that the forested savannas (both dystrophic and mesotrophic ones) presented a greater floristic similarity with the typical savannas. This result may be not only associated with similar soil characteristics (Marimon-Júnior & Haridasan 2005; Maracahipes-Santos *et al.* 2017), but also with the geographic proximity of these areas, since some forest species have physiological and ecological characteristics that allow them to settle in areas of savannas (Hoffmann *et al.* 2004; Pinheiro & Monteiro 2006; 2008).

Also in agreement with our first hypothesis, we indicated that fire and soil unequivocally determined variations in floristic composition throughout the Transition, indicating a role of environmental drivers acting on local scales (Murphy & Bowman 2012; Dantas *et al.* 2013). However, from a spatial point of view, the filters selected for the canonical model act on broader scales - note that the first eigenvectors (MEM 1, MEM 2 etc.) have this characteristic, while the latest eigenvectors act on finer scales (Borcard *et al.* 2011). This suggests a possible dispersion limitation at great distances, a fact that contradicts our second hypothesis. However, further discussions on possible neutral processes should be developed with caution, because we did not work with abundance data. If such data were available, the protocol suggested by Diniz-Filho *et al.* (2012) could be applied to test a possible association between spatial contribution and neutral dynamics. An additional caution we recommend here is to ensure that spatial processes are being correctly estimated, which is a critical issue on variance partition framework (Clappe *et al.* 2018). In fact, we took into account such caution by performing the method of Moran Spectral Randomization (Clappe *et al.* 2018).

Our results also suggest that fire is probably a relevant factor, since 'Cluster 6' formed by the variables 'flammability index' and 'grass cover' was one of the most influential in the main axes of the canonical model, besides being the variable that most contributed to explain the model as a whole. This result may be associated with the land use, which can increase forest flammability, and grasses are the first to settle after deforestation (Brando *et al.* 2014). Thus, our results show that these factors, associated with drought events and intense fires, may favor the substitution of forest types along the Transition in grass-dominated ecosystems, as demonstrated by Silvério *et al.* (2013) for the Amazon Forest.

The canonical model (tb-RDA) also showed a notable influence of 'Cluster 5' both on the first and second axes of the tb-RDA diagram (Fig. 5), and also for the model as a whole. This is a synthetic variable formed by environmental predictors related to soil moisture. These results, together with cluster and ordination analyses, reinforce that, among the predictors used in this study, soil moisture is one of the most important factors influencing the variation of the floristic variations along the Cerrado-Amazon transition.

Most of the variance (>80 %) was not explained. This may be due to the absence of some important predictor variables in the model, which may contribute to the variation of the floristic composition, or to random events that are not related to space and that would be able to increase the competition among plant species, thereby decreasing their recruitment limits (Hurt & Pacala 1995; Favretto 2017). In addition to the environmental predictors used here (climate, fire and soil), ecophysiological characteristics, such as the incorporation of nutrient limitation, may also influence vegetation distribution patterns along the Cerrado-Amazon transition (Dionizio *et al.* 2018).

Our study reinforces the knowledge about the patterns responsible for shaping vegetation patterns on large tropical ecosystem transitions, which may differ when compared to extratropical communities in South America, an important fact to be considered in conservation strategies (Rezende *et al.* 2018). In addition, our results show the importance of deterministic processes, especially those related to the finer scales (soils and fire), and dispersal constraints (since spatial processes seem to be highly relevant), as possible modulators of these patterns, which could suggest a general macroecological rule for tropical transition zones (Bueno *et al.* 2017). We indicate the predictive capacity of the climate, which is not a surprise, because recent literature has shown, for instance, that precipitation is a major factor driving species distribution in the Cerrado and Amazon domains (*e.g.*, Oliveira-Filho & Ratter 2002; Esquivel-Muelbert *et al.* 2016; but see Bueno *et al.* 2018). However, edaphic and fire-related variables were more useful in predicting floristic variation in our study. In fact, the detection of limiting factors for species distribution is a hot issue for current research on possible biological responses to climate change, particularly in biogeographical transition zones (Sommer *et al.* 2018).

Transition areas often do not receive attention for biodiversity conservation strategies, although these areas may generate adaptive responses to environmental changes (Smith *et al.* 2001). Taking into account this fact, and also that the Cerrado-Amazon transition area is situated in a strongly anthropized area (Marimon *et al.* 2006), the correspondence between the environmental heterogeneity found throughout the Transition and our results demonstrate once again the utmost importance of conserving biogeographical transition zones.

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