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Functional diversity and regeneration traits of tree communities in the Amazon-Cerrado transition

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Abstract

In central Brazil, there are strong gradients and discontinuities in vegetation structure and composition between the forests of southern Amazonia, and the open savannas of South America's Cerrado. These transitions are often controlled by disturbance processes, and the ability of vegetation to respond to climatic and environmental changes may depend on the regeneration traits of the different floras present. In this study we aim to assess the regeneration traits of tree communities of the Amazon-Cerrado transition and to understand how they differ among and within the markedly different vegetation types. We sampled 39 one-hectare long-term monitoring plots that include typical cerrado (TC=10), cerradão (CD=3), gallery forests (GF=3), floodplain forests (FF=6), seasonal and open rainforests (SF=17). The regeneration traits assessed included dispersal syndrome (zoochory, anemochory, and autochory), fruit consistency (dry and fleshy), number of seeds per fruit, and diaspore dimensions (width and length). We found differences among the vegetation types, in all regeneration traits. And these tended to be aggregate by vegetation structure, being similar for cerrado and cerradão species, and similar for SF, FF and GF (more forested vegetation). Vegetation types did not differ in functional diversity, however, while regeneration traits among seasonal and open rainforests were well-dispersed, in floodplain forests they were more clustered. Tree species depend substantially on fauna (zoochoric species between 42 and 86% in vegetation) for the dispersal across all habitats here, consisting of the dominant dispersal strategy. By incorporating these strategies into the tree recruitment and establishment study, we will be improving our understanding of the dynamic and tree species richness of neotropical forests and savannas.

Keywords: functional trait, seed dispersal, fruit, forest, savanna, ecological strategy

1. Introduction

Regeneration traits are important elements in plant community ecology, affecting the processes of dispersal, germination, colonization, and establishment of trees in the environment (Vandelook et al., 2012; Romero-Saritama and Pérez-Rúiz, 2016). The regeneration in plant communities is the process whereby mature individuals of a population are replaced by new individuals of the next generation through the regeneration traits (i.e., seed production, fruit size, dispersal, and seedling emergence)

(Grubb, 1977). Species use distinct regeneration strategies as direct responses to different selective pressures, which allows their coexistence in communities (Hutchings, 1986; Houle, 1991). Hence, understanding the factors that affect forest regeneration is crucial for practical restoration in the face of disturbance and for enabling the recovery of these environments (Vieira and Scariot, 2006). Understanding the complex network of biotic mechanisms that influence and control forest recovery is also key for a deeper understanding of tropical forest ecology (Powers et al., 2009). For example, changes in plant-pollinator interactions can affect seed dispersal and seedling recruitment, potentially reducing population size or promoting local extinction (Girão et al., 2007).

Environmental conditions form the basis for the selective pressures that directly influence the mechanisms responsible for plant regeneration (Houle, 1991; Grime, 2006). Studies have highlighted how fire regimes, rainfall, temperature, resource availability (light and nutrients), and the frequency and intensity of drought events are among the main environmental factors that affect the regeneration of tropical vegetation types (e.g. Vargas-Rodrigues et al., 2005). Consequently, the regeneration of tropical species results from adaptation to abiotic factors, which directly affect species functional traits. Nevertheless, there is potentially a wide range of regeneration strategies associated with the environmental conditions of regions where communities are established (van Schaik et al., 1993). Studies of regeneration traits in savanna and forest show that plant regeneration strategies are strongly related to habitat, and this plays an important role in community assembly (Ribeiro et al., 2015; Escobar et al., 2021).

Forest and savanna are influenced by different environmental filters, with fire occurrence, groundwater depth, and hight light availability in savannas (Hoffman et al., 2009). And air humidity, soil moisture, canopy closure, and nutrient content increasing towards the forest (Hoffman et al., 2004; Torello-Raventos et al., 2013). These sets of environmental filters have been linked to describe what is currently known about regenerative strategies in forests and savannas. In open savannas of the Cerrado, wind dispersion predominates at the end of the rainy season and in the dry season (Kuhlmann and Ribeiro, 2016) and pronounced post-fire resprouting (Scalon et al., 2020). While in the tropical forests, dispersal by animals occurs much more distributed throughout the year, with germination and seedling development under a closed canopy (van Schaik et al., 1993; Ribeiro et al., 2015).

Vegetation in the Amazon-Cerrado transition separates the two largest South American biomes, the Amazon and the Cerrado (Marques et al., 2019). Tree populations in the Amazon-Cerrado transition are mostly composed of fast turnover species ("hyperdynamic", Marimon et al., 2014) but have also recently experienced net declines in abundances due to land-use change and extreme climate events (e.g. Nogueira et al., 2019; Marimon et al., 2020). How they regenerate will be a critical factor in determining the ecological stability of a large area of forest in central South America. Different patterns of regeneration may be expected among the different woody vegetation types in the Amazon-Cerrado ecotone. Given that the region is characterized by complex interactions among environmental factors (Marimon et al., 2006) and different vegetation types are subject to different natural and anthropogenic environmental pressures. Several vegetation types are found in the transition zone between Cerrado and Amazonian forests. These include typical cerrado (typical savanna), cerradão (a dense and tall transitional woodland formation) (Ratter et al., 1973), gallery forests (Marimon et al., 2002), and floodplain forests (Marimon et al., 2015). Seasonal evergreen, seasonal semi-deciduous (dry forests), and open rainforests are the true Amazonian forests in the transition zone. (Ivanauskas et al., 2008). As a continuum from savanna vegetation of the Cerrado, passing through transitional forests such as cerradão and dry forests to the rainforests in the Amazonia. The environmental conditions in which these vegetation types differ provide a great opportunity to investigate the relationship between habitat and regeneration traits.

In this study, we aimed to assess how functional diversity (a multitrait index) and regeneration traits vary within and among the vegetation types of the Amazon-Cerrado ecotone. We investigated and tested the following questions and hypotheses: a) *How do regeneration traits differ between transitional vegetation types?* We expect that a higher proportion of species bearing fleshy and large fruits would be found in moist forests, with a greater proportion of wind-dispersed species with smaller diaspores in drier forests and savannas. This is because environments with greater availability of water during the year often have a higher proportion of species with fleshy fruits dispersed by animals (Howe and Smallwood, 1982; Tabarelli et al., 2003; Correa et al., 2015); b) *Does regeneration traits tend to cluster or diverge?* We expected that functional trait clustering would be found, as phylogenetic and functional aggregation has been reported elsewhere in tropical forests (Webb et al., 2002; Vamosi et al., 2009); c) *Which regeneration trait is the best predictor?* We hypothesize that between our set of traits, fruit dimensions are the best predictors. Since for zoochoric species, tall plants with large fruits may attract highly mobile dispersers, which can take seeds long distances (Thomson et al., 2011). Thus, influencing the seed dispersal range, which is strongly related to the local species composition (Howe and Smallwood, 1982). For this purpose, we determined dispersal syndrome, fruit consistency, number of seeds per fruit, fruit length, and fruit width for 196 tree species from a unique and complex set of vegetation types occurring in the Amazon-Cerrado transition zone.

2. Materials and methods

2.1 Study area

We worked across the Amazon-Cerrado transition, with plots established from the southern region of Pará State, skirting the southern edge of the Xingu Indigenous Land, to the central-northern region of Mato Grosso State (Figure 1). Our analysis is based on 39 one-hectare long-term monitoring plots, classified as typical cerrado (TC=10), cerradão (CD=3), gallery forests (GF=3), and floodplain forests (FF=6). For this study we grouped the vegetation types: semideciduous seasonal forest, evergreen seasonal forest, and open rainforest in a single class, named seasonal and open rainforests (SF=17). Because these are the typical forest types and representatives of the peripheral region of the Amazonia Forest in the transition zone with the Cerrado (Ratter et al., 1973; Pires and Prance, 1985). The cerradão is a transitional forest, characterized by the presence of species from both savanna and forest (Ratter et al., 1973) (Table 1). All the plots were censused using RAINFOR protocols (e.g., Phillips et al., 2009; Marimon et al., 2014).

The climate of the region is tropical with dry winters (“Aw”) and monsoon tropical (“Am”), according to the Köppen classification system (Alvares et al., 2013). The average annual rainfall ranges from 1,511 to 2,353 mm, and the average annual temperature varies from 24.1 to 27.3 ° C (Hijmans et al., 2005).

2.2 Data collection

Species lists from the most recent inventories (between 2014 and 2016) carried out by the research team at the Plant Ecology Laboratory of the Mato Grosso State University (UNEMAT) in Nova Xavantina were used. Data were deposited in the ForestPlots.net forest monitoring database (Lopez-Gonzalez et al., 2011). In these inventories, plants were included if the stem diameter was at least 10 cm, measured at 1.30 m (forest vegetation) or 0.30 m above ground level (savanna). Families were classified according to the APG IV (Chase et al., 2016) system, and the Flora of Brazil 2020 (http://floradobrasil.jbrj.gov.br/) was consulted for identifying species. Voucher materials have been deposited in the following herbaria: NX (UNEMAT - Mato Grosso

State University - Nova Xavantina, Mato Grosso State), UB (University of Brasilia, Brasilia, Federal District), IBGE (Brazilian Institute of Geography and Statistics, Brasilia, Federal District), and CEN (Embrapa Genetic Resources and Biotechnology, Brasilia, Federal District).

2.3 Regeneration traits

Trait data were obtained from herbarium collections and available bibliography, with values determined for each species present in the 39 plots studied. The regeneration traits used were: dispersal syndrome, fruit consistency, number of seeds per fruit, fruit length, and fruit width. Dispersal syndrome (zoochory, anemochory, and autochory), fruit consistency (dry and fleshy), and the number of seeds per fruit were determined based on diaspore characteristics (seed and fruit), which were obtained from field observations and the specialized literature (Pott and Pott, 1994; Lorenzi, 1998; Barroso et al., 2000; Perez-Harguindeguy et al., 2016). Diaspore length and width data obtained from herborized samples available online (http: //splink.cria.org.br, http://fm1.fieldmuseum.org/vrrc, http://sweetgum.nybg.org/science/ vh/, and other virtual herbaria) were also used, and only samples collected within the bo rders of the Mato Grosso State were selected. Five fruit replicates (five herbarium specimens) per species were measured (Thompson et al., 1993), and a database was created with the functional traits of the more dominant species that composed up to 80% of the basal area of each plot, following the method recommended by Garnier et al. (2004). The aim was to understand how the environment shapes vegetation characteristics and how functional traits affect local productivity.

2.4 Analyses

To test for differences in regeneration traits between vegetation types, we compared the functional traits using Generalized Linear Mixed Models (GLMM) in `lme4` package (Bates et al., 2015), with the vegetation type as predictors (fixed effect) and plots as random effect. We fitted the null model and an alternative model for each trait and tested statistical similarity between the null model and the alternative model by an ANOVA. To choose the best model, we used Akaike information criteria (AIC) for the significant alternative models. We use the Tukey tests *a posteriori* for multiple comparisons of values between groups (vegetation type) using the `multcomp` package

(Hothorn et al., 2008). We also performed an ordination based on a principal component analysis (PCA) using the `vegan` package in a matrix consisting of the functional traits of each species per vegetation type (Oksanen et al., 2017).

To verify if the regeneration traits tend to cluster or diverge, first we calculate the Functional Diversity Index (FD), for this a functional dendrogram was built from a matrix (species × functional traits) transformed into a distance matrix. Gower distance was used to treat categorical (dispersal syndrome and fruit consistency) and quantitative data (number of seeds per fruit, fruit length, and fruit width) (Pavoine et al., 2009) in the `ade4` (Dray et al., 2007) and `ape` packages (Paradis et al., 2004). Null models were used to test whether functional traits were clustered or dispersed, and to test whether the observed patterns of species coexistence differed from what would be expected by chance regarding the regeneration traits. The null models were created by FD values of 1,000 communities built at random and compared based on the species pool of each vegetation type. Next, the standardized effect size of FD was calculated and t-tests were performed for samples, with the means of the standardized effect values being compared in relation to the zero mean using the `Picante` package (Kembel et al., 2010): *Standardized effect size (Z)* = - (obsFD - rndFD)/sd.rndFD. The obsFD is the observed FD (Functional diversity index), rndFD is the FD mean of null communities, and sd.rndFD is the standard deviation of the 1,000 random values of the FD (see Cianciaruso et al., 2012).

Standardized effect size values of FD higher than zero indicate functional diversity higher than what would be expected by chance (functional clustering), and values lower than zero indicate functional diversity lower than what would be expected by chance (functional dispersion) (Webb, 2000).

To determine which regeneration traits were the best predictors among the set of functional traits, we used the Bayesian average model with the `BMS` package (Zeugner and Feldkircher, 2015), with the functional traits as explanatory variables and the vegetation types as the response variable. We choose the hyperparameter on Zellner's (g-prior) for the regression coefficients. The Bayesian average models are an extension of the usual Bayesian inference methods, which use the Bayes theorem to produce posterior models and parameters, allowing the model selection by the complete enumeration of the model space (Hoeting et al., 1999; Fragoso et al., 2018). All analyses were performed in the R program (R Core Team, 2018), with the significance level set at 5%.

3. Results

Regeneration traits were compiled for all 196 tree species found on the studied sites. These included 60 species in the typical cerrado (TC), 27 in cerradão (CD), 22 in gallery forests (GF), 23 in floodplain forests (FF), and 103 in seasonal and open rainforests (SF). Fruit dimensions were smaller for seasonal and open rainforests species (Fruit length = 2.17±2; Fruit width = 1.34±1.02) and larger for typical cerrado species (Fruit length = 3.95±3.48; Fruit width = 1.94±1.28) (Figure 2 and Supplementary Table 1). Fruit lengths of species in seasonal and open rainforests were significantly shorter than those in the cerradão and typical cerrado (Figure 2 and Supplementary Table 1). In general, fruit length increase following a gradient of vegetation from the most forested and dense vegetation (SF) to the savanna and open areas (TC).

The fruit width in seasonal and open rainforests species was only significantly smaller than typical cerrado species (Figure 2 and Supplementary Table 1). Floodplain forest species have a few numbers of seeds per fruit (1.83±1.45) compared to other vegetation types (Figure 2 and Supplementary Table 1).

Thus, the highest percentage zoochory (59 to 89%) were recorded in more forested vegetation (SF, FF, and GF) and the lowest in typical cerrado (42.01±11.71) and cerradão (44.03±5.27); these two vegetation types also showed the highest proportion of dry fruits (TC = 53.75±10.65; CD = 44.03±5.27) (Figure 2 and Supplementary Table 1). Species that were wind-dispersed (anemochoric) had significantly larger fruits than the autochoric and zoochoric species in all vegetation types (Supplementary Table 4 and Supplementary figure 1). However, when comparing species of the same dispersal type among vegetation types, fruit dimensions were similar, for example, anemochoric species of typical cerrado were similar in length to anemochoric species of seasonal and open rainforests (Supplementary Table 4 and Supplementary Figure 1).

In ordination space, species tended to group based on their regeneration traits instead of by the type of vegetation, forming functional groups structured by dispersal syndrome and fruit type (percentage of variance explained, PC1 = 48% and PC2 = 16%) (Figure 3). Three main clusters, represented by anemochoric species with dry fruits, zoochoric species with fleshy fruits, and autochoric species, were observed (Figure 3). We found a big division between more forested vegetation (GF, FF and SF), typical cerrado (TC) and cerradão (CD). With clear occurrence of species of typical cerrado that are an exception, standing with forest species. These tree species are: *Curatella americana* L., *Guapira graciliflora* (Mart. ex J.A.Schmidt) Lundell, *Guapira noxia*

(Netto) Lundell and *Myrcia splendens* (Sw.) DC.. Savanna species with small fleshy fruits dispersed by zoochory.

Vegetation types did not differ in functional diversity (FD index) of regeneration traits (Figure 4). However, the functional diversity of seasonal and open rainforests and of floodplain forests were different from what would be expected by chance, with Z values significantly different from zero (Figure 5). For seasonal and open rainforests, the mean Z-value was much lower than zero, which implies the presence of species with a wide range of regeneration traits. By contrast, the mean of floodplain forests was higher than zero, which is an indicator of communities formed by species with similar functional traits (functional clustering).

The best regeneration traits model among the set of functional traits, for different vegetation types, was composed of dispersal syndrome, with a posterior model probability of 85% indicating that this is clearly the most important predictor (*Posterior Inclusion Probabilities* / PIP = 0.97) (Figure 6 and Supplementary Table 6).

4. Discussion

Our results showed differences among the vegetation types in all the regeneration traits examined. Which results in great variation in functional characteristics and ecological strategies among the vegetation types of the Amazon-Cerrado ecotone. Our hypothesis about variation of regeneration traits among vegetation types has been partially confirmed with a higher proportion of species bearing fleshy and small fruits dispersed by animals found in forest areas, and a greater proportion of wind-dispersed species with big dry fruits in dry forests and savannas. Regarding community assembly based on functional diversity, the seasonal and open rainforests showed overdispersion of regeneration traits, in floodplain forests by contrast these were markedly clustered. Contrary to our expectations, our results showed that dispersal syndrome (anemochory, autochory, and zoochory) was the most effective variable among the set of regeneration traits.

4.1 Variation of regeneration traits among vegetation types

These differences in functional traits highlight variability in re-colonization capacity, competitive vigor, and response to disturbance (Romero-Saritama and Pérez-Rúiz, 2016; Cornelissen et al., 2003) throughout the Amazon-Cerrado transition. In this case, heterogeneity in fruit size, consistency, and dispersal strategy indicates a spectrum in terms of diaspore permanence in the soil, as large-sized fruits found in typical cerrado species, in general, tend to remain in the soil in the seed bank for a shorter length of time, forming a transient soil seed bank (Salazar et al., 2011). Other studies have also shown variability in functional regeneration capacity between dry and evergreen forests (Romero-Saritama and Pérez-Rúiz, 2016), savannas (García-Nuñes and Azócar, 2004), and fragmented areas in the Atlantic Forest (Girão et al., 2007). The results of this study show similar variability between different vegetation types at a broad spatial scale.

Species of the cerradão and typical cerrado have larger fruits than those in forest vegetation. These fruits have higher exposure in the environment, requiring investment in resistance adaptations (Romero-Saritama and Pérez-Ruiz, 2016). We also observed that more forested vegetation had smaller fruits (SF, FF, and GF) which would suggest they have a richer seed bank, also formed by fruits with seeds inside. Since smaller fruits have a high capacity to contribute to the seed bank and attract dispersing agents, maintaining a more distributed dispersion throughout the year (Marimon and Felfili, 2006). Cerrado species are instead likely to rely on other types of regeneration strategies, such as resprouting capacity. Resprouting capacity is more pronounced in savanna species because it permits a rapid response to the impacts of fire and also a strategy for hydric seasonality (Hoffmann et al., 2009). In general, within and between communities, different sets of regeneration traits characterize the species, so that species with low capacity to contribute to seed banks may have good resprouting or dispersal capacity over long distances (Escobar et al., 2021).

Overall, a greater proportion of species with animal-dispersed seeds was found than the wind-dispersed or self-dispersed species. Zoochory is usually the dominant dispersal syndrome in tropical forests, and it is well represented even in environments where fruits are seasonally scarce (Jordano et al., 2007). The dispersal peak for wind-dispersed species occurs during the dry season, while animal-dispersed species takes place throughout the year (van Schaik et al., 1993; Escobar et al., 2018). Thus, here as elsewhere forest trees appear to depend strongly on animals for successful dispersal, which may represent an adaptive advantage in reaching new environments where seedlings can survive away from the zone closest to the parent tree, where they are more likely to encounter reduce predation rates and less conspecific competition (Travesset et al., 2014). Correa et al. (2015) found similar results in 1-ha plots when comparing different vegetation types in neotropical forests in the Colombian Amazon, with zoochory dominant in all plots, but with a high proportion of autochory in places with high levels of disturbance. Regarding the consistency of fruits, a similar pattern was found as in other studies, a predominance of dry fruits in dry forests and savannas and fleshy fruits in more humid forests (Howe and Smallwood, 1982; Tabarelli et al., 2003; Vieira and Scariot, 2006).

The lowest number of seeds per fruit recorded for floodplain forest species may reflect selective pressure in a harsh physical environment for ensuring the seed survive (Jordano, 2014). Fruits with few large seeds increase the chances of seedling establishment, especially when there are limited resources in the environment, reflecting the general trade-off between dispersal and establishment (Parciak, 2002). On the other hand, a large number of small seeds also favours dispersal away from the parent tree due to their greater mobility. Seed number per fruit (seed output) is an important indicator of potential seed production and is inversely related to the seed mass, reflecting per seed resource investment (Henery and Westoby, 2001). In this context, the water present in floodplain forests is an important abiotic filter in the seed production stage (Larson and Funk, 2016), clearly selecting local species that invest resources in the production of few seeds and probably of greater mass. The seeds of high production species are possibly dispersed away from the parent tree because they are lighter and easily dispersed by wind or animals (Thomson et al., 2011).

4.2 Functional diversity and community assembly

The functional diversity of regeneration traits did not differ among the vegetation types of the Amazonian-Cerrado transition. Thus, the amplitude of regeneration traits and the part of the niche space occupied by species are similar (Tilman, 2001; Mason et al., 2005). Functional diversity may be interpreted as reflecting the diversity of niches and ecological functions (Lavorel and Garnier, 2002). It was expected that the functional diversity in forest vegetation types like SF, FF, and GF would be higher because, in these areas, there is higher species richness and, according to Tilman et al. (2014), richness is positively correlated with functional diversity. We did not find differences in the functional diversity between vegetation types, possibly due to the type or quantity of functional traits. Choosing more, or including other fruit or seed traits in the analysis (e.g. seed mass, nutrient concentration in the fruits or partitioning the zoochory by type of animal disperser) could have affected the functional diversity in the vegetation types by increasing (or decreasing) the dimension of the functional space (Petchey and Gaston, 2002).

Considering that functional traits influence how species use the resources present in the environment, complementarity in the use of resources may increase primary productivity and enable more species to coexist (Tilman et al., 1997). Besides, different responses from different species to environmental factors (e.g. fire and extreme climate conditions) contribute to the maintenance of ecosystem function in the long-term (Grime, 1998). In this context, the functional variation that exists in the seasonal and open rainforests of the Amazon-Cerrado transition may enhance the efficiency and complementarity with which populations re-establish themselves, with lower competition, leading to higher species richness and productivity.

On the other hand, the "insurance hypothesis" affirms that a community with redundant species has greater resistance to disturbances. In these communities, important ecosystem functions, such as seed dispersal and fruit set, are more likely to still be performed even after species are lost (Yachi and Loreau, 1999). They may also contribute ecosystem functions to other areas with fewer functional groups. In our study region, seasonal and open rainforests are largely structured based on complementarity, whereas floodplain forests have functional redundancy that ensures that dispersal and re-establishment are more likely to be safely performed in environments subject to a certain restricted set of physical conditions.

We expected that there would be functional clustering of regeneration traits in all communities in which there were strong environmental filters, such as fire for the typical cerrado (Cianciaruso et al., 2012) and water for gallery and floodplain forests (Marimon et al., 2015). However, such clustering was only clearly found in floodplain forests, where species are influenced by strong environmental filters as seasonal flooding, fire, and drought (Maracahipes et al., 2014; Silva et al., 2018). This suggests that the regeneration traits of the vegetation types of the Amazon-Cerrado transition show functional clustering in the presence of severe environmental filters. Another factor that may have caused functional clustering in addition to fire and flooding may have been a restricted pool of dispersers due to flooding, for example reducing zoochory in which dispersal by birds is important. The dispersal and frugivory network has a strong relationship with plant traits so that changes in this interaction can restrict the number and identity of the dispersing agents (González-Castro et al., 2015). It is also possible that the characters chosen here were insufficient to detect patterns of environmental filtering in typical cerrado. According to Cianciaruso et al. (2012), regeneration traits of fruits and seeds are not affected by fire, and dispersal and pollination syndromes play a secondary role in the regeneration of the cerrado, where the ability to resprout is the main strategy.

Regeneration traits play a key role in the maintenance of Amazon Forest biodiversity via niche partitioning, as the traits of co-occurring species differ from those expected from null models (Kraft et al., 2008; Paine et al., 2011). The traits analyzed showed a strong relationship with the competitive vigor and colonization capacities of the species, such as seed production, dispersal, germination, and emergence (Cornelissen et al., 2003). Therefore, the observed functional dispersion reflected the role of competitive hierarchies (Mayfield and Levine, 2010) in structuring forests of the Amazon-Cerrado transition.

4.3 The importance of dispersal syndrome for vegetation types

The dispersal syndrome was the species regeneration trait that best explained the differences in the regeneration functional structure between vegetation types. In fact, different proportions of anemochory, autochory, and zoochory are fundamental to the regeneration classification of vegetation types, especially in distinguishing forests (where the proportion of zoochoric species is higher) from savannas (anemochory and zoochory in similar proportions). Elsewhere, variations in the dispersal syndrome can be characteristic markers of very different tropical vegetation types, perhaps, most notably the fact that in humid forests fleshy fruits dispersed by animals are typical, while in tropical dry forests it is the wind-dispersed fruits that often dominate (Howe and Smallwood, 1982). This result is related to the metabolic cost for the production of fleshy fruits, so that areas with greater availability of water (and nutrients), have a much greater capacity to produce fleshy fruits as a resource for dispersing animals (Tabarelli et al., 2003; Correa et al., 2015). Additionally, our results showed a drastic change in the proportions of anemochory and zoochory between the vegetation types, following a gradient of cover (savanna-forest). The complexity in the structure of the forested areas increases the occurrence of frugivores mainly due to the contrast between the vegetation and the fruits, favouring, for example, the dispersion by the birds (Camargo et al., 2013) and also may limit wind flow, consequently, limiting wind dispersal (Escobar et al., 2021). Thus, the zoochory proportions observed in this study for different types of vegetation can be used as an indicator of the structural complexity of the environments concerning the occurrence of dispersing animals. In this context, seasonal and open rainforests are the most complex environments that best favour the presence of dispersers.

Overall, we found that regeneration strategies differ markedly from the use of small, animal-dispersed fruits in forest vegetation types, to large often wind-dispersed fruits in the savanna. These two functional groups of species represent two distinct functional modes ("strategies") of tree establishment and reproduction. The evaluated traits were sufficient to distinguish the forest from savanna areas, but not to distinguish among forest types. Here, we observed functional clustering (standardized effect size of FD) that until then was in agreement for savanna vegetation but not yet registered for floodplain forests that are also subject to the effect of fire. This is helps to understand the relationship between ecological processes and the diversity of regeneration strategies in these forests. These results enhance our understanding of how these vegetation types will respond to possible disturbances. With regional environmental changes and global climate change strongly affecting the entire transitional region between South America's two largest biomes, such understanding can help us to better predict the stability of biomes and the ability of different species and vegetation types to track these changes.

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Figure Legends

Figure 1. Location of the 39 1-ha plots established in the Amazon-Cerrado transition. TC = typical cerrado, CD = cerradão, GF = gallery forests, FF= floodplain forests, SF = seasonal and open rainforests.

Figure 2. Raincloud plots showing the variation of the regeneration traits between different vegetation types in the Amazon-Cerrado transition. The red dot represents the mean for each vegetation and statistical differences are represented by different letters. The Raincloud plot provides an overview of probability distribution and statistical inference via medians and confidence intervals, combining box plot and violin plot. TC = typical cerrado, CD = cerradão, GF = gallery forests, FF = floodplain forests, SF = evergreen, seasonal and open rainforests.

Figure 3. Ordination produced by the analysis of the principal components of regeneration traits and species found in the vegetation types of the Amazon-Cerrado transition, using the first two dimensions. The traits closest to the axes showed higher eigenvalues. Colored dots represent the species in each vegetation type. ANE = anemochory, AUT = autochory, ZOO = zoochory, N/Seeds = number of seeds per fruit, Length = fruit length, Width = fruit width. TC = typical cerrado, CD = cerradão, GF = gallery forests, FF = floodplain forests, SF = seasonal and open rainforests. Details of the position and length of the vectors are given in Supplementary Table 5 and Supplementary Figure 2).

Figure 4. Box-plot showing the median, upper and lower quartile of functional diversity calculated as FD index with no significant difference between different vegetation types in the Amazon-Cerrado transition TC = typical cerrado, CD = cerradão, GF = gallery forests, FF = floodplain forests, SF = seasonal and open rainforests.

Figure 5. Standardized effect size of functional diversity of regeneration traits in different vegetation types in the Amazon-Cerrado transition. The * symbol indicates significant non-zero values ($P<0.05$). Confidence intervals = 95%. TC = typical cerrado, CD = cerradão, GF = gallery forests, FF = floodplain forests, SF = seasonal and open rainforests.

Figure 6. A Bayesian average model of regeneration traits from different vegetation types in the Amazon-Cerrado transition. Dispersion = dispersal syndrome, Fruit consist. = fruit consistency, Width = fruit width, Length = fruit length, No. seeds = number of seeds per fruit. The Y-axis contains the regeneration traits as predictors of vegetation types while the X-axis shows an accumulated probability of models. Positive coefficients are indicated by blue, negative coefficients by orange, and white indicates non-inclusion of the respective predictor.

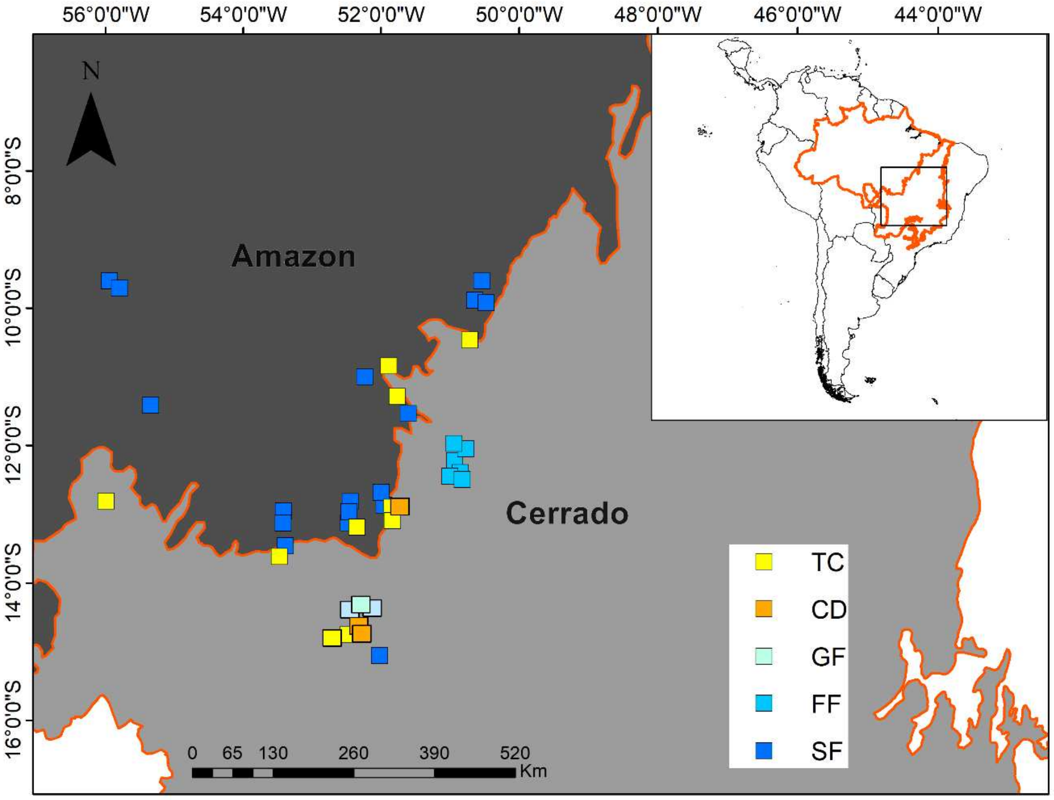
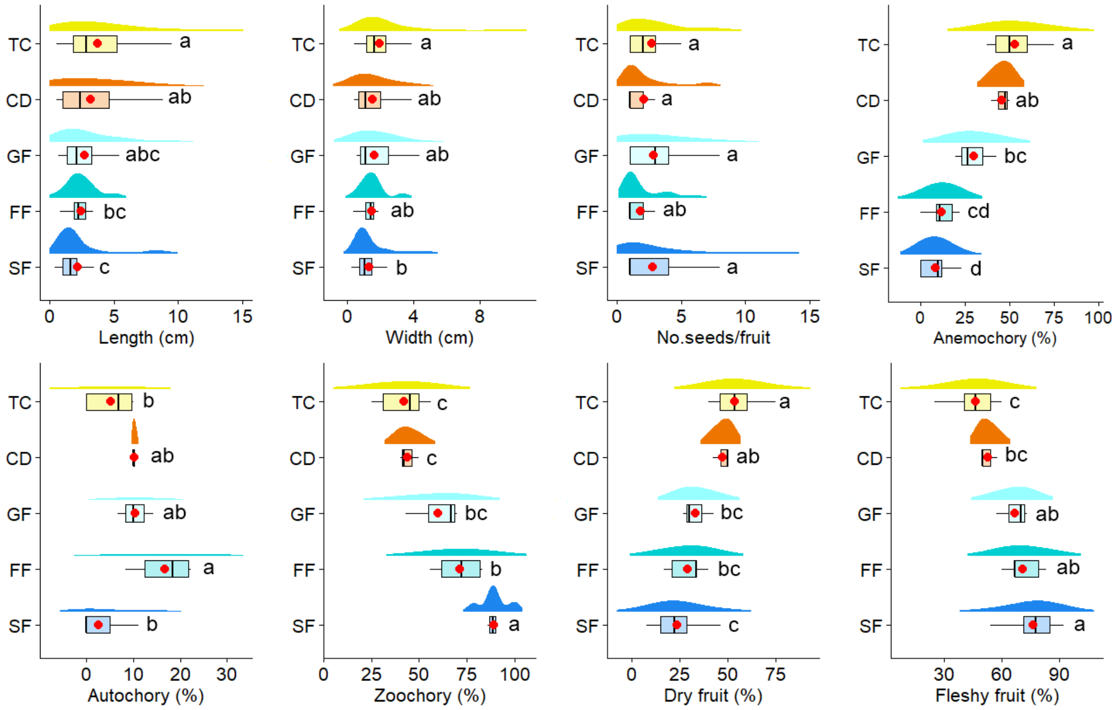


Figure 1.



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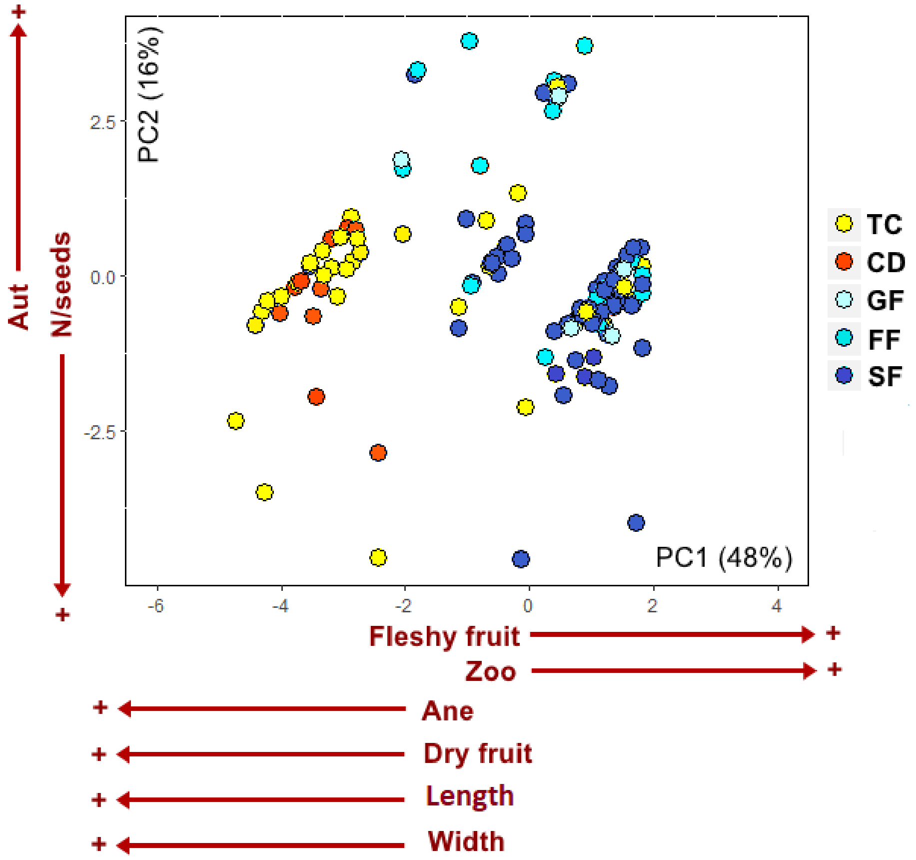

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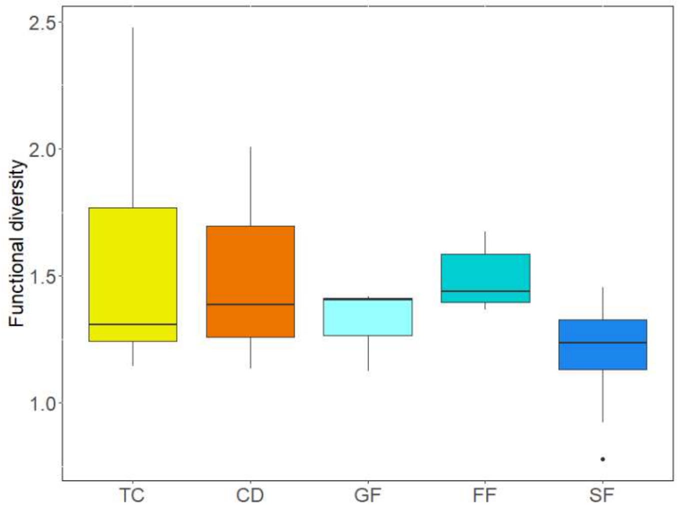

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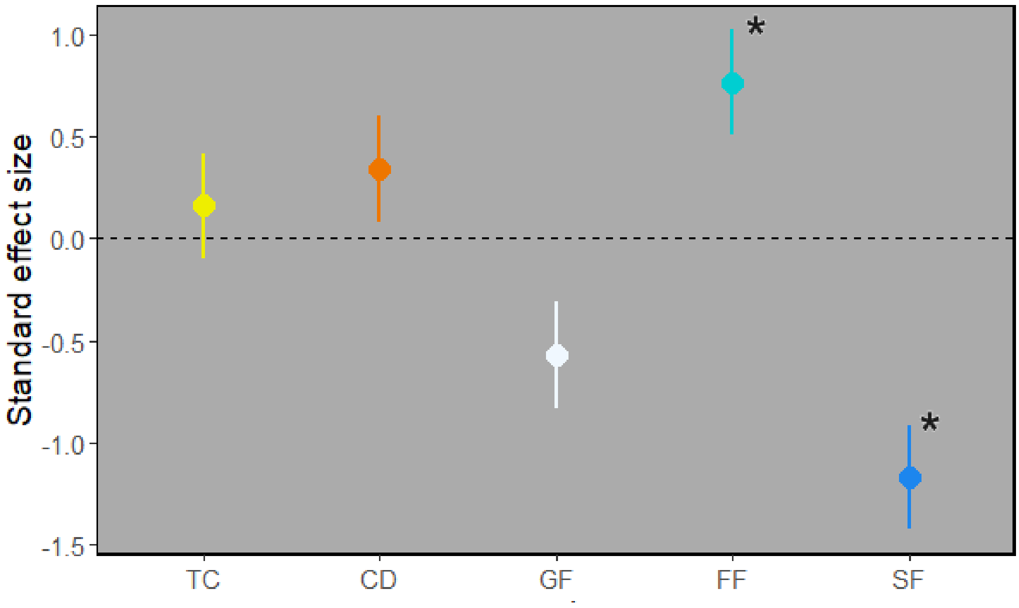

Figure 5.

Figure 6.

Table 1. Structural parameters for vegetation types in in the Amazon-Cerrado transition. H = mean tree height (m); LAI = mean leaf area index (m²/m²); BA = mean tree basal area (m²/ha^{-1}); TD = mean tree density. The means were calculated using the values of the plots of each vegetation type. The biome for vegetation type was defined by the occurrence of plots (see Figure 1).

Vegetation type	**Acroym**	**Biome**	**H**	**LAI**	**BA**	**TD**
Typical cerrado	TC	Amazonia/Cerrado	5.80	1.6	8.49	404.8

Cerradão	CD	Cerrado	8.34	2.8	13.71	465.6
Gallery forest	GF	Cerrado	9.48	3.6	20.63	248.6
Floodplain forest	FF	Cerrado	10.67	3.4	25.25	811.5
Seasonal and open rainforests	SF	Amazonia/Cerrado	12.51	6.1	19.01	490.8