



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

Wesley Jonatar Alves da Cruz^{a,*}, Beatriz Schwantes Marimon^a, Ben Hur Marimon Junior^a, Izabel Amorim^a, Paulo S. Morandi^a, Oliver L. Phillips^b

^a Programa de Pós-graduação em ecologia e conservação (PPGEC), Universidade do Estado de Mato Grosso – UNEMAT, Campus de Nova Xavantina, MT 78690-000, Brasil

^b University of Leeds, School of Geography, Leeds, LS2 9JT, United Kingdom

ARTICLE INFO

Edited by Gerhard Overbeck

Keywords:

Functional trait
Seed dispersal
Fruit
Forest
Savanna
Ecological strategy

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. 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. By considering regeneration traits in the study of tree recruitment and establishment, we will increase our understanding about the dynamics of tree communities in neotropical forests and savannas.

1. Introduction

Regeneration traits are important elements in plant community ecology, affecting the processes of dispersal, germination, colonization, and establishment of plants in the environment (Vandelook et al., 2012; Romero-Saritamá 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). Different 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 community

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

* Corresponding author.

E-mail addresses: wesleyjonatar@gmail.com, wesley.jonatar@unemat.br (W.J.A. Cruz), biamarimon@unemat.br (B.S. Marimon), bhmjunior@gmail.com (B.H. Marimon Junior), bebeellamorim@gmail.com (I. Amorim), morandibio@gmail.com (P.S. Morandi), O.Phillips@leeds.ac.uk (O.L. Phillips).

<https://doi.org/10.1016/j.flora.2021.151952>

Received 5 April 2021; Received in revised form 5 October 2021; Accepted 9 October 2021

Available online 13 October 2021

0367-2530/© 2021 Elsevier GmbH. All rights reserved.

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).

Different processes drive community dynamics in forest and savanna, with the open savanna environment being characterised by occurrence of fire and high light availability, and forests characterised by a closed canopy, higher air humidity and often also higher soil moisture and soil nutrient conditions (Hoffman et al., 2004, 2009; Torello-Raventos et al., 2013). These sets of environmental conditions have been linked to describe what is currently known about regenerative strategies in forests and savannas. In open savannas of the Cerrado, wind dispersal predominates at the end of the rainy season and in the dry season (Kuhlmann and Ribeiro, 2016), as well as with pronounced post-fire resprouting (Scalon et al., 2020). In contrast, in the tropical forest, dispersal by animals occurs 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 species with a short life cycle ("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, as the region is characterized by complex interactions among environmental factors (Marimon et al., 2006). 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). These vegetation types form 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 multi-trait 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 vegetation types along the savanna-forest transition?* 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 fruits in drier forests and savannas (Tabarelli et al., 2003; Correa et al., 2015); b) *Do 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 hypothesized that in our set of traits, fruit dimension would be the best predictor, as for zoochoric species, tall plants with large fruits may attract highly mobile dispersers that can take seed long distances (Thomson et al., 2011). To test these hypotheses, 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 (Fig. 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), floodplain forests (FF = 6), seasonal and open rainforests (SF = 17). The latter category includes the typical forest types, that are representatives of the peripheral region of the Amazonia Forest in the transition zone with the Cerrado: semideciduous seasonal forest, evergreen seasonal forest, and open rainforest (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 1511 to 2353 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 borders 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 abundant species that composed up to 80% of the basal area of each plot, following the method recommended by Garnier et al. (2004).

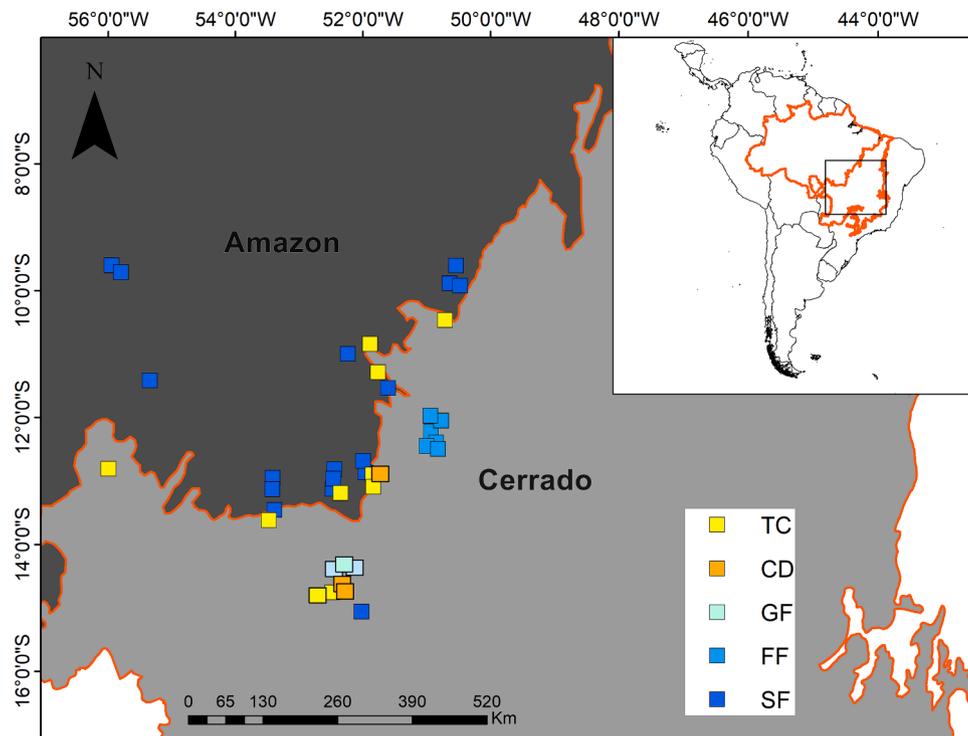


Fig. 1. Location of the 39 1-ha plots established in the Amazon-Cerrado transition. TC = typical cerrado, CD = cerradão, GF = gallery forests, FF = floodplain forests, SF = seasonal and open rainforests. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1

Structural parameters for vegetation types in the Amazon-Cerrado transition. H = mean tree height (m); LAI = mean leaf area index (m^2/m^2); BA = mean tree basal area ($\text{m}^2/\text{ha}^{-1}$); 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 Fig. 1).

Vegetation type	Acronym	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

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 \times 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 1000 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): $\text{Standardized effect size } (Z) = -(\text{obsFD} - \text{rndFD})/\text{sd.rndFD}$. 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 1000 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) (Fig. 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 (Fig. 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 (Fig. 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 (Fig. 2 and Supplementary Table 1).

The highest percentage of zoochory was recorded in more forested vegetation (GF = 59.84 ± 14.80 , FF = 71.11 ± 12.06 , and SF = 89.11 ± 6.86) 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) (Fig. 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%) (Fig. 3). Three main clusters, represented by anemochoric species with dry fruits, zoochoric species with fleshy fruits, and autochoric species, were observed (Fig. 3). We found a clear division between more forested vegetation (GF, FF and SF), typical cerrado (TC) and cerradão (CD). Some typical cerrado species were found to be associated to forest species: *Curatella americana* L., *Guapira graciliflora* (Mart. ex J.A.Schmidt) Lundell, *Guapira noxia* (Netto) Lundell and *Myrcia splendens* (Sw.) DC., all of them species with small fleshy fruits dispersed by zoochory.

Vegetation types did not differ in functional diversity (FD index) of regeneration traits (Fig. 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 (Fig. 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) (Fig. 6 and Supplementary Table 6).

4. Discussion

Our results showed differences among the vegetation types in all the regeneration traits examined, resulting in great variation in functional characteristics and ecological strategies among the vegetation types of

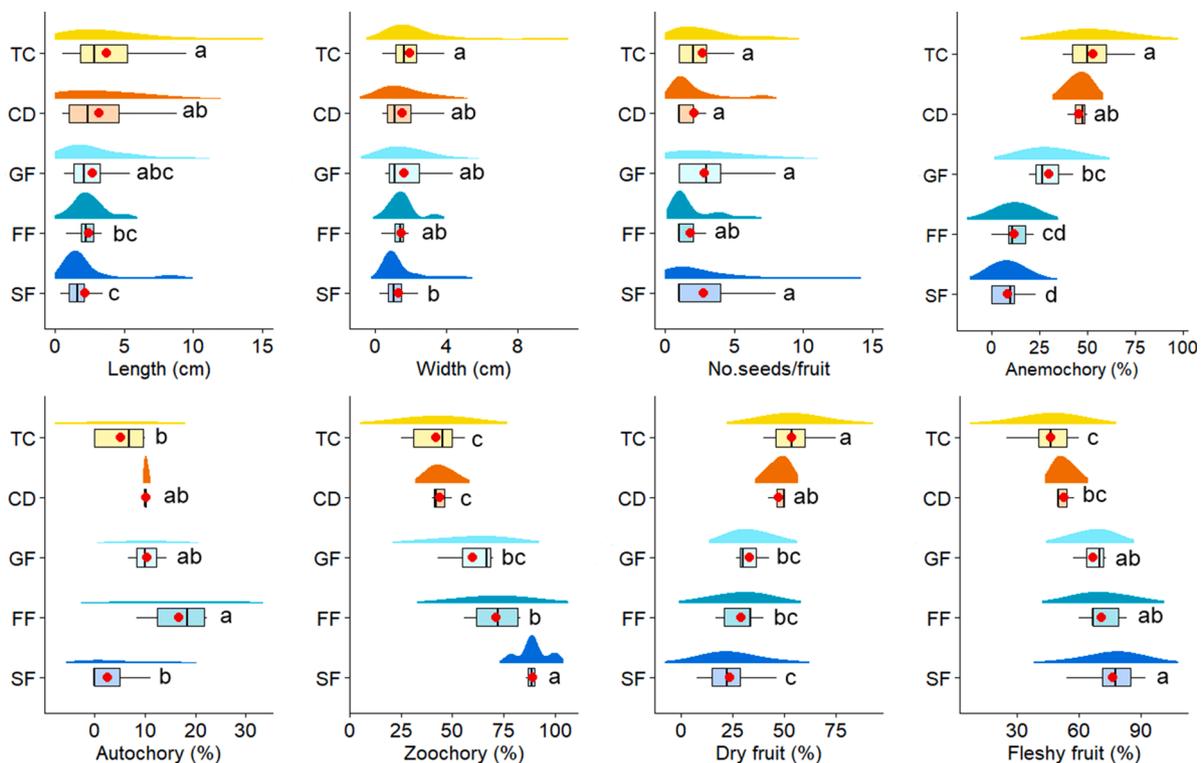


Fig. 2. Raincloud plots showing the variation of the regeneration traits between different vegetation types in the Amazon-Cerrado transition. The red dot represents the mean for each vegetation and statistical differences are represented by different letters. The Raincloud plot provides an overview of 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. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

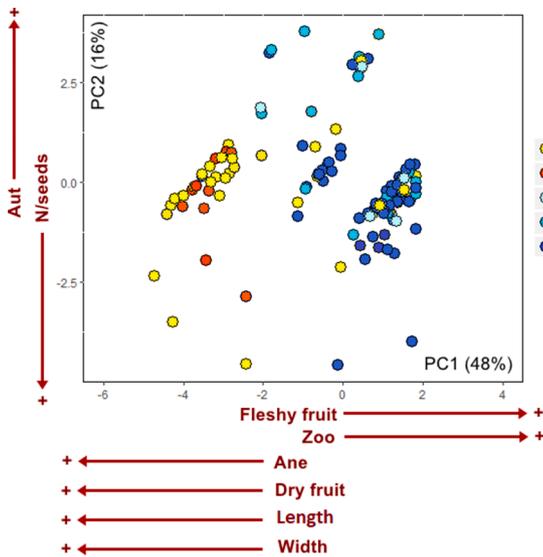


Fig. 3. Ordination produced by the analysis of the principal components of regeneration traits and species found in the vegetation types of the Amazon-Cerrado transition, using the first two dimensions. The traits closest to the axes showed higher eigenvalues. Colored dots represent the species in each 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). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

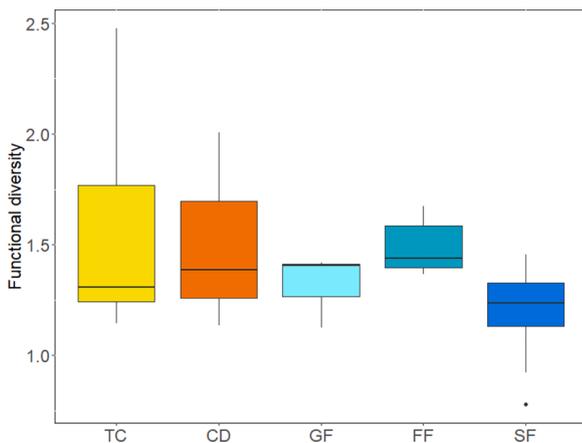


Fig. 4. Box-plot showing the median, upper and lower quartile of functional diversity calculated as FD index with no significant difference between different vegetation types in the Amazon-Cerrado transition TC = typical cerrado, CD = cerradão, GF = gallery forests, FF = floodplain forests, SF = seasonal and open rainforests. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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 important

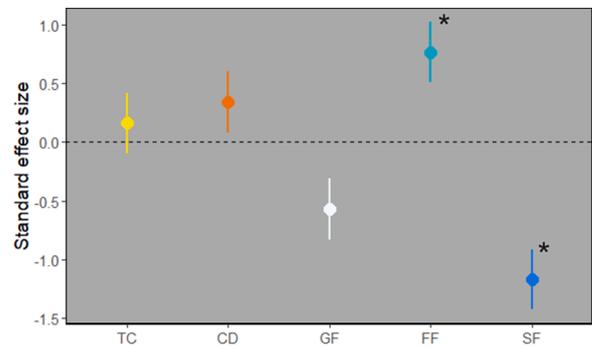


Fig. 5. Standardized effect size of functional diversity of regeneration traits in different vegetation types in the Amazon-Cerrado transition. The * symbol indicates significant non-zero values ($P < 0.05$). Confidence intervals = 95%. TC = typical cerrado, CD = cerradão, GF = gallery forests, FF = floodplain forests, SF = seasonal and open rainforests. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

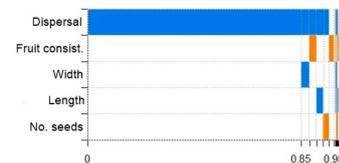


Fig. 6. A Bayesian average model of regeneration traits from different vegetation types in the Amazon-Cerrado transition. Dispersal = dispersal syndrome, Fruit consist. = fruit consistency, Width = fruit width, Length = fruit length, No. seeds = number of seeds per fruit. The Y-axis contains the regeneration 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. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

variable among the set of regeneration traits.

4.1. Variation of regeneration traits among vegetation types

These differences in functional traits highlight variability in recolonization capacity, competitive vigor, and response to disturbance (Romero-Saritamá and Pérez-Ruíz, 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-Saritamá and Pérez-Ruíz, 2016), savannas (García-Nuñez 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 other vegetation types. These fruits have higher exposure in the environment, requiring investment in resistance adaptations (Romero-Saritamá and Pérez-Ruíz, 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. This is due to the fact that 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 is 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-aided dispersal 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 (Traveset 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 seed survival (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 (Petchev 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 functionally 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 analysed 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 difference 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 fruit favouring, for example, dispersal by 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 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.

CRedit authorship contribution statement

Wesley Jonatar Alves da Cruz: Writing – original draft, Writing – review & editing, Investigation, Formal analysis, Visualization. **Beatriz Schwantes Marimon:** Conceptualization, Visualization, Investigation, Resources, Supervision, Project administration, Funding acquisition. **Ben Hur Marimon Junior:** Conceptualization, Resources, Funding acquisition. **Izabel Amorim:** Data curation. **Paulo S. Morandi:** Formal analysis, Visualization. **Oliver L. Phillips:** Conceptualization, Investigation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank to the support of the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) - Financing Code 001. We are grateful to Fundação de Amparo à Pesquisa do Estado de Mato Grosso (FAPEMAT) with scholarships granted to students who participated in the research (WJAC, IA). We thank the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) that financed the Projeto Ecológico de Longa Duração (PELD), Cerrado-Amazon transition: ecological and socio-environmental bases for conservation, stage III (#441244/2016–5) and the PVE project (#401279/2014–6) to OLP. Thanks go to the team of the Laboratório de Ecologia Vegetal (LABEV) of the Universidade do Estado de Mato Grosso (UNEMAT), for their help with field and laboratory work, and to RT for the valuable comments in the manuscript.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.flora.2021.151952.

References

- Alvares, C.A., Stape, J.L., Sentelhas, P.C., de Moraes, G., Leonardo, J., Sparovek, G., 2013. Köppen’s climate classification map for Brazil. *Meteorol. Z.* 22 (6), 711–728. <https://doi.org/10.1127/0941-2948/2013/0507>.
- Barroso, G.M., Morim, M.P., Peixoto, A.L., Ichaso, C.L.F., 2000. *Frutos e Sementes: Morfologia Aplicada à Sistemática De Dicotiledôneas*. Universidade Federal de Viçosa, Viçosa.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67 (1), 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Camargo, M.G.G., Cazetta, E., Schaefer, H.M., Morellato, L.P.C., 2013. Fruit color and contrast in seasonal habitats—a case study from a cerrado savanna. *Oikos* 122 (9), 1335–1342. <https://doi.org/10.1111/j.1600-0706.2013.00328.x>.
- Chase, M.W., Christenhusz, M.J.M., Fay, M.F., Byng, J.W., Judd, W.S., Soltis, D.E., et al., 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Bot. J. Linn. Soc.* 181 (1), 1–20. <https://doi.org/10.1111/boj.12385>.
- Cianciaruso, M.V., Silva, I.A., Batalha, M.A., Gaston, K.J., Petchey, O.L., 2012. The influence of fire on phylogenetic and functional structure of woody savannas: moving from species to individuals. *Perspect. Plant Ecol. Evol. Syst.* 14 (3), 205–216. <https://doi.org/10.1016/j.ppees.2011.11.004>.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., et al., 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust. J. Bot.* 51 (4), 335–380. <https://doi.org/10.1071/BT02124>.
- Correa, D.F., Álvarez, E., Stevenson, P.R., 2015. Plant dispersal systems in Neotropical forests: availability of dispersal agents or availability of resources for constructing zoochorous fruits? *Glob. Ecol. Biogeogr.* 24 (2), 203–214. <https://doi.org/10.1111/geb.12248>.
- Dray, S., Dufour, A.B., Chessel, D., 2007. The ade4 package-II: two-table and K-table methods. *R News* 7 (2), 47–52.
- Escobar, D.F., Silveira, F.A., Morellato, L.P.C., 2018. Timing of seed dispersal and seed dormancy in Brazilian savanna: two solutions to face seasonality. *Ann. Bot.* 121 (6), 1197–1209. <https://doi.org/10.1093/aob/mcy006>.
- Escobar, D.F., Silveira, F.A., Morellato, L.P.C., 2021. Do regeneration traits vary according to vegetation structure? A case study for savannas. *J. Veget. Sci.* 32 (1), e12940. <https://doi.org/10.1111/jvs.12940>.
- Fragoso, T.M., Bertoli, W., Louzada, F., 2018. Bayesian model averaging: a systematic review and conceptual classification. *Int. Stat. Rev.* 86 (1), 1–28. <https://doi.org/10.1111/insr.12243>.
- García-Núñez, C., Azócar, A., 2004. *Ecología de la regeneración de árboles de la sabana*. *Ecotropicos* 17 (1–2), 1–24.
- Garnier, E., Cortez, J., Billès, G., Navas, M.L., Roumet, C., Debussche, M., et al., 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85, 2630–2637. <https://doi.org/10.1890/03-0799>.
- Girão, L.C., Lopes, A.V., Tabarelli, M., Bruna, E.M., 2007. Changes in tree reproductive traits reduce functional diversity in a fragmented Atlantic forest landscape. *PLoS ONE* 2 (9), e908. <https://doi.org/10.1371/journal.pone.0000908>.
- González-Castro, A., Yang, S., Nogales, M., Carlo, T.A., 2015. Relative importance of phenotypic trait matching and species’ abundances in determining plant-avianseed dispersal interactions in a small insular community. *AoB Plants* 7, plv017.
- Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* 86 (6), 902–910. <https://doi.org/10.1046/j.1365-2745.1998.00306.x>.
- Grime, J.P., 2006. *Plant Strategies, Vegetation Processes and Ecosystem Properties*, 2nd ed. Wiley, New York.
- Grubb, P.J., 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52 (1), 107–145.
- Henery, M.L., Westoby, M., 2001. Seed mass and seed nutrient content as predictors of seed output variation between species. *Oikos* 92 (3), 479–490. <https://doi.org/10.1034/j.1600-0706.2001.920309.x>.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25 (15), 1965–1978. <https://doi.org/10.1002/joc.1276>.
- Hoeting, J.A., Madigan, D., Raftery, A.E., Volinsky, C.T., 1999. Bayesian model averaging: a tutorial. *Stat. Sci.* 382–401.
- Hoffmann, W.A., Orthen, B., Franco, A.C., 2004. Constraints to seedling success of savanna and forest trees across the savanna-forest boundary. *Oecologia* 140 (2), 252–260. <https://doi.org/10.1007/s00442-004-1595-2>.
- Hoffmann, W.A., Adasme, R., Haridasan, M.T., de Carvalho, M., Geiger, E.L., Pereira, M.A., et al., 2009. Tree topkill, not mortality, governs the dynamics of savanna-forest boundaries under frequent fire in central Brazil. *Ecology* 90 (5), 1326–1337. <https://doi.org/10.1890/08-0741.1>.
- Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. *Biomet. J.* 50 (3), 346–363. <https://doi.org/10.1002/bimj.200810425>.
- Houle, G., 1991. Regenerative traits of tree species in a deciduous forest of north eastern North America. *Ecography* 14 (2), 142–151. <https://doi.org/10.1111/j.1600-0587.1991.tb00645.x>.

- Howe, H.F., Smallwood, J., 1982. Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.* 13 (1), 201–228. <https://doi.org/10.1146/annurev.es.13.110182.001221>.
- Hutchings, M.J., 1986. Plant population biology. In: Moore, P.D., Chapman, S.B. (Eds.), *Methods in Plant Ecology*. Blackwell Scientific Publications, Boston, pp. 377–435.
- Ivanaukas, N.M., Monteiro, R., Rodrigues, R.R., 2008. Classificação fitogeográfica das florestas do Alto Rio Xingu. *Acta Amazon* 38 (3), 387–402. <https://doi.org/10.1590/S0044-59672008000300003>.
- Jordano, P., 2014. Fruits and frugivory. In: Gallagher, R.S. (Ed.), *Seeds: The Ecology of Regeneration in Plant Communities*. CABI, Wallingford, pp. 18–61.
- Jordano, P., García, C., Godoy, J.A., García-Castano, J.L., 2007. Differential contribution of frugivores to complex seed dispersal patterns. *Proc. Natl. Acad. Sci. U.S.A.* 104, 3278–3282. <https://doi.org/10.1073/pnas.0606793104>.
- Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, S.P., et al., 2010. Picante: r tools for integrating phylogenies and ecology. *Bioinformatics* 26, 1463–1464. <https://doi.org/10.1093/bioinformatics/btq166>.
- Kraft, N.J., Valencia, R., Ackerly, D.D., 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* 322 (5901), 580–582. <https://doi.org/10.1126/science.1160662>.
- Kuhlmann, M., Ribeiro, J.F., 2016. Evolution of seed dispersal in the Cerrado biome: ecological and phylogenetic considerations. *Acta Bot. Brasiliica* 30, 271–282. <https://doi.org/10.1590/0102-33062015abb0331>.
- Larson, J.E., Funk, J.L., 2016. Regeneration: an overlooked aspect of trait-based plant community assembly models. *J. Ecol.* 104 (5), 1284–1298. <https://doi.org/10.1111/1365-2745.12613>.
- Lavorel, S., Garnier, É., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.* 16 (5), 545–556. <https://doi.org/10.1046/j.1365-2435.2002.00664.x>.
- Lopez-Gonzalez, G., Lewis, S.L., Burkitt, M., Phillips, O.L., 2011. ForestPlots.net: a web application and research tool to manage and analyse tropical forest plot data. *J. Veget. Sci.* 22, 610–613. <https://doi.org/10.1111/j.1654-1103.2011.01312.x>.
- Lorenzi, H., 1998. *Árvores brasileiras: Manual de Identificação e Cultivo de Plantas Arbóreas Nativas Do Brasil*, 2. Instituto Plantarum de Estudos da Flora Ltda, Nova Odessa.
- Maracahipes, L., Marimon, B.S., Lenza, E., Marimon-Junior, B.H., de Oliveira, E.A., Mews, H.A., et al., 2014. Post-fire dynamics of woody vegetation in seasonally flooded forests (impuncas) in the Cerrado-Amazonian Forest transition zone. *Flora-Morphol., Distrib. Funct. Ecol. Plants* 209 (5–6), 260–270. <https://doi.org/10.1016/j.flora.2014.02.008>.
- Marimon, B.S., Colli, G.R., Marimon-Junior, B.H., Mews, H.A., Eisenlohr, P.V., Feldpausch, T.R., et al., 2015. Ecology of floodplain Campos de murundum savanna in southern Amazonia. *Int. J. Plant Sci.* 176 (7), 670–681. <https://doi.org/10.1086/682079>.
- Marimon, B.S., Felgili, J.M., Lima, E.S., 2002. Floristics and phytosociology of the gallery forest of the Bacaba Stream, Nova Xavantina, Mato Grosso, Brazil. *Edinburgh J. Bot.* 59 (2), 303. <https://doi.org/10.1017/S0960428602000124>.
- Marimon, B.S., Felgili, J.M., 2006. Chuva de sementes em uma floresta monodominante de *Brosimum rubescens* Taub. e em uma floresta mista adjacente no Vale do Araguaia, MT, Brasil. *Acta Bot. Brasiliica* 20, 423–432. <https://doi.org/10.1590/S0102-33062006000200017>.
- Marimon, B.S., Lima, E.D.S., Duarte, T.G., Chieregatto, L.C., Ratter, J.A., 2006. Observations on the vegetation of northeastern Mato Grosso, Brazil. IV. An analysis of the Cerrado-Amazonian Forest ecotone. *Edinburgh J. Bot.* 63 (2–3), 323–341. <https://doi.org/10.1017/S0960428606000576>.
- Marimon, B.S., Marimon-Junior, B.H., Feldpausch, T.R., Oliveira-Santos, C., Mews, H.A., Lopez-Gonzalez, G., et al., 2014. Disequilibrium and hyperdynamic tree turnover at the forest-cerrado transition zone in southern Amazonia. *Plant. Ecol. Divers.* 7 (1–2), 281–292. <https://doi.org/10.1080/17550874.2013.818072>.
- Marimon, B.S., Oliveira-Santos, C., Marimon-Junior, B.H., Elias, F., de Oliveira, E.A., Morandi, P.S., et al., 2020. Drought generates large, long-term changes in tree and liana regeneration in a monodominant Amazon forest. *Plant. Ecol.* 1–15. <https://doi.org/10.1007/s11258-020-01047-8>.
- Marques, E.Q., Marimon-Junior, B.H., Marimon, B.S., Matricardi, E.A., Mews, H.A., Colli, G.R., 2019. Redefining the Cerrado-Amazonia transition: implications for conservation. *Biodivers. Conserv.* 29, 1501–1517. <https://doi.org/10.1007/s10531-019-01720-z>.
- Mason, N.W., Moullot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111 (1), 112–118. <https://doi.org/10.1111/j.0030-1299.2005.13886.x>.
- Mayfield, M.M., Levine, J.M., 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecol. Lett.* 13 (9), 1085–1093. <https://doi.org/10.1111/j.1461-0248.2010.01509.x>.
- Nogueira, D.S., Marimon, B.S., Marimon-Junior, B.H., Oliveira, E.A., Morandi, P., Reis, S.M., et al., 2019. Impacts of fire on forest biomass dynamics at the southern amazon edge. *Environ. Conserv.* 46 (4), 285–292. <https://doi.org/10.1017/S0376892919000110>.
- Oksanen, F.J., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., et al., 2017. *Vegan: Community Ecology Package*. R package version 2.4-4. 5. <http://cran.r-project.org/>. (accessed in February 2018).
- Paine, C.E.T., Baraloto, C., Chave, J., Herault, B., 2011. Functional traits of individual trees reveal ecological constraints on community assembly in tropical rain forests. *Oikos* 120, 720–727. <https://doi.org/10.1111/j.1600-0706.2010.19110.x>.
- Paradis, E., Claude, J., Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20, 289–290. <https://doi.org/10.1093/bioinformatics/btg412>.
- Parciak, W., 2002. Seed size, number, and habitat of a fleshy-fruited plant: consequences for seedling establishment. *Ecology* 83 (3), 794–808. [https://doi.org/10.1890/0012-9658\(2002\)083\[0794:SSNAH\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[0794:SSNAH]2.0.CO;2).
- Pavoine, S., Vallet, J., Dufour, A.B., Gachet, S., Daniel, H., 2009. On the challenge of treating various types of variables: application for improving the measurement of functional diversity. *Oikos* 118 (3), 391–402. <https://doi.org/10.1111/j.1600-0706.2008.16668.x>.
- Perez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, C., et al., 2016. Corrigendum to: new handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot.* 64 (8), 715–716. <https://doi.org/10.1071/BT12225.CO>.
- Petchey, O.L., Gaston, K.J., 2002. Functional diversity (FD), species richness and community composition. *Ecol. Lett.* 5, 402–411. <https://doi.org/10.1046/j.1461-0248.2002.00339.x>.
- Phillips, O., Baker, T., Feldpausch, T., Brienen, R., Almeida, S., Arroyo, L., Vásquez, R., 2009. *RAINFOR Field Manual For Plot Establishment and Remasement*. Moore Foundation, Leeds, UK.
- Pires, J.M., Prance, G.T., 1985. The vegetation types of the Brazilian Amazon. In: Prance, G.T., Lovejoy, T.E. (Eds.), *Key Environments: Amazonia*. Pergamon Press, Oxford (UK), pp. 109–145.
- Pott, A., Pott, V.J., 1994. *Plantas Do Pantanal*. EMBRAPA-Pantanal, Brasília.
- Powers, J.S., Becknell, J.M., Irving, J., Pérez-Aviles, D., 2009. Diversity and structure of regenerating tropical dry forests in Costa Rica: geographic patterns and environmental drivers. *For. Ecol. Manage.* 258 (6), 959–970. <https://doi.org/10.1016/j.foreco.2008.10.036>.
- R Core Team, 2018. *A Language and Environment For Statistical Computing*. R Foundation for Statistical Computing, Vienna. <https://www.r-project.org/>. accessed in February 2018.
- Ratter, J.A., Richards, P.W., Argent, G., Gifford, D.R., 1973. Observations on the vegetation of northeastern Mato Grosso: I. The woody vegetation types of the Xavantina-Cachimbo Expedition area. *Philos. Trans. R. Soc. London. B, Biol. Sci.* 266 (880), 449–492.
- Ribeiro, L.C., Barbosa, E.R., van Langevelde, F., Borghetti, F., 2015. The importance of seed mass for the tolerance to heat shocks of savanna and forest tree species. *J. Veg. Sci.* 26 (6), 1102–1111. <https://doi.org/10.1111/jvs.12314>.
- Romero-Saritamá, J.M., Pérez-Ruíz, C., 2016. Rasgos morfológicos regenerativos en una comunidad de especies leñosas en un bosque seco tropical tumbesino. *Rev. Biol. Trop.* 64 (2), 859–873. <https://doi.org/10.15517/RBT.V64I2.20090>.
- Salazar, A., Goldstein, G., Franco, A.C., Miralles-Wilhelm, F., 2011. Timing of seed dispersal and dormancy, rather than persistent soil seed-banks, control seedling recruitment of woody plants in Neotropical savannas. *Seed Sci. Res.* 21 (2), 103–116. <https://doi.org/10.1017/S0960258510000413>.
- Scalon, M.C., Bicalho, F.D.M.C., Cruz, W.J.A., Marimon-Júnior, B.H., Marimon, B.S., e Oliveras, I., 2020. Diversity of functional trade-offs enhances survival after fire in Neotropical savanna species. *J. Veg. Sci.* 31 (1), 139–150. <https://doi.org/10.1111/jvs.12823>.
- Silva, A.P.G., Mews, H.A., Marimon-Junior, B.H., De Oliveira, E.A., Morandi, P.S., Oliveras, I., 2018. Recurrent wildfires drive rapid taxonomic homogenization of seasonally flooded Neotropical forests. *Environ. Conserv.* 45 (4), 378–386. <https://doi.org/10.1017/S0376892918000127>.
- Tabarelli, M., Vicente, A., Barbosa, D.C.A., 2003. Variation of seed dispersal spectrum of woody plants across a rainfall gradient in north-eastern Brazil. *J. Arid Environ.* 53 (2), 197–210. <https://doi.org/10.1006/jare.2002.1038>.
- Thompson, K.B.S.R., Band, S.R., Hodgson, J.G., 1993. Seed size and shape predict persistence in soil. *Funct. Ecol.* 7, 236–241. <https://doi.org/10.2307/2389893>.
- Thomson, F.J., Moles, A.T., Auld, T.D., Kingsford, R.T., 2011. Seed dispersal distance is more strongly correlated with plant height than with seed mass. *J. Ecol.* 99 (6), 1299–1307. <https://doi.org/10.1111/j.1365-2745.2011.01867.x>.
- Tilman, D., 2001. *Functional diversity*. In: Levin, S.A. (Ed.), *Encyclopedia of Biodiversity*. Academic Press, San Diego, pp. 109–120.
- Tilman, D., Isbell, F., Cowles, J.M., 2014. Biodiversity and ecosystem functioning. *Annu. Rev. Ecol. Syst.* 45, 471–493. <https://doi.org/10.1146/annurev-ecolsys-120213-091917>.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E., 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277 (5330), 1300–1302. <https://doi.org/10.1126/science.277.5330.1300>.
- Torello-Raventos, M., Feldpausch, T.R., Veenendaal, E., Schrod, F., Saiz, G., Domingues, T.F., et al., 2013. On the delineation of tropical vegetation types with an emphasis on forest/savanna transitions. *Plant. Ecol. Divers.* 6 (1), 101–137. <https://doi.org/10.1080/17550874.2012.762812>.
- Traveset, A., Heleno, R., Nogales, M., 2014. The ecology of seed dispersion. In: Fenner, M. (Ed.), *Seeds: The Ecology of Regeneration in Plant Communities*. CABI, Publishing, Wallingford, pp. 62–93.
- Vamosi, S.M., Heard, S.B., Vamosi, J.C., Webb, C.O., 2009. Emerging patterns in the comparative analysis of phylogenetic community structure. *Mol. Ecol.* 18 (4), 572–592. <https://doi.org/10.1111/j.1365-294X.2008.04001.x>.
- van Schaik, C.P., Ter borgh, J.W., Wright, S.J., 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annu. Rev. Ecol. Syst.* 24 (1), 353–377.
- Vandelook, F., Verdú, M., Honnay, O., 2012. The role of seed traits in determining the phylogenetic structure of temperate plant communities. *Ann. Bot.* 110 (3), 629–636. <https://doi.org/10.1093/aob/mcs121>.
- Vargas-Rodríguez, Y.L., Vázquez-García, J.A., Williamson, G.B., 2005. Environmental correlates of tree and seedling-sapling distributions in a Mexican tropical dry forest. *Plant. Ecol.* 180 (1), 117–134. <https://doi.org/10.1007/s11258-005-30269>.

- Vieira, D.L., Scariot, A., 2006. Principles of natural regeneration of tropical dry forests for restoration. *Restor. Ecol.* 14 (1), 11–20. <https://doi.org/10.1111/j.1526-100X.2006.00100.x>.
- Webb, C.O., 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *Am. Nat.* 156 (2), 145–155. <https://doi.org/10.1086/303378>.
- Webb, C.O., Ackerly, D.D., McPeck, M.A., Donoghue, M.J., 2002. Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.* 33 (1), 475–505. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150448>.
- Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Nat. Acad. Sci.* 96 (4), 1463–1468. <https://doi.org/10.1073/pnas.96.4.1463>.
- Zeugner, S., Feldkircher, M., 2015. Bayesian model averaging employing fixed and flexible priors: the BMS Package for R. *J. Stat. Softw.* 68 (4), 1–37. <http://hdl.handle.net/10.18637/jss.v068.i04>.