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

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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 diasporic dimensions (width and length). We found differences among the vegetation types, in all regeneration traits. These tended to 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-Saritama and Pérez-Ruíz, 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 Scarlott, 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, wesleyjonatar@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).

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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; Torell-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 (Kubhmann 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 be the same or different? 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.ibjb.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 Brasília, 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 diaspora 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 herbarized samples available online (http://splink.cria.org.br, http://fm1. fieldmuseum.org/vrvtc, 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).
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 the \textit{lme4} package (\cite{bates2015lme4}), 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 \textit{a posteriori} for multiple comparisons of values between groups (vegetation type) using the \textit{multcomp} package (\cite{hothorn2008multcomp}).

We also performed an ordination based on a principal component analysis (PCA) using the \textit{vegan} package in a matrix consisting of the functional traits of each species per vegetation type (\cite{oksanen2017vegan}).

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) (\cite{pavoine2009gower}) in the \textit{ade4} (\cite{dray2007ade4}) and \textit{ape} packages (\cite{paradis2004ape}). 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 \textit{Picante} package (\cite{kembel2010picante}):

\[
\text{Standardized effect size (Z)} = \frac{\text{obsFD} - \text{rndFD}}{\text{sd.rndFD}}.
\]

The observed FD (Functional diversity index), \text{obsFD} is the FD mean of null communities, and \text{sd.rndFD} is the standard deviation of the 1000 random values of the FD (see \cite{cianciaruso2012functional}).

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) (\cite{webb2000functional}).

To determine which regeneration traits were the best predictors among the set of functional traits, we used the Bayesian average model with the \textit{BMS} package (\cite{zeugner2015bayesian}), 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 (\cite{hoeting1999bayesian, fragoso2018bayesian}). All analyses were performed in the R program (\cite{rcoreteam2018rprogram}), with the significance level set at 5%.

\begin{table}[h]
\centering
\caption{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 (m$^2$/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).}
\begin{tabular}{lcccc}
\hline
Vegetation type & Acronym & Biome & H & LAI & BA & TD \\
\hline
Typical cerrado & TC & Amazonia/Cerrado & 5.80 & 1.6 & 8.49 & 404.8 \\
Cerrado & 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 \\
\hline
\end{tabular}
\end{table}
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 (Fig. 2 and 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
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regeneration traits among vegetation types has been partially confirmed

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Regarding community assembly based on functional diversity, the sea-

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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.

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sonal and open rainforests showed overdispersion of regeneration traits,

in floodplain forests by contrast these were markedly clustered. Con-

trary to our expectations, our results showed that dispersal syndrome

(anemochory, autochory, and zoochory) was the most important

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-Ruíz, 2016; Cornellissen 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-Ruíz, 2016), savannas (García-Nunes 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 cerrado and typical cerrado have larger fruits than

other vegetation types. These fruits have higher exposure in the envi-

ronment, requiring investment in resistance adaptations (Romero-Sar-

itama 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

variable among the set of regeneration traits.
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 Scarioni, 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 (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 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.

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Supplementary materials


References

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