Functional diversity and assembly rules of two deciduous seasonal forests in Southeastern Brazil

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Abstract

Deciduous seasonal forests (DSFs) have a peculiar floristic composition, with species capable of surviving periods of high water deficit in the year. Our goal was to demonstrate that abiotic filters lead to the assembly of two DSFs communities that have high floristic dissimilarity. For this, we carry out the environmental characterization of the areas and use the CWM, FRic and FDis indices for regional recognition of functional patterns. The local assessment of the assembly rules was carried out using null models. We found differences in the FRic and FDis indeces between the areas, which was attributed to the different floristic influences exercised on the communities. However, in both, the typical attributes of dry formations were dominant (CWM), indicating that, on the regional scale of study, the dry season acts as a filter in the composition of species in the communities. On a local scale, stochastic dispersion was identified as the most influential mechanism in the assembly of communities. We conclude that deterministic and stochastic processes act in the assembly of the studied communities, and the proportion of each of these depends on the scale, with abiotic filtration predominating on a regional scale and stochastic dispersion events on a local scale.

Keywords: Environmental filtering, functional attributes, null model, tropical dry forests.

1. Introduction

The ecological functions exercised by plant communities are based on functional traits, which are defined as morphological, physiological, and phenological attributes of an organism that influence its individual performance (Tilman 2001, Villéger et al. 2008, Laliberté and Legendre 2010, Ricotta et al. 2014). These traits affect the fitness of individuals through their effects on growth, reproduction, and survival in certain environments (Medeiros et al. 2018, Raymundo et al. 2019; Subedi et al. 2019;). Because they are related to species niches (Soberón 2007, Thuiller et al. 2007), the variability of these functional diversity traits reflects the processes of assembling communities (Mouchet et al. 2010, Mason et al. 2013).

The species composition of a community is the result of ecological processes, known as hierarchical filters, which act at different scales and under different conditions, selecting species according to their functional traits (Keddy 1992, Gotzenberger et al. 2012). Dispersion, habitat filtering and biotic interactions are the three processes that dominate this theory (Kraft et al. 2015, Cadotte and Tucker 2017). Thus, species are filtered first by factors that act at global scales, such as randomness, historical speciation patterns, extinction, migration, and dispersion processes. At regional scales, the performance of abiotic factors, such as climate and physical restrictions of the environment, is predominant. Finally, biotic interactions (facilitation or competition) operate at the local scale (Valladares et al. 2015, Blanchard et al. 2019).

Under adverse conditions such as extreme cold or drought, a strong pattern of abiotic filtering is expected, determining the set of species capable of surviving in that particular environment. In these circumstances, the competitive hierarchy between species is increased (Menezes et al. 2020). This is because biotic interactions can be strongly influenced by the abiotic context, since the construction of communities is also dependent on the relationship between the intrinsic growth rates of the species and the environment. Thus, in stressful sites, the competition of a species with those better adapted (higher rates of local growth) may result in patterns of presence/absence and abundances similar to those expected by a strict environmental filter (Kraft et al. 2015, Cadotte and Tucker 2017).

Deciduous seasonal forests (DSFs) occur in regions of accentuated climatic seasonality, with a marked dry season, and are generally associated with rocky limestone outcrops (Gonzaga et al. 2017). Because of these stressful conditions, the plants growing there show extraordinary adaptations to survive, among them, high wood density, smaller leaf size and deciduousness (Raymundo et al. 2018, Pooter et al. 2019). Moreover, DSFs include floristically very distinct communities (Gonzaga et al. 2013). This dissimilarity is attributed to the input from the adjacent biomes, which provides them with high α and β diversity (Silva et al. 2020). Although there is this floristic diversity, when studying dry forests, some authors have found that functional diversity responds to the environmental gradient, resulting in trait convergence as the environment becomes more restrictive (Méndez-Toribio et al. 2017, Raymundo et al. 2018, Menezes et al. 2020;).

The vulnerability of these forests in the face of the current climate change scenario and the intense anthropic activity (Pennington et al. 2018) make it urgent to improve our understanding of this physiognomy. Changes in the structure and functioning of communities affect ecosystem services and human well-being. Therefore, detecting how this vegetation works is important to ensure the conservation of its unique diversity, and to promote restoration actions such as the introduction of species with specific functional characteristics, among others.

Unfortunately, little is known about the functioning and processes that structure DSFs at different spatial scales and with a different floristic composition. For this reason, this work aimed to contribute to the recognition, on a regional and local scale, of the functional patterns and the assembly mechanisms of two DSF communities that are in different vegetation contacts and have high β diversity. We intended to prove that, despite the high floristic dissimilarity, abiotic filtration is predominant in species composition of those vegetation communities, on a regional and local scale.

We specifically seek to respond: I) regional scale: do the communities in the studied areas have similar composition and functional diversity? II) local scale: is it possible to identify the predominant filtering process in the assembly of each community? We hypothesize that: I) the areas are functionally similar. We believe that the restrictions imposed by abiotic filters are predominant to the floristic differences resulting from the stochastic dispersion events arising from the adjacent biome; and II) there is a pattern of functional convergence caused by the direct effects of abiotic filtering on the survival of individuals and also on the biotic interactions between them.

2. Materials and Methods

2.1. Study areas

The study was carried out in two areas of deciduous seasonal forests located in the municipalities of Paracatu and Presidente Juscelino in the state of Minas Gerais, Brazil. The Paracatu area (17º3’16.6”S and 46º49’23.5”O) has 100 ha and is in the core region of the Cerrado. The area in Presidente Juscelino (18º38’40”S and 44º04’57”O) has 150 ha and is located in a transitional zone Cerrado-Atlantic Forest (Figure 1). The two sites have steeply sloping relief, outcroppings of limestone rocks (belonging to the Bambuí group), predominant Lithic Neossols, and seasonal climate according to the Köppen classification (Figure 1, Table 1). These two communities were previously studied by Silva et al. (2020) and showed high β diversity, sharing only 23.4% of their species. Both areas are protected and are in a good state of conservation.

2.2. Sampling of vegetation

We installed 25 plots of 20 × 20 m, perpendicular to the land declivity, totaling 1 ha of sampled surface in each area. In Paracatu the plots were randomly distributed, while in Presidente Juscelino the plots were systematically allocated and distributed in five transects, 50 m between transects and 20 m between plots.

In each plot we surveyed all live trees with a diameter at breast height over 5 cm, which were labeled with numbered aluminum platelets. The inventories were conducted in 2016 and 2017 in Paracatu and PresidenteJuscelino, respectively.

Botanical samples from unidentified individuals were collected in the field and deposited at the Jeanine Felfili Dendrological Herbarium (HDJF) of the Federal University of the Valleys of Jequitinhonha and Mucuri (UFVJM). Identifications were based on specialized literature, specialists' expertise, and comparisons with the samples in the herbaria of the Federal University of Minas Gerais (BHCB/UFMG), University of Brasília (UnB), IBGE Ecological Reserve, and Embrapa Genetic Resources (CEN). The species were classified into families according to the APG system, Angiosperm Phylogeny Group IV (APG IV, 2016). We checked spelling and nomenclatural synonyms using databases from the Missouri Botanic Garden (MOBOT) and the International Plant Names Index (IPNI).

2.3. Environmental characterization

Environmental data were collected from all plots used for the tree survey in both areas. We analyzed physical and chemical edaphic characteristics, as well as the topography and rockiness of the fragments. In particular, we assessed the contents of sand, silt, clay, K^+, Ca^{2+}, Mg^{2+}, Ca^{2+}+Mg^{2+}, pH, potential acidity (H + Al), sum of bases (SB), base saturation (V), organic matter (OM), potential CTC (T) and effective CTC (t), altitude (Alt), slope (Slp), and percentage of exposed rock (Roc). Precipitation and temperature data (Table 1) extracted from the WorldClim version 2.1 (Fick and Hijmans, 2017) were also used for environmental characterization.

The physical-chemical properties of the soils were obtained averaging five samples collected from the top 20 cm depth in each plot. These sample collections were made randomly in Presidente Juscelino and in the center of the plots and at each of the four vertices in Paracatu. We measured the slope of each plot, calculating the difference between the maximum and minimum elevations of the plot corners (Espírito-Santo et al. 2002).

The percentage of rock cover was assessed by adapting the method of Braun Blanquet (1979). Thus, classes were assigned through nominal values: 0 = absence of surface rocks; 1 = 0%–25%; 2 = 26%–50%; 3 = 51%–75%; and 4 = 76%–100%.

2.4. Functional classification of species

The sampled species were classified according to the following traits, whose attributes are in parentheses: 1) EG: Ecological Group (PI = pioneer, NPI = non-pioneer); 2) DS: Seed dispersal syndrome (Ane = anemochory, Aut = autochory, Zoo = zoochory); 3) PS: Pollination syndrome (Anemo = anemophilous, Zoop= zoophilous); 4) DT: Seed desiccation tolerance (Ort = orthodox, Rec = recalcitrant), and 5) WD: Wood density (light, medium, and heavy), according to Borchert's criteria (1994 a, b), disregarding the shell, being: (a) light wood, species with wood density < 0.5 g cm^{-3}; (b) medium wood, density of 0.5–0.8 g cm^{-3}; (c) heavy wood, density > 0.8 g cm^{-3}. The classifications were based on specialized literature and knowledge of the authors (Table S2).

2.5. Composition and functional diversity

The functional composition of each area was estimated using the community-weighted mean (CWM) or “weighted average values of the traits within a community,” proposed by Garnier et al. (2004). This index quantifies the average, weighted by the abundance of species, for each functional trait. The higher the value of the CWM, the more relevant the attribute is in the community structure. Consequently, it is possible to obtain the functional identity of the fragments (Garnier et al., 2007, Leps et al. 2011).

Functional diversity was analyzed using functional richness (FRic) (Villéger et al. 2008) and functional dispersion (FDis) indices (Laliberté and Legendre 2010). FRic represents the size of the functional space occupied in the community without considering the abundance of species. FDis is a measure of functional divergence and measures the average distance of each species in the functional space in relation to the centroid of all other species present in the community, and reflects the contribution of each species in proportion to its abundance (Laliberté and Legendre 2010). These indices were identified as those that best represented the processes that act in the structuring and distribution of species in communities in response to the environment (Mason et al. 2013).

For data processing, two matrices were created: one with the abundance of each species in each plot (sample unit) and another with the respective traits of each species. Since the variables are categorical, the trait matrix was converted into a functional dissimilarity matrix, calculated by the Gower distance (Botta-Dukat 2005), and transformed into a numerical matrix through a principal coordinates analysis (PCoA). With the values of the axes resulting from the PCoA, the functional diversity indices were calculated using the dbFD function of the FD package (Laliberté and Legendre 2010) in R version 3.5.1 R (R Development Core Team 2018). The CWM was calculated using the same package.

2.6. Data analysis and null models

2.6.1. Environmental variables

The environmental variables of the areas, including mean annual temperature and mean annual precipitation, were evaluated by principal component analysis (PCA), using PC-ORD version 6.0 for Windows (Mccune and Mefford 2011). After a preliminary analysis, only variables whose eigenvalues were greater than 0.5 in one of the ordering axes or those not correlated with each other were selected. Highly redundant variables with the chosen ones were rejected. Consequently, sand, clay, acidity, H+Al, SB, OM, Slp, Roc, and precipitation (highly correlated with temperature) were maintained.

2.6.2. Composition and Functional Diversity

Regional Scale

In this analysis we compared the CWM values of the attributes of each trait in order to test the hypothesis that the areas have a similar functional composition and are mainly subject to abiotic filtration on a regional scale. This comparison was made at the area level, based on the CWM value of the attributes obtained in the plots, to determine the functional identity of each of the communities (e.g., the PI and NPI values of the GE trait of each plot were compared). The Mann–Whitney test (Mann and Whitney 1947) was used for traits with two levels (EG, PS, and DT) and the Kruskal–Wallis test (Zar 1996) was followed by the Mann–Whitney test when there was a significant difference ($p < 0.05$) in traits with three levels (DS and WD).

Additionally, the functional diversity indices (FRic and FDis) between the areas were compared using the Mann–Whitney test. These processes were conducted using the Past program, version 3.23 (Hammer et al, 2009).

2.6.3. Null Models

Local Scale

To test the hypothesis of the prevalence of abiotic filtering acting also on a local scale, we determined whether the observed values of FRic and FDis were higher or lower than expected by chance, using null models (Mason et al. 2013). The models were created based on the original null model of Connor and Simberllof (1979) complemented with other approaches (Bernard-Verdier et al. 2012, Gotzenberger et al. 2012, Luzuriaga et al. 2015, Loranger et al. 2016, Liu et al. 2018). The set of data measured for species richness and abundance in each plot was used in the models for each area in which it was collected, to maintain the taxonomic characteristics of each community (Connor and Simberllof 1979).

Unlike FRic, FDis considers the abundance of species, so a null model was created for each of the two indexes. For FRic, a presence/absence matrix was used, which was randomized with 1000 interactions, keeping the species richness constant. For FDis, another set of 1000 interactions was created where the abundances were randomized (between one and the maximum observed abundance of each species). The species frequency was used as the probability of their occurrence in each plot.

To determine the significance of the difference between the observed values and those of the communities simulated by null models, we calculated a P-value (Eq. 1) and the standardized effect sizes, separately, for each index, FRic and FDis (SESFRic and SESFDis, respectively; Eq. 2) (Loranger et al. 2016):

$$P = \frac{\Sigma(nullvalues<observedvalue)+\frac{\Sigma(nullvalues=observedvalues)}{2}}{1001} \qquad \text{(Eq. 1.)}$$

$$\text{SES}= 2(\text{P}-0.5) \qquad \text{(Eq. 2)}$$

A value of SES < −0.95 indicates higher convergence of traits than expected by chance, which suggests that abiotic filtering (Cadotte and Tucker, 2017) can be the main mechanism for assembling communities. In contrast, an SES > 0.95, which indicates higher divergence of traits than expected by chance, suggests that limiting similarity (biotic interactions) can be the predominant process in structuring communities (Loranger et al. 2016, Kubota et al. 2018). SES values between −0.95 and 0.95 mean no difference to what is expected by chance and indicate stochastic dispersion processes (Kubota et al. 2018). In addition, we investigated the relationships between SESFRic and SESFDis values and the environmental gradient using Spearman's correlation coefficient (*S*).

3. Results and Discussion

3.1. Environmental analysis

The PCA performed for the environmental characteristics of the fragments explained a significant proportion (80.93%) of the total variation in the data, which was included in two axes (axis 1: 47.53%, p <0.01; axis 2: 33.39%, p <0.01) (Figure 2). The first axis described an environmental gradient positively correlated with clay content in the soil (0.78) and slope (0.79) and negatively correlated with OM (−0.85), sand contents (−0.97), and mean annual precipitation (−0.98).The second axis reflected a gradient positively correlated with the SB (0.92) and rockiness (0.72), and negatively correlated with potential acidity (−0.81) (Figure 2).

The ordering separated the areas and converged in three distinct groups, two referring to the parcels of Paracatu and the other to those of Presidente Juscelino (Figure 2). In the latter, there was greater slope and higher clay content. Additionally, the layout of their plots along the ordering axes in the graph suggested that, despite the smoother gradient compared to Paracatu, plots in Presidente Juscelino were highly heterogeneous. In contrast, in Paracatu, there was a higher content of sand and OM, whereas the layout of its plots indicated a more pronounced gradient resulting in two distinct environments. One of those environments included more acidic and less fertile soils than the other, which in turn had greater fertility and rockiness. It is important to highlight that although the areas present seasonality of the same duration (five months of drought), the volume of precipitation was higher in Paracatu (Table 1) and, although not very discrepant, it probably contributed to the edaphic differentiation between the areas.

The process of soil formation takes considerable time, and is dependent on a range of factors involving the climate, parent material, relief and biota (Jenny 1941, Mocek et al. 2011). Paracatu and Presidente Juscelino, have the same type of parent material, which is limestone. However, the same source material can generate soils with different characteristics depending on the interaction of the other factors involved in their genesis (Augusto et al. 2017). From the environmental data evaluated in this study, we observed that one of the possible factors that would explain the differences in the edaphic properties of the areas would be the difference in precipitation between them (Figure 2). A similar result was found by Gonzaga et al. (2017), who studied this same phytophysiognomy.

Rainfall is a fundamental element in the process of soil formation and, although the difference in annual rainfall volume between areas is not significant in a short period of time, this aspect was fundamental in their separation (Figure 2). Higher rainfall results in greater weathering, which in the long run causes leaching and acidification of the soil through the depletion of carbonate and base cations (Kramer and Chadwick 2018). For this reason, we believe that the Paracatu area, which is located in a region with higher rainfall levels than Presidente Juscelino, would be subject to more intense weathering over time, which would have resulted in soils with more pronounced acidity.

In addition, edaphic gradients can be influenced by topographic conditions, which on a local scale, alter soil drainage and fertility conditions (Nakashima et al. 2017). From the results generated by the PCA, it is possible to infer that the slope was a factor that also differentiated the areas, being greater in Presidente Juscelino. In places with higher slopes, water infiltration is less, causing less intense leaching, and less loss of nutrients (Zhang et al. 2020). It is impossible to determine the proportion that each of these factors exerted in the formation and dynamics of these soils. However, we understand that the isolated effect of none of these aspects would be strong enough to cause the edaphic differences found in the areas. Unlike this, we believe that the different interaction between them, over time, was responsible for the distinctions in the weathering processes of each location, which resulted in soils with different characteristics.

Regional Scale

3.2. Community-weighted mean

Regarding CWM, both fragments included a higher component in the community with anemochory dispersion, anemophilous pollination, orthodox seeds, and heavy WD (Table 2), revealing that they had a similar dominant functional composition, corroborating our first hypothesis. There was only a difference in relation to the ecological group (EG), in which the CWM showed a significantly higher amount of pioneer species in Presidente Juscelino, whereas in Paracatu there was no difference between these attributes.

The highest CWM value for the Ane attribute found in both fragments a matched the expectations for dry forests. In these environments, wind dispersion is more important compared to humid forests where there is a prevalence of seeds dispersed by animals (Gentry, 1983, Macedo et al. 2019). The results also showed a large number of individuals with orthodox seeds. This result is consistent with the fact that in these forests seeds can tolerate low moisture levels, remaining viable until the beginning of the rainy season, when they germinate (Mayrinck et al. 2019). This explains why the Ort attribute was dominant and therefore more important than the Rec attribute in both communities (Table 2).

Additionally, we found that both communities were dominated by species with heavy wood, such as *Anadenanthera colubrina* (Vell.) Brenan, *Aspidosperma pyrifolium* Mart., *Myracrodrum urundeuva* Allemao, and *Machaerium acutifolium* Vogel, which are common in this vegetation type (Table S1). Higher density of the wood is strongly associated with the capacity of the species to avoid hydraulic failures generated by the water deficit, such as cavitation and embolism, which cause the death of plants during drought (Markesteijn et al. 2011, Choat et al. 2016).

We suggest that the similarity found between areas is due to the fact that the same abiotic filtration process, in this case the five month dry season, prevailed over other factors in the functional composition of the two communities. Climate is widely known as the main factor that shapes the patterns of species composition and diversity at a regional scale (Towers and Dwyer 2018). Thus, the stress imposed by the dry season in the regions where the DSF occurs (Ribeiro and Walter 2008, Gonzaga et al. 2017) would filter species with similar ecological functions, capable of maintaining viable populations under such conditions (Medeiros et al. 2018, Towers and Dwyer, 2018, González-M et al. 2019).

3.3. Functional richness and functional dispersion

The FRic and FDis indices were significantly different between fragments, with higher values in Presidente Juscelino (Figure 3), rejecting our hypothesis that posed no distinction between communities.

Higher values of FRic and FDis indicated a greater diversity of functional strategies (Villéger et al. 2008, Laliberte and Legendre 2010). From the coexistence theory point of view, the increase in environmental heterogeneity offers more opportunities for niche partitioning, which was reflected by greater functional diversity and greater species richness (Chesson and Warner 1981, Price et al. 2017). Thus, the highest values of FRic and FDis found in Presidente Juscelino were consistent with the fact that this area was more heterogeneous. This area showed greater variation in altitude, greater slope and less rocky, as observed through the PCA (Figure 2). Other studies have also shown that environmental heterogeneity enhances the variety of attributes, generating greater functional diversification (Price et al. 2017, Stark et al. 2017, Towers & Dwyer, 2018).

However, Presidente Juscelino revealed a smoother and less stressful edaphic gradient than Paracatu, presenting less acidic and more clayey soils. Thus, this environment is more favorable to plants, as it enables the survival and development of individuals with diverse traits resulting in greater functional diversity (Soboleski et al. 2017, Menezes et al. 2020). Therefore, we believe that these conditions allowed certain functionally different species to colonize the area through stochastic dispersion processes (Tuiller et al. 2007, Mason et al. 2011, Gotzenberger et al. 2012, Cadotte et al. 2017). This is because the Presidente Juscelino forest is located in an ecotonal area, with floristic influence from the Cerrado and the Atlantic Forest (Silva et al. 2020). This scenario may have contributed to increase the functional diversification of this area, incorporating typical attributes of humid regions in the community composition (Gentry, 1983, Poorter et al. 2019). Our results corroborate this discussion, since the presence of species, typical of the Atlantic Forest, such as *Annona sylvatica* A.St.-Hil (N PI, Zoo, Zoop, Rec, Light), *Deguelia costata* (Benth.) Az.-Tozzi (PI, Ane, Zoop, Ort, Medium), *Senegalia tenuifolia* (L.) Britton & Rose (PI, Aut, Zoop , Ort, Light), among others, was verified in the area (Table S1).

In contrast, the Paracatu area primarily had more sandy soils, which potentiated the water deficit soils because the predominance of this texture results in less water retention capacity (Gonzaga et al. 2017). Therefore, soil with greater acidity and high sandiness, combined to a higher mean annual temperature make the Paracatu area more stressful for plants. Consequently, in this environment, there was less functional amplitude, as observed with the values of FRic and FDis (Figure 3).

Thus, from our results we observe that abiotic and stochastic factors are acting in the assembly of the studied communities on a regional scale. However, although the areas are floristically distinct and there are species with traits typical of the adjacent biome in Presidente Juscelino, indicating dispersion events in the assembly of this community, the functional composition (CWM) of this area was the same as that of Paracatu. This means that the dominant functional traits of the two areas are the same and, therefore, in general the plants of the two communities have performed the same function in the environment.

Local Scale

3.4. Null model

The comparison of the observed functional diversity indices with those generated by the null model did not indicate the predominance of functional convergence (SES <−0.95) or abiotic filtering as the main process of assembling the studied communities. Contrary to our expectations, most of the values of SESFRic and SESFDis did not differ from that expected by chance; that is, it remained between the range −0.95 to 0.95 (Figure 4a, b, c, and d), revealing the prevalence of stochastic dispersion processes (Kubota et al. 2018). However, some plots had SES values that exceeded the significance thresholds (−0.95 and 0.95), indicating convergence and functional divergence at the local scale.

The distribution and species richness of plant communities are strongly influenced by their dispersion patterns (Poschlod et al. 2013). In addition, anemochory represents a pattern of random distribution (Polli et al. 2020). This is consistent with our results, since the two communities presented anemochory as one of the dominant functional traits, which resulted in a stochastic dispersion pattern. It is worth mentioning that this discussion refers to the local scale of study. This shows that, despite the dominance of the ANE trait in both areas (regional scale), individuals are randomly distributed within each of these environments.

In addition, we can complement this discussion from different points of view. One of them is related to the study scale. In this study, to understand the community assembly processes, we reduced the observation scale, obtaining SESFRi and SESFDis values at the plot level. Shipley et al. (2012) suggested that as the spatial scale decreases, the population size is also reduced. In this way, fluctuations in germination and mortality rates dominate population dynamics, even though the probabilities of reproduction, survival, and growth of species are influenced by their attributes. Therefore, under these conditions, a pattern of stochasticity may be observed in the community assemblage.

Additionally, Fang et al. (2019) found that stochastic processes are more often observed leading to the composition of the community when only interspecific diversity is considered, as in this work. Meanwhile, intraspecific variation can reflect the relative importance of deterministic processes (e.g., environmental filtering, limiting similarity). Other works have also indicated the importance of using intraspecific traits in studies of ecosystems and communities based on characteristics. Siefert et al. (2015) confirmed that intraspecific trait variation (ITV) is generally responsible for a significant proportion of total functional diversity within and between communities. In addition, they demonstrated that the relative extent of these traits varies predictably between traits, species richness and spatial scale. Furthermore, Bastias et al. (2017) suggested that in addition to the relative importance of ITV, neutral processes or equalization mechanisms can act as potential drivers shaping the community assembly in hyperdiverse forests.

Another point to consider is that SES values of some plots exceeded the significance thresholds -0.95 and 0.95, indicating convergence and functional divergence respectively (Figure 4). This indicates that in addition to the prevalence of stochastic processes, deterministic factors are acting in the assembly of the studied communities. Unfortunately, the set of environmental variables used in this work showed significant correlations only between the variables H + Al (S = -0.49, p = 0.012) and Slope (S = 0.43, p = 0.032) and the SESFDis in PresidenteJuscelino, all other correlations were not significant (Table S3).

Thus, although the correlations are weak, it is possible to infer that, in Presidente Juscelino, the potential acidity influences the functional convergence pattern of some plots, since this presented a negative correlation with the SESFDis values. In contrast, slope showed a positive correlation with the SESFDis, revealing that part of the functional divergence found in the plots is due to this variable. Soil acidity is commonly considered a limiting factor for plant development, while higher slopes are favorable to greater functional diversity (Moraes et al. 2016, Soboleski et al. 2017). In this case, steeper slopes provide different levels of solar radiation, consequently interfering with evapotranspiration rates and soil moisture, resulting in more diverse and milder environments for plants (Ebel 2013, Chapman and McEwan 2018). In addition, some environmental aspects that we did not measure such as the topographic position and those already mentioned, soil moisture and incidence of light, among others, can strongly affect the functional traits at the community level (Mendivelso et al. 2013, Méndez-Toribio et al. 2017).

To sum up, the prevalence of stochastic processes does not necessarily exclude deterministic processes of operating. In fact, deterministic and stochastic dispersion processes can dynamically interact to drive the community pattern and are not mutually exclusive (Gotzenberger et al. 2012, Valladares et al. 2015). Thus, they can structure the species composition of a community simultaneously, and their effects can be interactive (Shipley et al. 2012, Fang et al. 2019).

4. Conclusions

This study allowed us to conclude that environmental filtration and stochastic processes participate in the assembly of the two communities, acting in different proportions on a regional and local scale.

Despite the high β diversity of the areas and the influence of dispersion events, arising from the adjacent vegetation, in the community of Presidente Juscelino, the dominant functional composition of the two areas was the same. The dominant traits in the two communities were those related to the adaptation of plants to severe periods of drought, which revealed the predominant role of abiotic filters in the assembly of communities on a regional scale. On a local scale, different from what we hypothesized, stochastic processes prevailed in the assembly of the two communities, with few plots showing functional convergence and divergence. Our set of environmental data was not adequate to answer which deterministic factors would be acting in the composition of these plots.

Finally, it is necessary to carry out broader studies, working in detail on different spatial features and scales, investigating other areas of seasonal deciduous forests, in order to confirm that the results found in this study reflect a general pattern for this phytophysiognomy.

5. Literature Cited

Angiosperm Phylogeny Group (APG IV). 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Bot. J. Linn. Soc*. 181: 1-20.

Augusto, L., D.L. Achat, M. Jonard, D. Vidal and B. Ringeval. 2017. Soil parent material—a major driver of plant nutrient limitations in terrestrial ecosystems. *Glob. Chang. Biol.* 23(9):3808-3824.

Bastias, C.C., C. Fortunel, F. Valladares, C. Baraloto, R. Benavides, W. Cornwell, L. Markesteijn et al. 2017. Intraspecific leaf trait variability along a boreal-to-tropical community diversity gradient. *PLoS One.*12(2):e0172495.

Bello, F.D., S. Lavorel, S. Lavergne, C.H. Albert, I. Boulangeat, F. Mazel and Thuiller, W. 2013. Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps. *Ecography*. 36(3):393-402.

Bernard-Verdier, M., M.L. Navas, M. Vellend, C. Violle, A. Fayolle and E. Garnier, 2012. Community assembly along a soil depth gradient: contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. *J. Ecol.* 100(6):1422-1433.

Blanchard, G., F. Munoz, T. Ibanez, V. Hequet, H. Vandrot, J. Girardi and P. Birnbaum. 2019. Regional rainfall and local topography jointly drive tree community assembly in lowland tropical forests of New Caledonia. *J. Veg. Sci.* 30(5):845-856.

Borchert, R. 1994a. Soil and stem water storage determine the phenology and distribution of tropical dry forest trees. *Ecology*. 75:1437-1449.

Borchert, R. 1994b. Water status and development of tropical trees during seasonal drought. *Trees*. 8:115-125.

Botta-Dukát, Z. 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *J. Veg. Sci.* 16(5):533-540.

Braun-Blanquet, J. 1979. Fitosociologia. Bases para el estudio de las comunidades vegetales. *Madrid: H. Blume Ediciones*, 820 p.

Cadotte, W and C.M. Tucker. 2017. Should environmental filtering be abandoned? *Trends Ecol. Evol.* 32(6):429-437.

Carvalho, F.A. and J.M. Felfili. 2011. Variações temporais na comunidade arbórea de uma floresta decidual sobre afloramentos calcários no Brasil Central: composição, estrutura e diversidade florística. *Act. Bot. Bras.* 25(1):203-214.

Chapman, J.I. and R.W. McEwan. 2018. The role of environmental filtering in structuring appalachian tree communities: Topographic influences on functional diversity are mediated through soil characteristics. *Forests*, 9(1):19.

Chesson, P.L. and R.R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems. *Am. Nat.* 117(6):923-943.

Choat, B., E. Badel, R. Burlett, S. Delzon, H. Cochard, S. Jansen. 2016. Noninvasive measurement of vulnerability to drought-induced embolism by x-ray microtomography. *Plant Physiol.* 170(1):273-282.

Connor, E.F. and D. Simberloff. 1979. The assembly of species communities: chance or competition? *Ecology*. 60(6):1132-1140.

Correia, L.P.D., M. Bouchard, É. Filotas, and F. Raulier. 2019. Disentangling the effect of drought on stand mortality and productivity in northern temperate and boreal forests. *J. Appl. Ecol.* 56(3):758-768.

Dexter, K.G., T. Pennington, A.T. Oliveira-Filho, M.L. Bueno, P.L. Silva de Miranda and D. Neves. 2018. Inserting tropical dry forests into the discussion on biome transitions in the tropics. *Front. Ecol. Evol.* 6(104):1-7.

Ebel, B.A. 2013. Simulated unsaturated flow processes after wildfire and interactions with slope aspect. *Water Resour. Res.* 49(12):8090-8107.

Espírito-Santo, F.D.B., A.D. Oliveira-Filho, E.L.M. Machado, J.S. Souza, M.A.L. Fontes and J.J.G.S.M. Marques. 2002. Variáveis ambientais e a distribuição de espécies arbóreas em um remanescente de floresta estacional semidecídua montana no campus da Universidade Federal de Lavras, MG. *Act. Bot. Bras.*16(3):331-356.

Fang, S., M.W. Cadotte, Z. Yuan, F. Lin, J. Ye, Z. Hao and X. Wang. 2019. Intraspecific trait variation improves the detection of deterministic community assembly processes in early successional forests, but not in late successional forests. *J. Plant Ecol.* 12(4):593-602.

Felfili, J.M., F.A. Carvalho and R.F. Haidar. 2005. Manual para o monitoramento de parcelas permanentes nos biomas Cerrado e Pantanal. Brasília: Universidade de Brasília, Departamento de Engenharia Florestal. 60 p.

Fick, S.E. and R.J. Hijmans. 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* 37(12):4302-4315.

Garnier, E., J. Cortez, G. Billès, M. Navas, C. Roumet, M. Debussche, G. Laurent et al. 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology*. 85 (9): 2630-2637.

Garnier, E., S. Lavorel, P. Ansquer,; H. Castro, P. Cruz, J. Dolezal, K. Grigulis, et al. 2007. Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. *Ann. Bot.* 99(5):967-985.

Gentry, A.H. 1983. Dispersal ecology and diversity in neotropical forest communities. *Disp. Dist.* 7:303-315.

Gonzaga, A.P.D., E.L.M. Machado, J.M. Felfili, and J.R.R. Pinto. 2017. Brazilian Decidual Tropical Forest enclaves: floristic, structural and environmental variations. *Rev. Bras. Bot.* 40(2):417-426.

Gonzaga, A.P.D., J.R.R. Printo, E.L.M. Machado and Felfili, J.M. 2013. Similaridade florística entre estratos da vegetação em quatro Florestas Estacionais Deciduais na bacia do Rio São Francisco. *Rodriguésia*, 64(1):11-19.

González-M, R., N. Norden, J.M. Posada, C. Pizano, H. García, Á. Idárraga-Piedrahita, R. López-Camacho et al. 2019. Climate severity and land-cover transformation determine plant community attributes in Colombian dry forests. *Biotropica*, 51(6):826-837.

Gotzenberger, L., F. De Bello, K.A. Brathen, J. Davison, A. Dubuis, A. Guisan, L. Pellissier et al. 2012. Ecological assembly rules in plant communities approaches, patterns and prospects. *Biol. Rev.* 87(1):111-127.

Hammer, O., D.A.T. Harper and P.D. Ryan, 2009. PAST–Palaeontological Statistics, Version 1.90. *University of Oslo, Oslo, Norway*.

Jenny, H. 1941. Factors of soil formation. *New York: McGraw-Hill*, 281 p.

Keddy, P.A. 1992. Assembly and response rules: two goals for predictive community ecology. *J. Veg. Sci.* 3(2):157-164.

Kraft, N.J., P.B. Adler, O. Godoy, E.C. James, S. Fuller and J.M. Levine, 2015. Community assembly, coexistence and the environmental filtering metaphor. *Funct. Ecol.* 29(5):592-599.

Kramer, M.G. and O.A. Chadwick. 2018. Climate-driven thresholds in reactive mineral retention of soil carbon at the global scale. *Nat. Clim. Change.* 8(12):1104.

Kubota, Y., B. Kusumoto, T. Shiono and W. Ulrich. 2018. Multiple filters affect tree species assembly in mid-latitude forest communities. *Oecologia*. 187(1):245-253.

Laliberté, E. and P. Legendre. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology*. 91(1):299-305.

Leps, J., F. De Bello, P. Smilauer and J. Dolezal. 2011. Community trait response to environment: disentangling species turnover vs intraspecific trait variability effects. *Ecography*. 34(5):856-863.

Liu, B., H.Y. Chen and J. Yang. 2018. Understory Community Assembly Following Wildfire in Boreal Forests: Shift From Stochasticity to Competitive Exclusion and Environmental Filtering. *Front. Plant Sci.* 9 (1854):1-12.

Loranger, J., B. Blonder, É. Garnier, B. Shipley, D. Vile, and C. Violle. 2016. Occupancy and overlap in trait space along a successional gradient in Mediterranean old fields. *Am. J. Bot.* 103(6):1050-1060.

Luzuriaga, A.L., J.M. González and A. Escudero. 2015. Annual plant community assembly in edaphically heterogeneous environments. *J. Veg. Sci.* 26(5):866-875.

Macarthur, R. and R. Levins. 1967. The Limiting Similarity, Convergence, and Divergence of Coexisting Species. *Am. Nat.* 101(921):377-385.

Macedo, W.S., L.S. Silva, A.R. Alves and A.R. Martins. 2019. Análise do componente arbóreo em uma área de ecótono Cerrado-Caatinga no sul do Piauí, Brasil. *Sci. Plena.* 15(1):1-11.

Mann, H.B. and D.R. Whitney. 1947. On a test of whether one of two random variables is stochastically larger than the other. *Ann. Math. Stat.*18(1):50-60.

Markesteijn, L., L. Poorter, H. Paz, L. Sack and F. Bongers. 2011. Ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits. *Plant. Cell. Environ.* 34(1):137-148.

Mason, N.W., F. De Bello, J. Dolezal and J. Leps. 2011. Niche overlap reveals the effects of competition, disturbance and contrasting assembly processes in experimental grassland communities. *J. Ecol.* 99(3):788-796.

Mason, N.W., F. De Bello, D. Mouillot, S. Pavoine and S. Dray. 2013. A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *J. Veg. Sci.* 24(5):794-806.

Mayrinck, R.C., L.C. Vilela, T.M. Pereira, A.G. Rodrigues-Junior, A.C. Davide and T.A. Vaz, 2019. Seed desiccation tolerance/sensitivity of tree species from Brazilian biodiversity hotspots: considerations for conservation. *Trees*, 33(3):777-785.

McCune, B. and M.J. Mefford. 2011. Multivariate Analysis of Ecological Data, version 6. *MjM Software*, Gleneden Beach, Oregon, U.S.A.

Medeiros, C.D., C. Scoffoni, G.P., John, M.K., Bartlett, F. Inman-Narahari, R. Ostertag, S. Cordell, C. Giardina and L. Sack. 2019. An extensive suite of functional traits distinguishes Hawaiian wet and dry forests and enables prediction of species vital rates. *Funct. Ecol.* 33(4):712-734.

Méndez-Toribio, M., G. Ibarra-Manríquez, A. Navarrete-Segueda and H. Paz. 2017. Topographic position, but not slope aspect, drives the dominance of functional strategies of tropical dry forest trees. *Environ. Res. Lett.* 12(8):085002.

Mendivelso, H.A., J.J. Camarero, O.R. Obregón, E. Gutiérrez and M. Toledo. 2013. Differential growth responses to water balance of coexisting deciduous tree species are linked to wood density in a Bolivian tropical dry forest. *Plos One*, 8(10):e73855.

Menezes, B.S., F.R. Martins, E.C.D. Carvalho, B.C. Souza, A.P. Silveira, M.I.B. Loiola and F.C. Araújo. 2020. Assembly rules in a resource gradient: Competition and abiotic filtering determine the structuring of plant communities in stressful environments. *Plos One*, 15(3):e0230097.

Mocek A. and W. Owczarzak. 2011. Parent material and soil physical properties. In: Gliński J, Horabik J, Lipiec J (Eds) *Encyclopedia of agrophysics. Encyclopedia of earth sciences series. Springer*, Dordrecht, the Netherldands.

Moraes, D.A., P.O. Cavalin, R.S. Moro, R.A. Oliveira, M.R. Carmo and M.C. Marques. 2016. Edaphic filters and the functional structure of plant assemblages in grasslands in southern Brazil. *J. Veg. Sci.* 27(1):100-110.

Mouchet, M.A., S. Villéger, N.W. Mason and D. Mouillot. 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Funct. Ecol.* 24(4):867-876.

Nakashima, M.R., G.B. Alves, A.M. Barreiros and J.P.Q. Neto. 2017. Dos solos à paisagem: uma discussão teórico-metodológica. *Revista da ANPEGE*, 13(20):30-52.

O'Brien, M.J., B.M. Engelbrecht, J. Joswig, G. Pereyra, B. Schuldt, S. Jansen, J. Kattge et al. 2017. A synthesis of tree functional traits related to drought-induced mortality in forests across climatic zones. *J. Appl. Ecol.* 54(6):1669-1686.

Pennington, T.R., C.E.R. Lehmann and L.M. Rowland. 2018. Tropical savannas and dry forests. *Curr.Biol.* 28(9):541-545.

Price, J., R. Tamme, A. Gazol, F. De Bello, K. Takkis, J.U. Diez, L. Kasari et al. 2017. Within-community environmental variability drives trait variability in species-rich grasslands. *J. Veg. Sci.* 28(2):303-312.

Polli, A., M.B. Romagnolo, L.A. Souza and Pastorini, L. H. 2020. Influence of the functional traits of seeds on germination dynamics and morphofunctional pattern of the seedlings. *Acta Sci., Biol. Sci.*, 42:e52154-e52154.

Poorter, L., D.M.A. Rozendaal, F. Bongers, J.F. Almeida-Cortez, A.M.A. Zambrano, F.S. Álvarez, J.L. Andrade et al. 2019. Wet and dry tropical forests show opposite successional pathways in wood density but converge over time. *Nat. Ecol. Evol.* 3(6):928-934.

Poschlod, P., M. Abedi, M. Bartelheimer, J. Drobnik, S. Rosbakh, and A. Saatkamp, 2013. Seed ecology and assembly rules in plant communities. *Veg. Ecol.* 2:164-202.

R Development Core Team. 2018. R: A Language and Environment for Statistical Computing. Version 3.4.1. Vienna: R Foundation for Statistical Computing. Available online at: http://www.r-project.org.

Raymundo, D., J. Prado-Junior, F.A. Carvalho, V.S. Do Vale, P.E. Oliveira and M.T. Van Der Sande. 2019. Shifting species and functional diversity due to abrupt changes in water availability in tropical dry forests. *J. Ecol.* 107(1):253-264.

Ribeiro, J. F. and B.M.T. Walter. 2008. As principais fitofisionomias do bioma cerrado. P. 151-212 in: Sano, SM; Almeida, SP; Ribeiro, JF Cerrado: Ecologia e flora. *Brasília: Embrapa Informação Tecnológica.*

Ricotta, C., G. Bacaro and M. Moretti, 2014. A new measure of functional evenness and some of its properties. *Plos One*. 9(8):el104060.

Sanaphre-Villanueva, L., J. Dupuy, J. Andrade, C. Reyes-García, H. Paz and P. Jackson. 2016. Functional diversity of small and large trees along secondary succession in a tropical dry forest. *Forests*. 7(8):163.

Shipley, B. C.E.T. Paine and C. Baraloto, 2012. Quantifying the importance of local niche-based and stochastic processes to tropical tree community assembly. *Ecology*, 93(4):760-769.

Siefert, A., C. Violle, L. Chalmandrier, C.H. Albert, A. Taudiere, A. Fajardo, L.W. Aarssen et al. 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecol. Lett.*, 18(12):1406-1419.

Silva, L.A., T.C. Ribeiro, A.P.D. Gonzaga and E.L.M. Machado. 2020. Diversity α and β in two fragments of Seasonal Deciduous Forest. *Floresta Ambient.* 27(4):e20180285.

Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecol. Lett.*10 (12):1115-1123.

Soboleski, V.F., P. Higuchi, A.C. Silva, R. Loebens, K. Souza, F. Buzzi-Junior, C.L. Lima et al. 2017. Variação de atributos funcionais do componente arbóreo em função de gradientes edáficos em uma floresta nebular no sul do Brasil. *Rodriguésia*, 68(2):291-300.

Stark, J. R. Lehman, L. Crawford, B.J. Enquist and B. Blonder, 2017. Does environmental heterogeneity drive functional trait variation? A test in montane and alpine meadows. *Oikos*. 126(11):1650-1659.

Subedi, S.C., M.S. Ross, J.P. Sah, J. Redwine and C. Baraloto. 2019. Trait-based community assembly pattern along a forest succession gradient in a seasonally dry tropical forest. *Ecosphere*. 10(4):e02719.

Thuiller, W., J.A. Slingsby, S.D. Privett and R.M. Cowling. 2007. Stochastic species turnover and stable coexistence in a species-rich, fire-prone plant community. *Plos One*. 2(9): 938.

Tilman, D. 2001. Functional Diversity. *Encyclopaedia of biodiversity*, 3(1):109-120.

Towers, I.R. and J.M. Dwyer. 2018. Regional climate and local-scale biotic acceptance explain native–exotic richness relationships in Australian annual plant communities. *Proc. R. Soc. Lond. B Biol. Sci.* 285(1886):20181328

Valladares, F., C.C. Bastias, O. Godoy, E. Granda and A. Escudero. 2015. Species coexistence in a changing world. *Front. Plant Sci.* 6:866.

Villéger, S., N.W.H. Mason and D. Mouillot, 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*. 89(8):2290-2301.

Zhang, W., H. Li, S.G. Pueppke, Y. Diao, X. Nie, J. Geng, D. Chen and J. Pang. 2020. Nutrient loss is sensitive to land cover changes and slope gradients of agricultural hillsides: Evidence from four contrasting pond systems in a hilly catchment. *Agric. Water Manag.* 237:106165.

Zar, J. H. 1999. *Biostatistical analysis*. Pearson Education India.

Wang, X., T. Wiegand, N.J.B. Kraft, N.G. Swenson, S.J. Davies, Z. Hao, R. Howe et al. 2016. Stochastic dilution effects weaken deterministic effects of niche-based processes in species rich forests. *Ecology*. 97(2):347-360.

Table 1. Environmental information for the two areas of deciduous seasonal forests, located in the municipalities of Paracatu and Presidente Juscelino, Brazil

Table 2. Variation in the community-weighted mean (CWM) values of the attributes of each trait in two areas of deciduous seasonal forests, located in the municipalities of Paracatu and Presidente Juscelino, Brazil

Figure 1. Location of areas of deciduous seasonal forests in Paracatu and Presidente Juscelino in the state of Minas Gerais, Brazil, showing its biomes.

Figure 2. Ordering diagram (PCA) of the environmental variables related to the areas of deciduous seasonal forests, located in Presidente Juscelino (●) and Paracatu (●), Brazil. Legend: H + Al = potential acidity, SB = sum of bases, OM = organic matter and Roc = percentage of exposed rock.

Figure 3. Variation in functional diversity indices between the two areas of deciduous seasonal forests, located in Paracatu and Presidente Juscelino, Brazil. Boxes with different letters are significantly different according to the Mann–Whitney test ($p < 0.05$). Legend: FRic = Functional Richness; FDis = Functional Dispersion; PAR = President Juscelino; PCT = Paracatu.

Figure 4. Representation of the SES (standardized effect size) values of functional richness (A and B) and functional dispersion (C and D) per plot. The dotted lines indicate the significance threshold: 0.95 and −0.95. Legend: SESFRic: SES of functional richness, SESFDis: SES of functional dispersion.

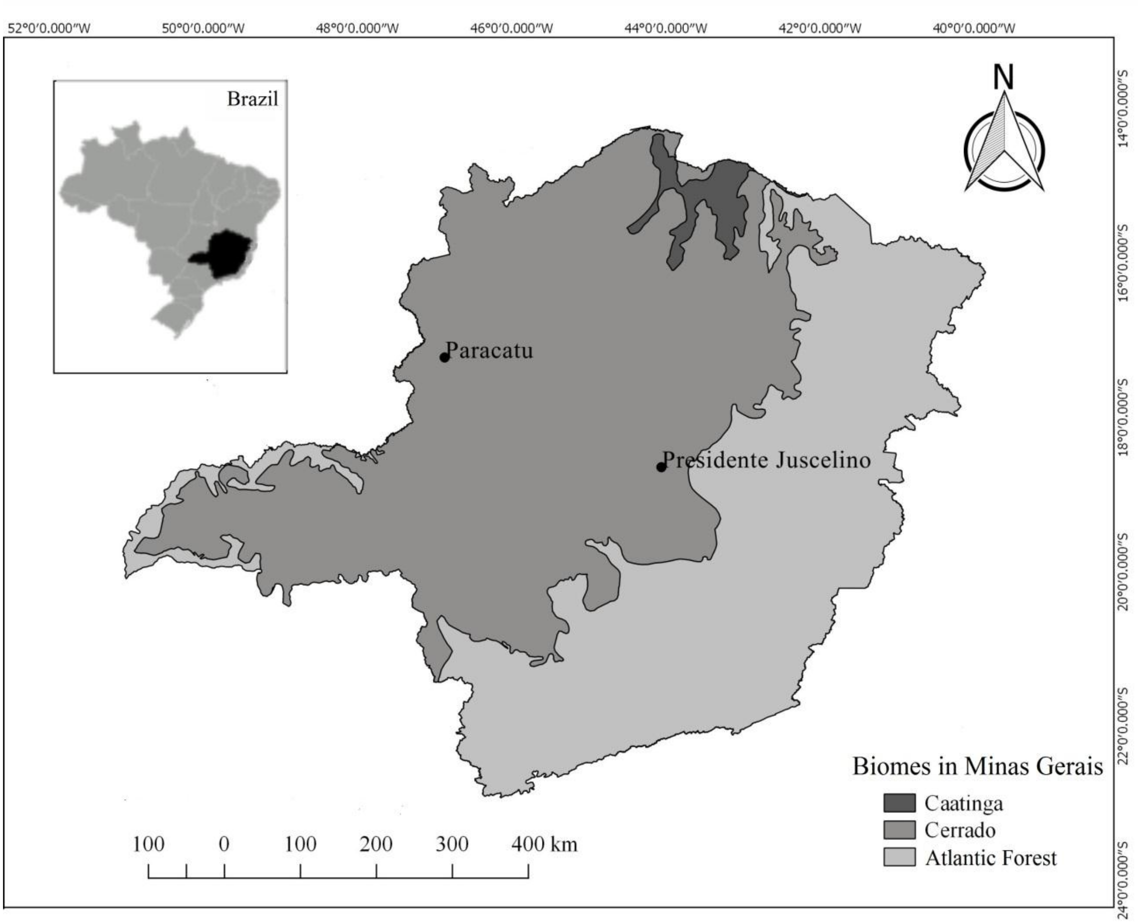
List of supplementary materials

Supplement 1. Table with functional classification of species of fragments sampled in the municipalities of Paracatu and Presidente Juscelino, Brazil.

Supplement 2. Table with functional attributes used in the classification of species and their ecological implications in the functions of the studied community.

Supplement 3. Table with Spearman correlation coefficient (*S*) between environmental variables and the SESFRic and SESFDis of Paracatu and Presidente Juscelino, Brazil.

Figure 1. Location of areas of Deciduous Seasonal Forest in Paracatu and Presidente Juscelino in the state of Minas Gerais, Brazil, showing its biomes.



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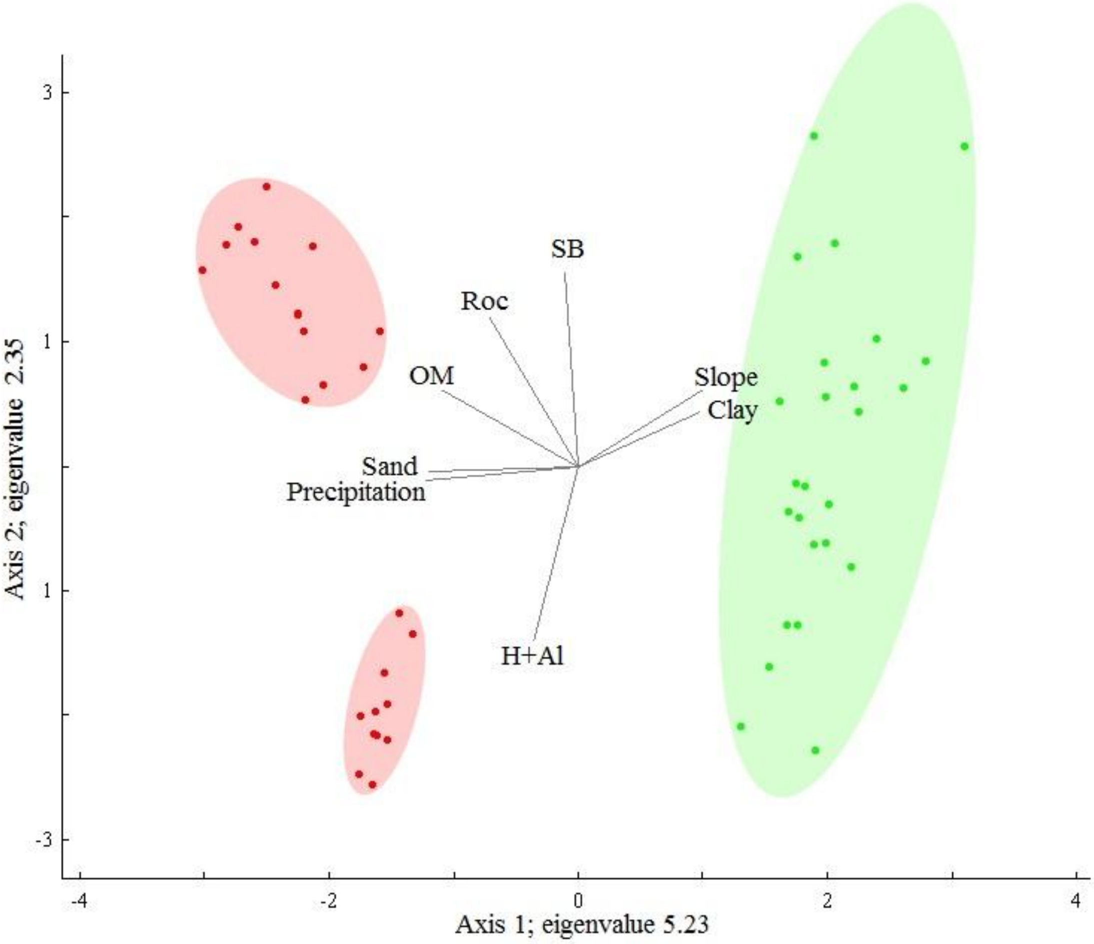

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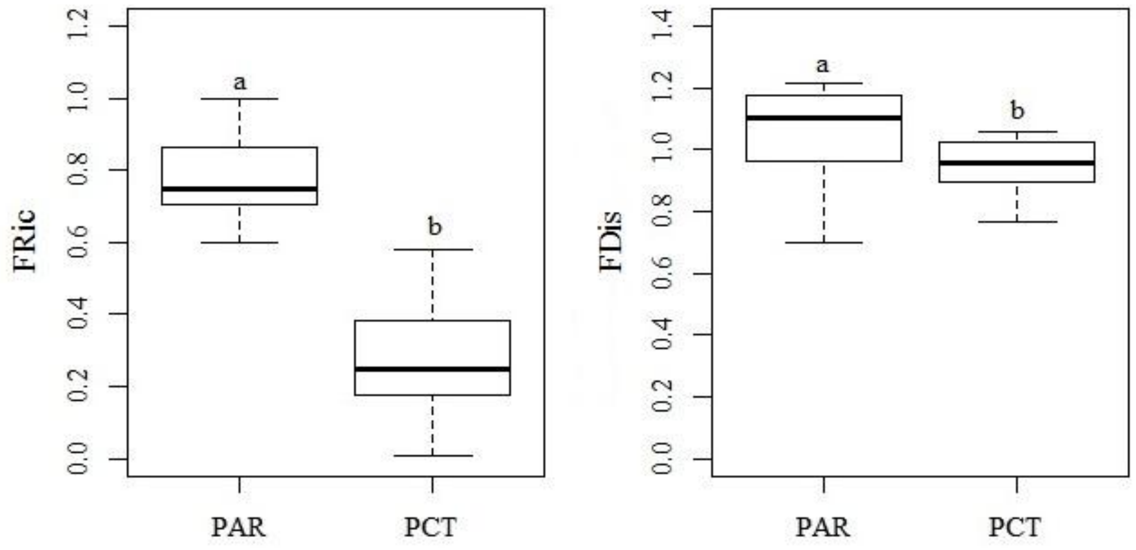

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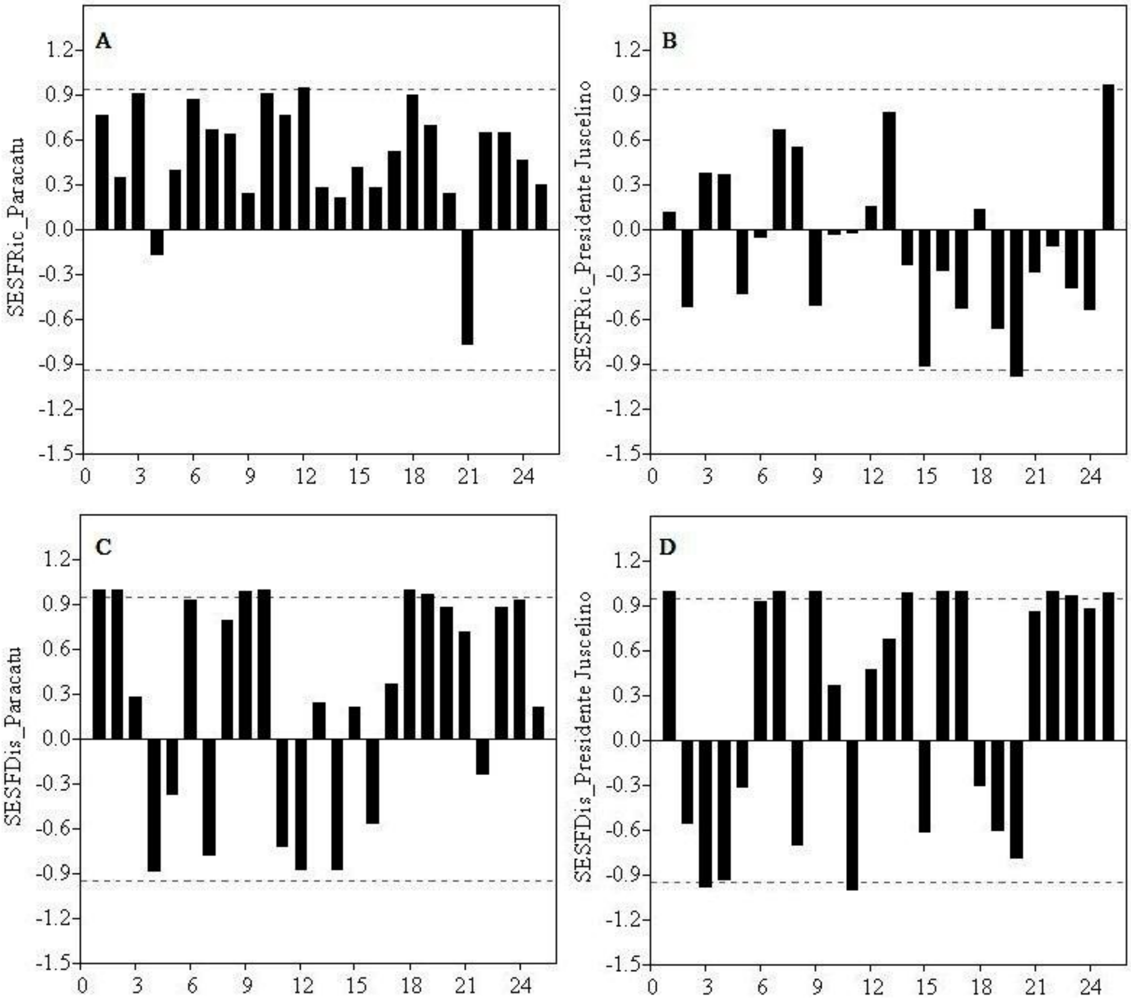

Table 1. Environmental information for the two areas of Deciduous Seasonal Forest, located in the municipalities of Paracatu and Presidente Juscelino, Brazil

	Paracatu	Presidente Juscelino
Altitude (m) (minimum and maximum)	598 a 695	687 a 826
Area (ha)	100	150
Climate (Köppen)	Aw	Cwa
Annual average temperature (°C)[b]	23.6	22.0
Annual rainfall (mm)[b]	1272	1116
Dry season (months/year)[a]	5	5

[a] Considering month with rainfall below 50 mm as dry months (Carvalho & Felfilli, 2011);
[b] Corresponding to an interval of 30 years (Fick & Hijmans, 2017).

Table 2. Variation in the community-weighted mean (CWM) values of the attributes of each trait in two areas of Deciduous Seasonal Forest, located in the municipalities of Paracatu and Presidente Juscelino, Brazil

Traits	Attributes	CWM_Paracatu	*p*	CWM_Presidente Juscelino	*p*
EG	NPI	0.53^a	*Ns*	0.62^a	<0.001
	PI	0.47^a	-	0.38^b	-
DS	Ane	0.45^a	<0.001	0.42^a	<0.001
	Aut	0.32^{ab}	-	0.20^b	-
	Zoo	0.23^b	-	0.38^{ab}	-
PS	Anemo	0.04^b	<0.001	0.03^b	<0.001
	Zoop	0.96^a	-	0.97^a	-
DT	Ort	0.81^a	<0.001	0.80^a	<0.001
	Rec	0.19^b	-	0.20^b	-
WD	Light	0.15^c	<0.001	0.24^b	<0.001
	Medium	0.31^b	-	0.17^c	-
	Heavy	0.52^a	-	0.59^a	-

EG = ecological group (PI: pioneers; NPI: non-pioneers); DS = dispersal syndrome (Ane: anemochory; Aut: autochory; Zoo: zoochory); PS = Pollination syndrome (Anemo: anemophilous; Zoop: zoophilous); DT = seed desiccation tolerance (Ort: orthodox; Rec: recalcitrant); WD = Wood density (light, medium, and heavy). Kruskal-Wallis and Mann-Whitney tests with significance level $\alpha = 0.05$ in which means followed by the same letter in the column for each characteristic do not differ; ns = not significant.

SUPPLEMENT 1

Table S1. Functional classification of species of areas sampled in the municipalities of Paracatu and Presidente Juscelino, Minas Gerais, Brazil. Tree species are arranged in alphabetical order. Where Ni = number of individuals; EG = Ecological group (PI: pioneers; NPI: non-pioneers); DS = Seed dispersal syndrome (Ane: anemochory; Aut: autochory; Zoo: zoochory); PS = Pollination syndrome (Anemo: anemophilia; Zoop: zoophilia); DT = Seed desiccation tolerance (Ort: orthodox; Rec: recalcitrant); and WD = Wood density (light, medium, and heavy).

Species	**Paracatu -MG**						**Presidente Juscelino -MG**					
	Ni	**EG**	**DS**	**PS**	**DT**	**WD**	**Ni**	**EG**	**DS**	**PS**	**DT**	**WD**
Agonandra brasiliensis Miers ex Benth. & Hook.	-	-	-	-	-	-	4	PI	Zoo	Zoop	Ort	Light
Albizia polycephala Benth.	1	PI	Aut	Zoop	Ort	Light	-	-	-	-	-	-
Allophylus sericeus (Cambess.) Radlk.	2	N PI	Zoo	Zoop	Ort	Light	-	-	-	-	-	-
Alseis floribunda Schot.	-	-	-	-	-	-	2	N PI	Ane	Zoop	Ort	Heavy
Anadenanthera colubrina (Vell.) Brenan	134	PI	Aut	Zoop	Ort	Heavy	177	PI	Aut	Zoop	Ort	Heavy
Annona mucosa Jacq.	1	N PI	Zoo	Zoop	Ort	Heavy	-	-	-	-	-	-
Annona neolaurifolia H.Rainer	-	-	-	-	-	-	13	N PI	Zoo	Zoop	Ort	Light
Annona sylvatica A.St.-Hil.	-	-	-	-	-	-	18	N PI	Zoo	Zoop	Rec	Light
Aralia warmingiana (Marchal) J. Wen	-	-	-	-	-	-	25	PI	Zoo	Zoop	Rec	Light
Aspidosperma cuspa (Kunth) S.F.Blake ex Pittier	39	N PI	Ane	Zoop	Ort	Medium	-	-	-	-	-	-
Aspidosperma pyrifolium Mart.	118	N PI	Ane	Zoop	Ort	Heavy	23	N PI	Ane	Zoop	Ort	Heavy
Aspidosperma subincanum Mart. ex A.DC.	-	-	-	-	-	-	2	N PI	Ane	Zoop	Ort	Heavy
Astronium fraxinifolium Schott ex Spreng.	13	PI	Ane	Anemo	Ort	Heavy	7	PI	Ane	Anemo	Ort	Heavy
Bauhinia catingae Harms	15	N PI	Aut	Zoop	Ort	Light	4	N PI	Aut	Zoop	Ort	Light
Brosimum gaudichaudii Trécul	1	N PI	Zoo	Anemo	Rec	Medium	1	N PI	Zoo	Anemo	Rec	Medium
Campomanesia velutina (Cambess.) O.Berg	15	N PI	Zoo	Zoop	Ort	Heavy	-	-	-	-	-	-
Casearia mariquitensis Kunth	5	N PI	Zoo	Zoop	Ort	Medium	-	-	-	-	-	-

Continue...

Species	Paracatu -MG						Presidente Juscelino -MG					
	Ni	**EG**	**DS**	**PS**	**DT**	**WD**	**Ni**	**EG**	**DS**	**PS**	**DT**	**WD**
Casearia rupestris Eichler	21	N PI	Zoo	Zoop	Rec	Heavy	3	PI	Zoo	Zoop	Rec	Heavy
Casearia sylvestris Sw.	3	N PI	Zoo	Zoop	Rec	Heavy	-	-	-	-	-	-
Ceiba pubiflora (A.St.-Hil.) K.Schum.	-	-	-	-	-	-	1	N PI	Ane	Zoop	Ort	Medium
Ceiba speciosa (A.St.-Hil.) Ravenna	8	N PI	Ane	Zoop	Ort	Light	-	-	-	-	-	-
Celtis iguanaea (Jacq.) Sarg.	16	PI	Zoo	Anemo	Ort	Medium	17	PI	Zoo	Anemo	Ort	Medium
Chrysophyllum flexuosum Mart.	4	N PI	Zoo	Zoop	Ort	Medium	-	-	-	-	-	-
Chrysophyllum marginatum (Hook. & Arn.) Radlk.	49	PI	Zoo	Zoop	Ort	Medium	-	-	-	-	-	-
Combretum duarteanum Cambess.	-	-	-	-	-	-	3	PI	Ane	Zoop	Ort	Light
Combretum leprosum Mart.	-	-	-	-	-	-	1	PI	Ane	Zoop	Ort	Medium
Copaifera langsdorffii Desf	2	N PI	Zoo	Zoop	Ort	Medium	-	-	-	-	-	-
Cordia glazioviana (Taub.) Gottschling & J.J.Mill.	-	-	-	-	-	-	3	N PI	Ane	Zoop	Ort	Medium
Cordia ochnacea DC.	-	-	-	-	-	-	1	PI	Ane	Zoop	Ort	Light
Cordiera concolor (Cham.) Kuntze	-	-	-	-	-	-	3	PI	Zoo	Zoop	Ort	Light
Cordiera sessilis (Vell.) Kuntze	-	-	-	-	-	-	1	N PI	Zoo	Zoop	Ort	Light
Coutarea hexandra (Jacq.) K.Schum.	12	N PI	Ane	Zoop	Ort	Light	20	N PI	Ane	Zoop	Ort	Light
Cupania vernalis Cambess.	-	-	-	-	-	-	4	N PI	Zoo	Zoop	Rec	Medium
Curatella americana L.	1	PI	Zoo	Zoop	Ort	Medium	-	-	-	-	-	-
Cyrtocarpa caatingae J.D.Mitch. & Daly	-	-	-	-	-	-	1	N PI	Zoo	Zoop	Otr	Heavy
Deguelia costata (Benth.) Az.-Tozzi	-	-	-	-	-	-	41	PI	Ane	Zoop	Ort	Medium
Dilodendron bipinnatum Radlk.	34	PI	Zoo	Zoop	Ort	Light	35	PI	Zoo	Zoop	Ort	Light
Dimorphandra mollis Benth.	1	PI	Zoo	Zoop	Ort	Heavy	-	-	-	-	-	-
Dipteryx alata Vogel	2	PI	Zoo	Zoop	Ort	Heavy	-	-	-	-	-	-
Diptychandra aurantiaca Tul.	1	N PI	Ane	Zoop	Rec	Heavy	-	-	-	-	-	-
Eriotheca gracilipes (K.Schum.) A.Robyns	-	-	-	-	-	-	1	N PI	Ane	Zoop	Ort	Light
Erythroxylum deciduum A.St.-Hil.	10	N PI	Zoo	Zoop	Rec	Medium	-	-	-	-	-	-

Continue...

Species	Paracatu -MG						Presidente Juscelino -MG					
	Ni	EG	DS	PS	DT	WD	Ni	EG	DS	PS	DT	WD
Erythroxylum pelleterianum A.St.-Hil.	3	N PI	Zoo	Zoop	Ort	Light	22	N PI	Zoo	Zoop	Ort	Light
Eugenia dysenterica DC.	1	PI	Zoo	Zoop	Rec	Heavy	-	-	-	-	-	-
Eugenia florida DC.	1	N PI	Zoo	Zoop	Rec	Heavy	6	N PI	Zoo	Zoop	Rec	Heavy
Ficus gomelleira Kunth & C.D. Bouché	14	PI	Zoo	Zoop	Ort	Light	11	PI	Zoo	Zoop	Ort	Light
Fridericia bahiensis (Schauer ex. DC.) L.G.Lohmann	-	-	-	-	-	-	4	PI	Ane	Zoop	Ort	Light
Guapira areolata (Heimerl) Lundell	-	-	-	-	-	-	4	N PI	Zoo	Zoop	Ort	Light
Guazuma ulmifolia Lam.	19	PI	Zoo	Zoop	Ort	Medium	1	PI	Zoo	Zoop	Ort	Medium
Guettarda viburnoides Cham. & Schltdl.	1	N PI	Zoo	Zoop	Ort	Medium	-	-	-	-	-	-
Handroanthus impetiginosus (Mart. ex DC.) Mattos	52	N PI	Ane	Zoop	Ort	Heavy	20	N PI	Ane	Zoop	Ort	Heavy
Handroanthus ochraceus (Cham.) Mattos	1	N PI	Ane	Zoop	Ort	Heavy	-	-	-	-	-	-
Handroanthus serratifolius (Vahl) S.O.Grose	-	-	-	-	-	-	1	N PI	Ane	Zoop	Rec	Heavy
Helicteres brevispira A.St.-Hil.	-	-	-	-	-	-	2	N PI	Aut	Zoop	Ort	Light
Hymenaea courbaril L.	9	N PI	Aut	Zoop	Ort	Heavy	-	-	-	-	-	-
Jacaranda brasiliana (Lam.) Pers.	6	PI/SI	Ane	Zoop	Ort	Medium	-	-	-	-	-	-
Kielmeyera coriacea Mart. & Zucc.	1	N PI	Ane	Zoop	Ort	Medium	-	-	-	-	-	-
Lecythis lanceolata Poir.	-	-	-	-	-	-	5	N PI	Ane	Zoop	Rec	Heavy
Luehea candicans Mart. & Zucc.	-	-	-	-	-	-	2	N PI	Ane	Zoop	Rec	Heavy
Luehea paniculata Mart. & Zucc.	6	PI	Ane	Zoop	Rec	Light	-	-	-	-	-	-
Machaerium acutifolium Vogel	1	N PI	Ane	Zoop	Ort	Heavy	98	N PI	Ane	Zoop	Ort	Heavy
Machaerium brasiliense Vogel	36	N PI	Ane	Zoop	Ort	Medium	13	N PI	Ane	Zoop	Ort	Medium
Machaerium hirtum (Vell.) Stellfeld	12	PI	Ane	Zoop	Ort	Medium	4	PI	Ane	Zoop	Ort	Medium
Machaerium nyctitans (Vell.) Benth.	-	-	-	-	-	-	3	PI	Ane	Zoop	Ort	Heavy
Machaerium opacum Vogel	-	-	-	-	-	-	1	PI	Ane	Zoop	Ort	Medium
Machaerium scleroxylon Tul.	4	N PI	Ane	Zoop	Ort	Heavy	17	N PI	Ane	Zoop	Ort	Heavy
Machaerium villosum Vogel	-	-	-	-	-	-	1	N PI	Ane	Zoop	Ort	Heavy

Continue...

Species	Paracatu -MG						Presidente Juscelino -MG					
	Ni	**EG**	**DS**	**PS**	**DT**	**WD**	**Ni**	**EG**	**DS**	**PS**	**DT**	**WD**
Maclura tinctoria (L.) Steud.	3	N PI	Zoo	Zoop	Rec	Heavy	1	N PI	Zoo	Zoop	Rec	Heavy
Magonia pubescens A.St.-Hil.	1	PI	Ane	Zoop	Ort	Medium	-	-	-	-	-	-
Maytenus aquifolia Mart.	-	-	-	-	-	-	1	N PI	Zoo	Zoop	Ort	Medium
Maytenus robusta Reissek	1	N PI	Zoo	Zoop	Ort	Medium	2	N PI	Zoo	Zoop	Ort	Medium
Myracrodruon urundeuva Allemão	108	N PI	Ane	Zoop	Ort	Heavy	86	N PI	Ane	Zoop	Ort	Heavy
Myrcia splendens (Sw.) DC.	4	PI	Zoo	Zoop	Ort	Medium	-	-	-	-	-	-
Myrciaria floribunda (H.West ex Willd.) O.Berg	1	N PI	Zoo	Zoop	Rec	Medium	-	-	-	-	-	-
Platycyamus regnellii Benth.	-	-	-	-	-	-	1	N PI	Aut	Zoop	Ort	Heavy
Platymiscium floribundum Vogel	-	-	-	-	-	-	1	N PI	Ane	Zoop	Rec	Heavy
Platypodium elegans Vogel	4	N PI	Ane	Zoop	Ort	Heavy	20	N PI	Ane	Zoop	Ort	Heavy
Pouteria gardneri (Mart. & Miq.) Baehni	1	N PI	Zoo	Zoop	Rec	Heavy	4	N PI	Zoo	Zoop	Rec	Heavy
Protium heptaphyllum (Aubl.) Marchand	2	N PI	Zoo	Zoop	Rec	Medium	-	-	-	-	-	-
Protium warmingianum Marchand	-	-	-	-	-	-	1	N PI	Zoo	Zoop	Rec	Medium
Pseudobombax tomentosum (Mart. & Zucc.) A.Robyns	14	PI	Ane	Zoop	Ort	Light	-	-	-	-	-	-
Qualea grandiflora Mart.	2	PI	Ane	Zoop	Ort	Heavy	-	-	-	-	-	-
Randia armata (Sw.) DC	1	N PI	Zoo	Zoop	Rec	Medium	-	-	-	-	-	-
Salacia crassifolia (Mart.) G.Don	-	-	-	-	-	-	1	N PI	Zoo	Zoop	Rec	Medium
Sapium glandulosum (L.) Morong	3	N PI	Zoo	Zoop	Ort	Light	2	N PI	Zoo	Zoop	Ort	Light
Schefflera macrocarpa (Cham. & Schltdl.) Frodin	-	-	-	-	-	-	1	PI	Zoo	Zoop	Ort	Light
Schefflera morototoni (Aubl.) Maguire. Steyerm. & Frodin	-	-	-	-	-	-	1	PI	Zoo	Zoop	Rec	Medium
Schinopsis brasiliensis Engl.	-	-	-	-	-	-	2	PI	Ane	Zoop	Ort	Heavy
Sebastiania brasiliensis Spreng.	117	PI	Aut	Zoop	Rec	Medium	-	-	-	-	-	-
Senegalia tenuifolia (L.) Britton & Rose	-	-	-	-	-	-	21	PI	Aut	Zoop	Ort	Light
Solanum granulosoleprosum Dunal	4	PI	Zoo	Zoop	Ort	Light	-	-	-	-	-	-
Sterculia striata A.St.-Hill. & Naudin	16	N PI	Aut	Zoop	Ort	Light	3	N PI	Aut	Zoop	Ort	Light

Continue...

Species	**Paracatu -MG**						**Presidente Juscelino -MG**					
	Ni	**EG**	**DS**	**PS**	**DT**	**WD**	**Ni**	**EG**	**DS**	**PS**	**DT**	**WD**
Swartzia macrostachya Benth.	-	-	-	-	-	-	1	N PI	Zoo	Zoop	Rec	Heavy
Syagrus romanzoffiana (Cham.)	-	-	-	-	-	-	1	N PI	Zoo	Zoop	Ort	Heavy
Tabebuia roseoalba (Ridl.) Sandwith	1	N PI	Ane	Zoop	Ort	Heavy	24	N PI	Ane	Zoop	Ort	Heavy
Talisia esculenta (A.St.-Hil.) Radlk.	-	-	-	-	-	-	5	N PI	Zoo	Zoop	Rec	Heavy
Trichilia catigua A.Juss.	-	-	-	-	-	-	41	N PI	Zoo	Zoop	Rec	Light
Trichilia elegans A.Juss.	6	N PI	Zoo	Zoop	Rec	Medium	-	-	-	-	-	-
Trichilia hirta L.	-	-	-	-	-	-	23	N PI	Zoo	Zoop	Rec	Medium
Trichilia pallens C.DC.	-	-	-	-	-	-	32	N PI	Zoo	Zoop	Rec	Heavy
Trichilia pallida Sw.	-	-	-	-	-	-	2	N PI	Zoo	Zoop	Rec	Medium
Trichilia clausseni C.DC.	-	-	-	-	-	-	6	N PI	Zoo	Zoop	Rec	Medium
Urera baccifera (L.) Gaudich. ex Wedd.	1	PI	Zoo	Zoop	Ort	Light	-	-	-	-	-	-
Zanthoxylum riedelianum Engl.	4	PI	Zoo	Zoop	Ort	Medium	1	PI	Zoo	Zoop	Ort	Medium
Zeyheria tuberculosa (Vell.) Bureau	-	-	-	-	-	-	3	PI	Ane	Zoop	Ort	Medium

SUPPLEMENT 2

Table S2. Functional attributes used in the classification of species and their ecological implications in the functions of the study community

Characteristics	Species description	Ecological implications
Ecological group [1]	a) Pioneer (young individuals and adults intolerant to the shade; dependent on light); b) Not pioneers (young individuals tolerant of shade, but who need light to grow; young individuals and adults tolerant to shade and able to survive in understory conditions).	Competition for light, stratification, regeneration time, soil cover, forest succession.
Seed dispersal syndrome [2]	a) Anemochory: diaspores are spread by the wind; b) Autochory: they disperse their seeds by gravity or by explosive dehiscence; c) Zoochory: diaspores are dispersed by animals.	Fertility, spatial distribution, genetic structuring, population viability, maintenance of dispersing fauna, environmental selection.
Pollination syndrome [2]	a) Anemophilous: pollinated by the wind; b) Zoophilous: pollinated by animals.	Propagation, trophic and phenodynamic structure, maintenance of local fauna.
Seed desiccation tolerance [3]	a) Orthodox: tolerate seed drying and low temperatures; b) Recalcitrants: do not tolerate desiccation of the seed and low temperatures.	Viability of the seed or seedling bank, germination process, forest succession, environmental selection.
Wood density [4]	a) Light wood: low-density wood (<0.5 gcm^{-3}) and low physical and structural resistance; b) Medium wood: intermediate density wood (from 0.5 to 0.8 gcm^{-3}), from low to medium physical and structural resistance; c) Heavy wood: wood with more lignified cells, high density (> 0.8 gcm^{-3}), and high physical and structural resistance.	Maximum height, longevity, relative growth rate, damage resistance, carbon storage, water storage.

Classification system proposed by: [1] = Cavalcante (2001); [2] = van der Pijl (1982); [3] = Davide & Silva (2008), [4] = Chave et al. (2009); Zanne et al. (2009); Borchert (1994 a,b).

Table S3. Spearman correlation coefficient (*S*) between environmental variables and the SESFRic and SESFDis of Paracatu and Presidente Juscelino, Brazil.

Environmental variables	Paracatu		Presidente Juscelino	
	SES_FRic	SES_FDis	SES_FRic	SES_FDis
	S	*S*	*S*	*S*
H+Al	0.106 ^{ns}	-0.297 ^{ns}	0.018 ^{ns}	-0.493*
SB	-0.019 ^{ns}	0.359 ^{ns}	-0.074 ^{ns}	0.123 ^{ns}
OM	0.019 ^{ns}	0.342 ^{ns}	-0.188 ^{ns}	-0.158 ^{ns}
Sand	0.061 ^{ns}	0.071 ^{ns}	-0.101^{ns}	0.21^{ns}
Clay	-0.169 ^{ns}	-0.268 ^{ns}	0.208 ^{ns}	0.069 ^{ns}
Roc	-0.015 ^{ns}	0.283 ^{ns}	-0.1 ^{ns}	0.355 ^{ns}
Slope	-0.104 ^{ns}	-0.008 ^{ns}	-0.332 ^{ns}	0.428**

H+Al = potential acidity; SB = sum of bases; OM = organic matter; Roc = percentage of exposed rock. SESFRic = standardized effect size of functional richness; SESFDis = standardized effect size of functional dispersion.* $p < 0,05$; ** $p < 0,01$; ns = not significant.