Phylogeny, traits, environment, and space in cerrado plant communities at Emas National Park (Brazil)

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ABSTRACT

Soil, drought, and fire are abiotic factors that may act as environmental filters in the cerrado, the Brazilian savanna. We used a framework to analyze environmental filtering in geographic and phylogenetic context, sampling woody species in one of the largest cerrado reserves. In 100 quadrats, we measured 10 functional traits on each woody individual. We also measured several soil variables, altitude and slope as a rough surrogate of water availability, interval between fires, and time since last fire. Almost all environmental variables were spatially auto-correlated. We found an overall trait clustering, but not an overall phylogenetic clustering. Nevertheless, we found a phylogenetic signal for some traits. Linking phylogeny, traits, environment, and space, we were able to detect a major dichotomy between two geomorphological units. The flat tableland was positively related with altitude, fire frequency, and nutrient-richer soil. Environmental filtering caused by water availability and fire lead to trait clustering, with smaller shrubs and trees that presented thicker barks, denser woods, sclerophylous leaves, highlighted by the prevalence of Myrtaceae. The other geomorphological unit, hilly terrain, was positively related with slope, low fire frequency, and nutrient-poorer soil. Environmental filtering was caused especially by nutrient-poor soil that lead to trait clustering, assembling taller trees, with thinner barks, lighter woods, and compound, large, tender, nutrient-richer leaves, distributed across many lineages, including Fabaceae. Hence, the high environmental variability in space with different environmental filters assembled different combination of plant traits and lineages, increasing the overall diversity in cerrado.

Introduction

The two main processes traditionally thought to structure ecological communities are limitations in similarity and environmental filtering (Emerson and Gillespie, 2008; Vamosi et al., 2009; Webb et al., 2002). Whereas the former leads to trait overdispersion, since similar species are prevented from co-occurring, the latter leads to trait clustering, since species with similar morphological and physiological traits are filtered (Emerson and Gillespie, 2008). If traits are conserved in the lineages, there will be a positive phylogenetic signal, and environmental filtering will also lead to phylogenetic clustering, that is, filtered species will also be closely related (Emerson and Gillespie, 2008). In this case, if environmental filters are spatially auto-correlated, there will be a spatial signal in the distribution of traits and taxa in the vegetation as well (Fortin and Dale, 2005; Pavoine et al., 2011). Phylogeny, traits, environment, and space are, thus, intertwined shaping vegetation units, even if there are few methods that combine them conceptually (Diniz-Filho et al., 2007; Kühn et al., 2009).

Recently, Pavoine et al. (2011) proposed a method that allows to analyze environmental filtering of plant species in a geographic and phylogenetic context. Their method describes environmental filters in terms of combinations of traits and abiotic variables, allowing spatial and phylogenetic signals to be detected (Pavoine et al., 2011). In their method, there are two main purposes in combining traits with phylogeny and environmental variables with space. First, associating traits with phylogeny determines whether the traits involved in environmental filters are evolutionarily conserved or convergent. In doing so, one can evaluate whether the turnover of trait states across habitats explains the distribution of specific lineages in space (Pavoine et al., 2011). Second, associating phylogeny with space at broad spatial scale determines whether historical processes, such as the history of the colonization, are

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predominant or interact with environmental factors in the species assembly (Pavoine et al., 2011).

The cerrado is the major savanna region in America and once covered about 2 million km² of Brazil's territory, especially in the Central Plateau (Gottsberger and Silberbauer-Gottsberger, 2006). The cerrado has a seasonal climate, with wet summer and dry winter, and occurs on nutrient-poor and acidic soils, with low cation exchange capacities and high levels of aluminum saturation (Gottsberger and Silberbauer-Gottsberger, 2006). The cerrado also undergoes frequent fires that favor the grassy ground layer, killing seedlings of woody species and hindering the development of adult woody individuals (Coutinho, 1990). So, soil characteristics, drought, and fire are abiotic factors that may act as environmental filters in the cerrado (Coutinho, 1990; Gottsberger and Silberbauer-Gottsberger, 2006), selecting from the pool those species that can persist within the community (Weiher and Reddy, 1995).

The cerrado presents a wide physiognomic variation, and when one looks at the landscape, one sees a mosaic of open and closed physiognomies, an evidence of spatial signal, which must be the consequence of the several spatially auto-correlated environmental factors acting upon the vegetation (Gottsberger and Silberbauer-Gottsberger, 2006). Generally, soil is considered the main environmental filter in the cerrado, since the less fertile the soil, the more open the physiognomy (Goodland and Pollard, 1973). However, fire and water availability also play important roles, since the higher the fire frequency (Coutinho, 1990) and the lower the water availability (Ferreira et al., 2007), the more open the physiognomy. These environmental filters are expected to assemble phenotypically similar species, since some combinations of traits will be favored. For example, nutrient-poor soil favors species with sclerophyllous leaves, drought favors deep-rooted trees, and high fire frequency favors trees with thick barks (Coutinho, 1990). Moreover, there is evidence of a positive phylogenetic signal for some traits in cerrado woody species (Silva and Batalha, 2011). So, if there is a spatial signal in the distribution of the cerrado vegetation, if there is trait clustering, and if there is, at least for some traits, a phylogenetic signal, then one may expect (1) different combinations of environmental variables in space; (2) different combinations of traits to be filtered according to these environmental variables and, consequently, different combinations of traits in space; and (3) lineages to be affected differently by these environmental variables and, consequently, lineages differently distributed in space.

Although the cerrado is among the most studied vegetation types in Brazil, a number of fundamental questions remain unanswered (Castro et al., 1999). Even if there are studies on environmental filtering (for example, Silva and Batalha, 2010), phylogenetic (for example, Silva and Batalha, 2011), and spatial signals (for example, Ferreira et al., 2007) in cerrado plant communities, an analysis combining all these aspects does, to the best of our knowledge, not yet exist. We used a new framework to analyze environmental filtering in the geographic and phylogenetic context (Pavoine et al., 2011), sampling woody species in one of the largest cerrado reserves. By linking phylogy, traits, environment, and space, we tried to answer the following questions: (1) are environmental variables spatially auto-correlated? (2) which combinations of traits is filtered by the environment? (3) which lineages are affected by these filters? (4) which combinations of environmental variables contribute to the assembly of the woody plant communities? and (5) do different combinations of environmental variables act on different geomorphological units?

Methods

We carried out this study in Emas National Park (ENP), one of the largest and most important cerrado reserves in South America, with about 133,000 ha, and located in the Brazilian Central Plateau (17°49′−18°28′S and 52°39′−53°10′W). The climate is tropical and humid, with wet summer and dry winter (Aw; Köppen, 1931). In the reserve, open cerrado physiognomies prevail, covering 68.1% of the total area, especially on the flat tableland (Ramos-Neto and Pivello, 2000). Closed cerrado physiognomies cover 23.1% of the reserve, mainly on the hilly terrain (Ramos-Neto and Pivello, 2000). Fire is frequent within the reserve, and a given point is burned every seven years on average (França et al., 2007).

We divided the study site into 10 strata according to time since last burning, using satellite images from 1973 to 2009. Then, we randomly placed 10 plots, each one with 5 m × 5 m, in each stratum. So, we placed 100 quadrats in total (Fig. 1), which allowed us to capture key characteristics in the study site. In each plot, from September 2009 to January 2010, we sampled all woody individuals with stem diameter equal to or higher than 3 cm at soil level (SMA, 1997). We identified all individuals to species level by comparing vouchers to ENP’s reference collection (Batalha and Martins, 2002) and used Plantminer (Carvalho et al., 2010) to search for families, authors, and synonyms concerning our species list.

For each individual sampled in the quadrats, we measured 10 functional traits that represent characteristics related to environmental filters, such as drought, fire, and nutrient-poor soils (Cornelissen et al., 2003; Pausas and Paula, 2005): basal area, height, bark thickness, wood density, leaf toughness, leaf size, specific leaf area, leaf nitrogen content, leaf phosphorus content, and leaf potassium content (see Cornelissen et al., 2003, for a detailed description of standard methods of measurement of these traits). For each trait and each species with two or more individuals, we calculated average values. For singleton species, we used the measured value of each trait. Instead of including only the most abundant species in the analyses, we used data of all species to avoid losing the generalization power of our analyses (Westoby, 1999).

In each quadrat, we determined, according to Silva and Batalha (2008), the following soil variables: pH, organic matter, available phosphorus, total nitrogen concentration, exchangeable potassium, exchangeable calcium, exchangeable magnesium, exchangeable aluminum, sum of bases, cation exchange capacity, base saturation, aluminum saturation, sand content, silt content, and clay content. We removed from subsequent analyses the parameter exchangeable magnesium, sum of bases, base saturation, aluminum saturation, silt content, and clay content, because they were highly correlated with other variables (R > 0.7). We also measured altitude and slope as a rough surrogate of water availability: in ENP, the higher the altitude and the lower the slope, the lower the water availability. Based on satellite images from 1984 to 2009, we determined mean interval between fires and time since last fire.

We constructed a phylogenetic tree for all sampled species with the Phylomatic software (Webb and Donoghue, 2005), estimating phylogenetic distances among species from different families from the current Phylomatic tree (R20091110). We improved tree resolution by consulting recent phylogenies of some families or orders: Fabaceae (Simon et al., 2009), Malpighiales (Wurdack and Davis, 2009), and Myrtaceae (Costa, 2009). We placed undated nodes evenly between dated nodes, using the “branch length adjustment” algorithm implemented in Phylomix (Webb et al., 2008).

Then, we followed the procedures described in Pavoine et al. (2011), using five matrices. First, with the coordinates of each quadrat, we constructed a spatial matrix S, defined as the eigenvectors of a neighboring matrix (Thioulouse et al., 1995), in which a value of one was given when two quadrats were neighbors and zero when they were not (Fig. 1). Second, with quadrats in rows and environmental variables in columns, we constructed an environmental matrix E. We log-transformed ‘slope’, ‘cation exchange capacity’, and ‘interval between fires’ to achieve normality. Then,
we standardized the matrix by the range. Third, with species in rows and functional traits in columns, we constructed a trait matrix \( T \). We log-transformed ‘basal area’, ‘height’, ‘leaf size’, and ‘leaf potassium content’ to achieve normality. Fourth, we constructed a phylogenetic matrix \( P \) based on the pairwise distances among species in the phylogenetic tree. Fifth, we constructed a species matrix \( L \), with species in rows, quadrats in columns, and abundances as entries.

To test whether the environmental variables were spatially auto-correlated, we used Moran’s test with 999 randomizations (Thioulouse et al., 1995). To test whether there was trait or phylogenetic clustering, we used, respectively, the TQE and the FQE tests with 999 randomizations (Pavoine et al., 2010). TQE and FQE are measures based on the quadratic entropy index (Rao, 1982) in such a way that trait and phylogenetic distances among species are incorporated to estimate respectively trait and phylogenetic diversities of communities (Pavoine et al., 2011). We looked for phylogenetic signal in each functional trait separately, using the root-skewness test (Pavoine et al., 2010). In this test, phylogenetic signal is found when species have more different trait values if they are distantly related on the phylogeny, that is, when the trait diversity is skewed to the root of the phylogenetic tree. Since we were interested in an overall description of environmental filters and traits, we used all environmental variables and all functional traits in the subsequent analyses.

We analyzed matrices \( S, E \), and \( T \) with principal component analyses and matrix \( P \) with principal coordinates analysis to produce, respectively, matrices \( X^*_c, X^*_s, X^*_f, \) and \( X^*_p \), which were standardized using the square root of the first eigenvalue of each analysis to produce, respectively, matrices \( X^*_c, X^*_s, X^*_f, \) and \( X^*_p \) (see figures 1 and 2 in Pavoine et al., 2011). We defined matrix \( R \) as \([X^*_c; X^*_f]\) and matrix \( Q \) as \([X^*_c; X^*_e]\), linked by matrix \( L \), which were analyzed in the RLQ approach with centered principal component analysis (Dolédec et al., 1996; Pavoine et al., 2011). The RLQ analysis was initially developed to study environmental filtering in ecological communities by assessing combinations of traits that have the highest covariances with combinations of environmental characteristics (Dolédec et al., 1996). We conducted all analyses in R [Development Core Team, 2009], using the “ade4” (Dray and Dufour, 2007), “ape” (Paradis et al., 2004), and “spdep” (Bivand, 2010) packages. We also used the functions provided by Pavoine et al. (2011).

Results

We sampled 531 individuals, belonging to 55 species, for which we constructed the phylogenetic tree (Fig. 2) and measured the functional trait values (Table 1). Fabaceae, with 10 species, and Myrtaceae, with nine species, were the richest families. All environmental variables (Table 2) except available phosphorus (\( P = 0.163 \)) and cation exchange capacity (\( P = 0.139 \)) were spatially auto-correlated (\( P < 0.005 \) in all other cases). We found an overall trait clustering (\( P = 0.0490 \), that is, lower trait diversity within each quadrant than expected by chance from all sampled species, but not an overall phylogenetic clustering (\( P = 0.359 \)). Nevertheless, we found significant phylogenetic signals for four traits, wood density (\( P = 0.042 \)), leaf size (\( P = 0.001 \)), leaf nitrogen content (\( P = 0.017 \)), and leaf potassium content (\( P = 0.009 \)), and marginally significant phylogenetic signals for three traits, height (\( P = 0.075 \)), specific leaf area (\( P = 0.087 \)), and leaf phosphorus content (\( P = 0.069 \)).

In the RLQ analysis, the first axis explained 23.8% of the variation and the second axis, 19.4%. Concerning the environmental variables, the first axis was positively related with time since last fire, interval between fires, sand proportion in soil, and slope (Fig. 3a). These areas were located especially in the hilly terrain, with closed cerrado physiognomies (Figs. 1 and 4a). The first axis was also negatively related with pH, exchangeable potassium, exchangeable aluminum, altitude, cation exchange capacity, exchangeable phosphorus, organic matter, and total nitrogen (Fig. 3a). These areas were located especially in the flat tableland, with open cerrado physiognomies (Figs. 1 and 4a). Concerning the traits, the first axis was positively related with leaf size, height, leaf nitrogen content, leaf phosphorus content (Fig. 3b), and several families including Fabaceae (Fig. 4b). The first axis was negatively related with leaf potassium content, specific leaf area, leaf toughness, wood density, bark thickness (Fig. 3b), and especially Myrtaceae (Fig. 4b).
Fig. 2. Phylogenetic tree assembled for the cerrado species sampled in Emas National Park, central Brazil (17° 49’ – 18° 28’ S, 52° 39’ – 53° 10’ W). The relationship among species was based on the current Phylomatic tree (tree R20091110, Webb and Donoghue, 2005). Fabaceae (FAB) and Myrtaceae (MRT) are the two families richest in species.

Discussion

We corroborated our expectation that we would find different combinations of environmental variables in space, since almost all variables we measured were spatially auto-correlated. When variability in environmental factors presents a spatial structure, the habitat is said to be heterogeneous, that is, spatial distributions are clumped (Ettema and Wardle, 2002). For example, fire occurrence within ENP is patchy, with some areas burned much more frequently than others (França et al., 2007). Fire, on its turn, may generate changes in nutrient concentrations, which become more clumped due to ash accumulation and litter deposition around trees (Rodrigues et al., 2009). Moreover, soil distribution and water availability are related to relief (Cole, 1986), which, in ENP, is also
heterogeneous, with two main geomorphological units, flat tableland and hilly terrain. So, if the environmental filters are spatially clumped and if they act upon the vegetation structure and composition, the cerrado will indeed be a heterogeneous landscape, with a mix of open and closed physiognomies (Gottsberger and Silberbauer-Gottsberger, 2006). Since the ‘habitat heterogeneity’ theory predicts that complex landscapes provide more niches and ways of exploiting resources, species diversity may increase (MacArthur and MacArthur, 1961).

Species diversity may increase in a heterogeneous landscape, but trait diversity is expected to decrease when environmental filters are speaking in the cerrado, nutrient-poor soils assemble shrubs and trees with sclerophyllous leaves that are able to tolerate aluminum toxicity (Gottsberger and Silberbauer-Gottsberger, 2006), frequent fires assemble smaller woody individuals with thick corky barks that prevent almost perfectly death by fire (Hoffman et al., 2005), and water shortage during the winter assembles shrubs and trees with long, deep roots that may extract water from deeper soil layers (Gottsberger and Silberbauer-Gottsberger, 2006). Since environmental variables were spatially auto-correlated, different combinations of them should lead to a spatial signal in the distribution of the traits as well.

Even if we found trait clustering, we did not find an overall phylogenetic clustering. On the one hand, we found a phylogenetic signal for wood density and most leaf traits; on the other hand, we did not find a phylogenetic signal in fire-related traits, such as
height, basal area, and thick bark. Contrary to other fire-prone vegetation types – for example, Mediterranean vegetation (Verdú and Pausas, 2007) – in the cerrado fire does not assemble phylogenetically related species, but only phenotypically similar species (Silva and Batalha, 2010). Whereas in Mediterranean vegetation, frequent fires appeared only in the Quaternary (Verdú and Pausas, 2007), in savannas, such as the cerrado, fire became frequent about 8 million years ago (Beering and Osborne, 2006). Thus, there was enough time for multiple colonizations of the cerrado by phylogenetically distant lineages (Silva and Batalha, 2010). Indeed, fire-related traits in the cerrado are not exclusive to specific families or older clades (Simon et al., 2009). A phylogenetic signal in wood density and leaf traits indicated that they were conserved in plant lineages and that there should also be a spatial signal, albeit weaker, in the distribution of clades.

Linking phylogeny, traits, environment, and space, we were able to detect a major dichotomy between the two geomorphological units. The flat tabletop was related with altitude, fire frequency, and nutrient-richer soil. It was located at higher altitudes, with deeper water tables. Even though many cerrado wood species present deep roots, there are hydraulic limitations to the amount of water that can be extracted from deeper soil layers (Franco, 2002). As a consequence, there were fewer trees, more grasses, which become highly flammable during the dry season, and higher fire frequency, which also leads to open cerrado physiognomies (Coutinho, 1990). Soil there was richer in nutrients, corroborating Silva and Batalha (2008), who found more fertile soils in sites with higher fire frequencies. In the flat tabletop, environmental filtering caused by water availability and fire lead to trait clustering, with smaller shrubs and trees that presented thicker barks, denser woods, sclerophyllous leaves. The phylogenetic variables highlighted the prevalence of Myrtaceae, which, despite the richer soil, presented the “low-resource strategy”, characterized by low relative growth rates, higher investment in leaf construction, low leaf water accumulation, and low leaf nutrient content (Craine, 2009).

The hilly terrain was positively related with slope, low fire frequency, and nutrient-poorer soil. In the steep relief, the less deep water table allows the establishment of woody individuals (Cole, 1986). The less developed grassy layer implies a lower fire frequency (Coutinho, 1990), which, in turn, implies a poorer soil (Silva and Batalha, 2008). In the hilly terrain, environmental filtering was caused especially by nutrient-poor soil that lead to trait clustering, assembling taller trees, with thinner barks, lighter woods, and compound, large, tender, nutrient-richer leaves. The phylogenetic variables emphasized the prevalence of many families, including Fabaceae, the family with most species in the area. In nutrient-poor soil, bacteria and cyanobacteria can make important contributions to nitrogen supply of cerrado plants by means of symbiosis with legume species that form root nodules (Gottsberger and Silberbauer-Gottsberger, 2006). Indeed, the proportion of nodulated trees is negatively correlated with soil nitrogen concentration (Lütteke, 1997). Moreover, compound leaves are frequent in Fabaceae (Malhado et al., 2010) and may be related to rapid-growth strategy, since these leaves allow species to invest relatively more energy into gaining height (Givnish, 1978).

## Table 2

<table>
<thead>
<tr>
<th>Environmental variable</th>
<th>Mean (sd)</th>
<th>Range (CV)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Altitude (m)</td>
<td>797.60 (40.08)</td>
<td>700.00–884.00 (5.03)</td>
</tr>
<tr>
<td>Slope (°)</td>
<td>2.07 (1.36)</td>
<td>0.30–8.70 (65.90)</td>
</tr>
<tr>
<td>pH</td>
<td>3.83 (0.18)</td>
<td>3.40–4.40 (4.59)</td>
</tr>
<tr>
<td>Organic matter (g kg⁻¹)</td>
<td>56.61 (16.61)</td>
<td>11.00–100.00 (29.34)</td>
</tr>
<tr>
<td>Nitrogen (mg kg⁻¹)</td>
<td>2035.05 (329.64)</td>
<td>1015.00–2746.00 (16.37)</td>
</tr>
<tr>
<td>Phosphorus (mg kg⁻¹)</td>
<td>6.55 (1.74)</td>
<td>1.00–13.00 (26.34)</td>
</tr>
<tr>
<td>Potassium (mmol kg⁻¹)</td>
<td>1.13 (0.36)</td>
<td>0.20–3.10 (31.56)</td>
</tr>
<tr>
<td>Calcium (mmol kg⁻¹)</td>
<td>1.51 (1.03)</td>
<td>1.00–10.00 (68.20)</td>
</tr>
<tr>
<td>Magnesium (mmol kg⁻¹)</td>
<td>1.36 (0.92)</td>
<td>1.00–9.00 (67.34)</td>
</tr>
<tr>
<td>Aluminum (mmol kg⁻¹)</td>
<td>18.43 (4.56)</td>
<td>5.00–38.00 (24.74)</td>
</tr>
<tr>
<td>Sum of bases (mmol kg⁻¹)</td>
<td>4.00 (2.14)</td>
<td>2.20–22.10 (53.50)</td>
</tr>
<tr>
<td>Cation exchange capacity (mmol kg⁻¹)</td>
<td>108.58 (34.53)</td>
<td>33.00–387.80 (31.80)</td>
</tr>
<tr>
<td>Base saturation (%)</td>
<td>3.92 (2.28)</td>
<td>1.00–23.00 (58.20)</td>
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<tr>
<td>Aluminum saturation (%)</td>
<td>81.99 (8.11)</td>
<td>18.00–92.00 (9.90)</td>
</tr>
<tr>
<td>Sand (%)</td>
<td>29.30 (17.88)</td>
<td>9.00–85.00 (61.02)</td>
</tr>
<tr>
<td>Silt (%)</td>
<td>4.40 (3.46)</td>
<td>1.00–13.00 (78.73)</td>
</tr>
<tr>
<td>Clay (%)</td>
<td>66.30 (16.96)</td>
<td>13.00–88.00 (25.58)</td>
</tr>
<tr>
<td>Fire interval (year)</td>
<td>2.99 (1.10)</td>
<td>1.18–8.00 (36.79)</td>
</tr>
<tr>
<td>Time since last fire (year)</td>
<td>5.14 (4.07)</td>
<td>0.00–15.00 (79.19)</td>
</tr>
</tbody>
</table>

## Fig. 3

Pearson’s correlations (a) between environmental variables and the coordinates of the sites on the first axis of the RQA analysis – Last Fire = time since last fire; Fire Int = mean interval between fires in the last 25 years; Sand = sand proportion in soil; Slo = slope; K = exchangeable potassium in soil; Al = exchangeable aluminum in soil; Alt = altitude; CEC = cation exchange capacity; P = exchangeable phosphorus in soil; OM = organic matter in soil; N = total nitrogen in soil; h = between species traits and the coordinates of the sites on the first axis of the RQA analysis – BA = basal area; H = height; Brk = bark thickness; Woo = wood density; Tgh = leaf toughness; LSz = leaf size; SLA = specific leaf area; N = leaf nitrogen content; P = leaf phosphorus content; K = leaf potassium content.
Fig. 4. Results of the RLQ analysis viewed on geographic area and phylogeny, based on coordinates of sites and species on the first axis. (a) Global coordinates of sites defined as the sum of environment- and space-based coordinates. The size of squares is proportional to the absolute values of site coordinates – white squares represent sites with negative coordinates, whereas black squares represent sites with positive coordinates; (b) global coordinates of species defined as the sum of trait- and phylogeny-based coordinates (see Fig. 2 for species names).

Based on our results, we may recommend conservation policies not only for ENP but for the cerrado as a whole. The relief was related to vegetation structure and composition and, thus, with trait and phylogenetic diversity, highlighted by the opposing strategies between the two families with highest species numbers, Myrtaceae and Fabaceae. But habitat vulnerability is not random in relation to relief. If crops are grown primarily on flat tablelands, sloping areas are preferably left as part of the reserve that landowners must preserve according to the Brazilian law (Carvalho et al., 2009). Thus, cerrado fragments are a non-random sample of the relief of a given region, being located mainly in hilly terrain, where open cerrado physiognomies are less frequent (Carvalho et al., 2009). If so, we may expect a higher vulnerability of Myrtaceae species and their attributes. Additionally, the adoption of a single fire management policy, as sometimes suggested by managers (França et al., 2007), would lead to higher trait and phylogenetic clustering, with loss of attributes and lineages. The statistical framework that links phylogeny, traits, environment, and space (Pavoine et al., 2011) allowed us to describe environmental filtering in terms of combinations of traits or abiotic factors and to determine spatial and phylogenetic signals. It seems to be a promising approach that should be applied in cerrado communities in other sites and at other scales.

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