Are the cerrado and the seasonal forest woody floras assembled by different processes despite their spatial proximity?

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Abstract

Aims
The Brazilian cerrado occupies land that could be occupied by seasonal forest, given current climatic conditions and their spatial proximity. Soil has been identified as one of the main determinants of cerrado and forest prevalence. We tested whether cerrado and seasonal forest woody floras were assembled by different processes. We postulated that soil nutrient availability would account for differences in the functional and phylogenetic structure of the cerrado and the seasonal forest.

Methods
In 100 5 × 5 m plots distributed along cerrado and seasonal forest patches in south-eastern Brazil, we sampled five individuals with a basal diameter ≥3 cm from 127 species and measured seven of their functional traits (plant height, basal area, tortuosity, leaf size, specific leaf area, leaf dry matter content, and leaf toughness). We constructed a phylogenetic tree and calculated the pairwise mean functional-phylogenetic distances (MFPDs), an approach that accounts for functional and phylogenetic information both separately and combined. We also sampled soils to a depth of 5 cm in each plot and had their chemical and physical properties determined. We related the MFPD to soil properties and compared MFPD between cerrado and forest species.

Important Findings
Phylogenetic distances were higher than functional distances in both cerrado and seasonal forest communities, suggesting trait convergence in both environments. Irrespective of the importance given to functional or phylogenetic information, most of the communities in the cerrado and in the seasonal forest fell within the null expectation, implying either that multiple assembly processes can occur simultaneously along the gradient of soil fertility, or that not all important traits were included. MFPD was related to soil nutrient status when only functional distances were considered. In this case, MFPD was lower in the cerrado than in the forest, indicating that soil nutrient availability influenced plant traits, with the low-nutrient soils in the cerrado constraining the range of variation in these traits. We found largely similar sorting mechanisms occurring in the cerrado and in the seasonal forest when we accounted for several important traits simultaneously along the phylogenetic distances. Nevertheless, we also found strong evidence for abiotic environmental filtering in the cerrado and for biotic filtering in the seasonal forest when relating MFPD to soil variables. Despite not being the only ecological force structuring these communities, soil nutrient status plays an important role in maintaining the functional distinctiveness of the two vegetation types.

Keywords: competition, functional traits, environmental filter, nutrient limitation, phylogeny, savanna

INTRODUCTION
Assembly rules are any constraint on species coexistence that determines whether species from a regional pool will colonize, survive and interact to form local communities (Götzenberger et al. 2012; HilleRisLambers et al. 2012). Since local communities are determined by a cumulative effect of dispersal and chance restrictions coupled with environmental filtering and biotic interactions (Götzenberger et al. 2012; HilleRisLambers et al. 2012), assembly rules embrace not only the ecological processes that directly influence structure and diversity of communities, but also the biogeographic processes that cause variation in the regional pool (Kraft and Ackerly 2014). Assessing assembly rules makes it possible to predict...

The occurrence of very different vegetation types occurring adjacent to each other despite being under a similar climate intrigues many plant ecologists around the world (Warman et al. 2013). A particular case occurs in Brazil, where cerrado and semi-deciduous seasonal forest are commonly found forming abrupt transitions (Dantas et al. 2013; Durigan and Ratter 2006; Hoffmann et al. 2012; Ratter et al. 1997; Viani et al. 2014). Despite occurring under the same climate and often adjacent to each other, few species are shared between them, suggesting that abiotic and biotic restrictions might be limiting their similarity, regardless of dispersal events (Ai et al. 2012). Studying assembly rules on both sides of the cerrado-forest boundary may give important insights into the processes maintaining and structuring cerrado and seasonal forest communities and, as a consequence, may help to define conservation goals.

One of the main factors that potentially maintain the cerrado-forest boundary is soil fertility (Durigan and Ratter 2006; Ruggiero et al. 2002). According to the habitat-filtering theory (Keddy 1992), low fertility may be a key environmental filter, selecting from the species pool those that have suitable traits to withstand local conditions and forcing species to converge towards the ‘most suitable’ trait values. Conversely, according to the limiting similarity theory (Diamond 1975; Pacala and Tilman 1994), competition for resources usually results in trait divergence, which enables stable coexistence among organisms. In this case, co-existing species are expected to have different functional attributes whereby resources are captured and exploited in different ways, reducing the chances of competitive exclusion (Grime 2006). Thus, while soil fertility may be a key environmental filter contributing to the lack of similarity in species composition between cerrado and forest (Hoffmann et al. 2012, Ruggiero et al. 2002), it can also promote diversification by limiting the similarity among its species (Grime 2006; Katabuchi et al. 2012; Simon et al. 2009). Regardless, in nutrient-poor soils, species tend to converge towards a retentive strategy, whereas, in nutrient-rich soils, species seem to have a mixture of strategies with respect to nutrient acquisition (Mason et al. 2012; Ordoñez et al. 2009).

Considering that soil must be one of the main factors influencing cerrado-forest prevalence, either by filtering out species from the regional pool, or by promoting diversity, we aimed to study the assembly processes in these two proximal but distinct vegetation types. To do so, we used a new approach for quantifying biodiversity by weighting the independent contribution of functional and phylogenetic distances in a single measure, the so-called ‘functional-phylogenetic distance’ (Cadotte et al. 2013). This measure of diversity can be considered both a phylogenetic distance that takes trait convergence or divergence into account and ‘a functional distance that accounts for information from unmeasured, phylogenetically correlated traits’ (Cadotte et al. 2013). Thereby, it is an advantageous tool because it simultaneously provides information on species similarity and unmeasured traits, enabling estimations of the evolutionary history and species distributions (i.e. through phylogenetic information; Swenson 2013), as well as more accurate information on species similarities based on direct morphological or physiological characteristics, allowing the identification of ecological strategies (i.e. through functional information; Swenson 2013).

Through sampling plant communities with respect to species composition, relatedness and functional traits linked to important ecological factors, such as resource use, resource conservation, space occupation, competitive vigour and stress tolerance, we aimed to answer the following questions: (i) Do functional traits present a positive phylogenetic signal? In the cerrado, phylogenetically auto-correlated traits have previously been found (Batalha et al. 2011); (ii) Are functional-phylogenetic distances lower in the cerrado than in the seasonal forest? We expect this to be the case if cerrado communities are mainly assembled by environmental filtering, given that their nutrient-poor soils promote trait clustering (Batalha et al. 2011), and if seasonal forest communities are mainly assembled by limiting similarity, given that they are subject to a more competitive environment (Viani et al. 2011); (iii) Are functional-phylogenetic distances related to soil features? Since soil is considered an important factor influencing cerrado-forest prevalence (Ruggiero et al. 2002), we expect functional-phylogenetic distances to increase towards richer soils.

**METHODS**

**Study site**

We carried out this study in Vaçununga State Park, located in Santa Rita do Passa Quatro municipality, south-eastern Brazil (21°43′05″S 47°35′49″W). The park is 590–740 m above sea level. Regional climate is classified as Cwa (Köppen 1931), with wet summers (from October to April) and dry winters (May to September). Mean annual temperature is 21.5°C and annual rainfall ~1500 mm (Pivello et al. 1998). The park covers 2071 ha and is divided into six fragments: one bigger and mainly covered by cerrado and five smaller and mainly covered by semi-deciduous seasonal forest. Soils are Neosols and Latosols, according to the Brazilian classification system (Embrapa 2012), or Entisols and Oxisols, according to the USDA classification system (Soil Survey Staff 2014). We established 100 25-m² plots in the three fragments that were accessible to researchers using random stratified sampling (Krebs 1998; Sutherland 2006). The number of plots in each vegetation type was proportional to the area covered by them in the three fragments, that is, 68 plots in the cerrado, representing its 1192 ha, and 32 plots in the seasonal forest, representing its 578 ha.
Soil data collection

In each plot, we collected soil samples at 0–5 cm depth. PH, organic matter, total nitrogen, available phosphorus, exchangeable potassium, calcium, magnesium, aluminium, sum of bases, base saturation, aluminium saturation, cation exchange capacity, and sand, silt and clay content were analysed at the Luiz de Queiroz College of Agriculture, at the University of São Paulo, following procedures described in Silva and Batalha (2008).

Trait data collection

We identified all woody individuals with stem diameter at the soil level equal to or higher than 3 cm (SMA 1997) to species level, comparing the collected material to vouchers lodged at the Botanical Institute of São Paulo herbarium or using identification keys based on vegetative characters (Batalha et al. 1998; Batalha and Mantovani 1999). We then randomly selected 5–10 individuals of each species to be sampled. For species with less than five individuals, we identified other individuals close to the plots in order to make up five individuals per species.

For each individual, we sampled seven functional traits that we considered relevant to assembly processes, by being related to either resource use, resource conservation, space occupation, competitive vigour or stress tolerance. These traits were height, basal area, tortuosity, leaf size, specific leaf area, leaf dry matter content and leaf toughness (Table 1).

We considered plant height to be the shortest distance between the highest photosynthetic tissue in the canopy and ground level, corresponding to the top of the canopy between the highest photosynthetic tissue in the canopy (specific leaf area, leaf dry matter content and leaf toughness traits were height, basal area, tortuosity, leaf size, specific leaf area, leaf dry matter content and leaf toughness). Thus, tortuosity varied from zero to one, and the higher the value, the more tortuous the plant.

Additionally, we collected five green leaves from each individual, from branches fully exposed to sunlight. We placed the leaves in plastic bags, put them in a thermal box, and took them to the laboratory, where we measured four functional traits: leaf size, specific leaf area, leaf dry matter content and leaf toughness (Table 1). Given that leaves were still fresh and wet at the time of measurement, we did not rehydrate them. We scanned the leaves and calculated their area using ImageJ software (Rasband 2014). We also weighed the leaves in an analytical balance accurate to 0.001 g to obtain their fresh masses. Then, we placed the leaves in paper bags, oven-dried them at 70°C for 72 hours, and weighed them again to obtain their dry masses. We divided leaf area by dry mass to obtain specific leaf area and dry mass by fresh mass to obtain leaf dry matter content. As a surrogate for leaf toughness, we measured the force to punch, punching with a dynamometer at both sides of the midrib and recording the force necessary to penetrate the leaf.

Phylogenetic data

After identifying the species in each plot, we built a phylogenetic tree, using Bell (2010) as reference. We improved tree resolution by consulting recent phylogenies of some clades, such as Fabaceae (Simon et al. 2009), Malpighiales (Wurdack and Davis 2009) and Myrtaceae (Costa 2009). After building the phylogenetic tree, we obtained a phylogenetic distance matrix using cophenetic distances.

Data analyses

To address the first question, we tested whether there was a positive or a negative phylogenetic signal in each functional trait using Blomberg’s K statistic (Blomberg et al. 2003). We considered K >1 to indicate a positive phylogenetic signal, meaning that closely related species have more similar traits than expected under the Brownian motion model (Blomberg et al. 2003, Zhang et al. 2017); K <1 to indicate a negative phylogenetic signal, meaning that closely related species are more divergent in their traits than expected under the Brownian motion model; and K close to 0 to indicate an absence of phylogenetic signal, so that closely related species are not more similar in their traits than distantly related species (Blomberg et al. 2003; Zhang et al. 2017).

As a mean of comparison, we plotted multiple density curves to analyse the distribution of each functional trait in the cerrado and in the seasonal forest.
To address the second question, we standardized each trait to zero mean and unit variance to obtain a functional distance matrix using Euclidean distances. Then, we computed the functional-phylogenetic distance matrix using three matrices: (i) the community matrix, containing communities as rows, species as columns and number of individuals as entries; (ii) the functional matrix, containing species as rows, traits as columns and mean trait values as entries and (iii) the phylogenetic matrix, containing species as rows and columns and the pairwise distances as entries. We then calculated the species functional-phylogenetic pairwise distances following Cadotte et al. (2013): \[ \text{FDPD} = (a \text{PD} + (1 - a) \text{FD})^{1/p}, \]

where FD is the functional distance, PD is the phylogenetic distance, and \( a \) and \( p \) are weighting parameters (Cadotte et al. 2013). The weighting parameter \( a \) goes from zero to one and adjusts the contribution of functional and phylogenetic distances: when it is close to zero, more importance is given to functional distances; when it is close to one, more importance is given to phylogenetic distances (Cadotte et al. 2013). The weighting parameter \( p \) is used to meet the mathematical restrictions of a distance metric and has to equal or exceed one (Cadotte et al. 2013).

To compare cerrado and forest communities, we calculated mean functional-phylogenetic distances (MFPDs) for each community, setting the parameter \( a \) to 0 (only functional distances were considered), 0.5 (functional and phylogenetic distances were given the same weight) and 1 (only phylogenetic distances were considered). In all cases, we set the parameter \( p \) to 2. We then ran Mann–Whitney tests (Zar 1999).

In addition, to test whether communities were under or overdispersed, we calculated the MFPDs for the entire range of weighting parameter \( a \), and plotted these distances against \( a \) (see Fig. 1). We compared the observed curves with those built from a null distribution based on 4999 randomizations that also accounted for different values of \( a \), ranging from 0 to 1. For the randomizations, the original species richness in each plot was kept fixed, but species identity varied. The species pool was given by the list of species presented across all plots in both vegetation types because together they represent better the regional pool of species. Nevertheless, as a matter of curiosity, we also generated randomizations by separating the cerrado and seasonal forest data, considering that each vegetation type would form a distinct local pool of species (see online supplementary Appendix 4). In both cases, the community was considered overdispersed when the observed curve was above the 0.975 quantile of the distribution and underdispersed when below the 0.025 quantile (Cadotte et al. 2013).

Importantly, we considered all seven traits simultaneously when calculating the MFPDs mainly because we were interested in knowing whether cerrado species were different from seasonal forest species in terms of performance. Thereby, we measured seven traits related to species performance (Table 1), since as many traits as possible should be included in an index of functional diversity as long as they are related to the

![Figure 1](https://academic.oup.com/jpe/article-abstract/11/5/740/4061481/1481)
process of interest (Petchey and Gaston 2006). In fact, using many traits is desirable for our method of calculating functional distances, as it uses ordination techniques to obtain the species pairwise functional distances from multidimensional trait space (Cadotte et al. 2013). The MFPD approach enables not only the incorporation of multiple traits, but also the detection of the effect of unmeasured traits, which is possible when combining functional and phylogenetic information (Cadotte et al. 2013).

Finally, we built linear models, using MFPDs as the response variable and soil variables as explanatory variables to address our third question. We repeated this procedure at three levels of a (0, 0.5 and 1), giving progressively more importance to phylogenetic distances (Cadotte et al. 2013). We conducted all analyses in R (R Development Core Team 2015), using the ‘ade4’ (Dray and Dufour 2007), ‘phytools’ (Revell 2012) and ‘vegan’ (Oksanen et al. 2013) packages, as well as the functions provided by Cadotte et al. (2013), which are currently included in the package ‘pez’ (Pearse et al. 2015).

**RESULTS**

We sampled 69 species belonging to 28 families in the cerrado and 65 species belonging to 30 families in the semi-deciduous seasonal forest (see online supplementary Appendix 1). Since there were seven species common to both vegetation types, overall there were 127 species, for which we measured the functional traits (see online supplementary Appendix 1) and obtained the phylogenetic tree (see online supplementary Appendix 2). Blomberg’s K values were always lower than one, but only significantly so for leaf toughness and specific leaf area (Table 2).

Cerrado species were shorter, had lower basal area, more tortuous stems, lower leaf size and specific leaf area and, as a consequence, had tougher leaves with higher dry matter content than the seasonal forest species (Fig. 2).

MFPDs were lower in the cerrado than in the forest when only functional distances were considered ($P < 0.001$; Table 3) and when phylogenetic and functional distances were given equal weight ($P = 0.022$; Table 3), but not when only phylogenetic distances were considered ($P = 0.130$; Table 3). Phylogenetic distances were higher than functional distances, particularly when analysing the curves of the MFPDs against the weighting parameter $a$, providing signatures that pairwise evolutionary relationships were convergent. As a consequence, curves of functional-phylogenetic distances as a function of the weighting parameter $a$ were always increasing (Fig. 3; see online supplementary Appendix 3). Among the 68 communities in the cerrado, eight were underdispersed at least for some values of $a$, whereas the other 60 were always within the null distribution (Fig. 3; see online supplementary Appendix 3). Among the 32 communities in the seasonal forest, three were underdispersed and three were overdispersed at least for some values of $a$, whereas the other 26 were always within the null distribution (Fig. 3; see online supplementary Appendix 3). Fig. 3 shows three communities with different patterns in each vegetation type, and patterns across all communities can be seen in online supplementary Appendix 3. We found similar patterns when we generated exclusive randomization for cerrado and for seasonal forest, even though with slight differences (see online supplementary Appendix 4).

Cerrado sites were, in general, less fertile than seasonal forest sites (Table 4) and we found a strong control of soil clay on the functional-phylogenetic distances (Fig. 4). The MFPDs were also related to soil organic matter, sum of bases, cation exchange capacity, though less strongly than to soil clay, when the relationships were tested individually (Fig. 4). Cerrado sites were remarkably clustered for almost all soil variables considered (Fig. 4) and a post-hoc Sorensen similarity index calculated for cerrado and forest plots indicated that cerrado plots were, on average, more similar to each other than the seasonal forest in regard to species composition, but still were not very similar ($s = 0.34$ for cerrado and $s = 0.16$ for seasonal forest).

**DISCUSSION**

As a whole, the cerrado and the seasonal forest had similar numbers of species, but few of them occurred simultaneously in both vegetation types. However, species and individual densities have been shown to be lower in the seasonal forest than in the cerrado (Miatto et al. 2016). Contrary to what we expected, none of the traits had a positive phylogenetic signal. Basal area, height, tortuosity and leaf size presented a random walk divergence in regards to species resemblance, whereas specific leaf area and leaf toughness presented a negative phylogenetic signal. The absence of phylogenetic signal in a given functional trait often occurs when the trait determines within-habitat diversity and so species are subject to rapid evolutionary rates due to adaptive radiation (Silvertown et al. 2006). Basal area and height are two allometrically related traits that determine species niche, and are labile for this reason (Westoby 1998). Leaf size is also a labile trait because of the multiple functions that a leaf carries out and the consequent trade-off required for its successful functionality.
Tortuosity, in contrast, is a trait driven by fire, and is related to scleromorphism (Sarmiento 1984).

Since fire in the cerrado tends to promote phenotypic but not phylogenetic underdispersion (Silva and Batalha 2010), it is reasonable that tortuosity had an absent phylogenetic signal.

The negative phylogenetic signal we found for specific leaf area and leaf toughness implies phylogenetic convergence. In this case, phylogenetically distant species were more similar for these traits than they would be if these traits had evolved following a Brownian motion (Blomberg et al. 2003). The negative phylogenetic signal we found for specific leaf area and leaf toughness implies phylogenetic convergence. In this case, phylogenetically distant species were more similar for these traits than they would be if these traits had evolved following a Brownian motion (Blomberg et al. 2003). The negative phylogenetic signal we found for specific leaf area and leaf toughness implies phylogenetic convergence. In this case, phylogenetically distant species were more similar for these traits than they would be if these traits had evolved following a Brownian motion (Blomberg et al. 2003).

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Figure 3: mean pairwise functional-phylogenetic distances (MFPD) as a function of the weighting parameter \( a \) for six communities in the Vaquinunga State Park, Brazil (21°41'00"–21°41'21"S and 47°34'37"–47°39'39"W). (a), (b) and (c) are communities from the cerrado. (d), (e) and (f) are communities from the seasonal forest. Dotted lines represent the observed mean pairwise distances. Dark grey, grey and light grey shading represents the 50, 90 and 95 confidence intervals of the null distributions. Solid lines represent the average of the null distributions. Species richness (S) is indicated. Three communities with different patterns in each vegetation type are represented: underdispersion (a) and (d); null distribution (b), (c) and (e); overdispersion (f). Patterns across all communities can be seen in online supplementary Appendix 3.

Table 4: mean, standard deviation and range of each soil feature in the cerrado and in the seasonal forest

<table>
<thead>
<tr>
<th>Soil feature (unit)</th>
<th>Cerrado</th>
<th></th>
<th>Seasonal forest</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean ± SD</td>
<td>Range</td>
<td>Mean ± SD</td>
<td>Range</td>
</tr>
<tr>
<td>pH</td>
<td>3.94 ± 0.12</td>
<td>3.7–4.2</td>
<td>4.25 ± 0.44</td>
<td>3.7–5.8</td>
</tr>
<tr>
<td>OM (mmol.kg(^{-1}))</td>
<td>20.37 ± 4.58</td>
<td>8 – 31</td>
<td>24.37 ± 9.21</td>
<td>13–46</td>
</tr>
<tr>
<td>N (mg.kg(^{-1}))</td>
<td>1144.11 ± 546.21</td>
<td>651 – 3199</td>
<td>1167.72 ± 308.23</td>
<td>770–1960</td>
</tr>
<tr>
<td>P (mg.kg(^{-1}))</td>
<td>2.30 ± 0.69</td>
<td>1.51 – 500</td>
<td>2.38 ± 0.63</td>
<td>1.44–4.47</td>
</tr>
<tr>
<td>Al (mmol.kg(^{-1}))</td>
<td>12.05 ± 2.18</td>
<td>7.50 – 19.21</td>
<td>10.07 ± 5.12</td>
<td>0.01–21.08</td>
</tr>
<tr>
<td>SB (mmol.kg(^{-1}))</td>
<td>1.71 ± 0.37</td>
<td>1.5 – 4.5</td>
<td>17.41 ± 23.57</td>
<td>3.1–124</td>
</tr>
<tr>
<td>CEC (mmol.kg(^{-1}))</td>
<td>47.38 ± 9.60</td>
<td>28.6 – 82.7</td>
<td>68.5 ± 28.95</td>
<td>31.7–155.4</td>
</tr>
<tr>
<td>Clay (g.kg(^{-1}))</td>
<td>89.25 ± 30.73</td>
<td>38 – 151</td>
<td>225.94 ± 115.25</td>
<td>100–443</td>
</tr>
</tbody>
</table>

pH, organic matter (OM), total nitrogen (N), available phosphorus (P), Aluminium (Al), sum of bases (SB), cation exchange capacity (CEC) and clay. A more complete version of this table is published in Miatto et al. (2016).
analysing the direct response to soil fertility. While cerrado species are selected only for a slow growth or conservative strategy, the forest species are selected for an acquisitive strategy, but with diversified traits that reduce niche overlap or improve a species’ competitive abilities.

When analysing communities that deviated from the null expectation, we found evidence for filtering in cerrado communities, some of which were underdispersed. However, we did not necessarily find evidence for limiting similarity in the seasonal forest. Some of the forest communities were also underdispersed at low and intermediate values of $a$, but some were overdispersed. It was at intermediate values that most of the deviations from the null model occurred when plotting the pairwise functional-phylogenetic distance against the weighting parameter $a$, implying that both measured and unmeasured functional traits were informative (Cadotte et al. 2013). When traits are convergent, as for specific leaf area and leaf toughness, and environmental filtering is the main ecological force, simultaneous phylogenetic overdispersion and phenotypic underdispersion are expected to occur (Webb et al. 2002). Conversely, phylogenetic random patterns and phenotypic overdispersion are expected to occur when...
competitive interactions are the main forces structuring the community (Webb et al. 2002). Hence, when a was set to 1, we should have found overdispersion in cerrado and no deviation from the null model in the forest. Instead, underdispersion occurred in both environments, which could have been caused by unmeasured traits that have some outstanding role into these assemblies (Cadotte et al. 2013).

Despite some evidence for environmental filtering in the cerrado and limiting similarity in the seasonal forest for a few communities, most of the cerrado and the seasonal forest communities lay within the null expectation when plotting pairwise functional-phylogenetic distances against the weighting parameter. This pattern was contrary to what we expected, and was likely due to a balance between environmental filtering and abiotic filtering in both environments. Indeed, multiple assembly processes can occur simultaneously along a gradient of soil fertility, with traits being selected differently at both extremes of the gradient (Cadotte et al. 2013; Spasojevic and Suding 2012). So, even if species were selected for a conservative strategy in the cerrado and for an acquisitive strategy in the forest, after they were able to colonize, establish and persist in both habitats, they necessarily must also interact with their neighbours, occupy niches and develop their competitive abilities (Mayfield and Levine 2010). Consequently, the traits we measured can be simultaneously constrained in their range due to soil nutrient status (more evident for cerrado), and become overdispersed within that range due to limiting similarity (Silvertown et al. 2006). Moreover, other factors such as space and light may have been promoting, or at least reinforcing, the limiting similarity in the seasonal forest due to the higher basal area and higher canopy closure in this vegetation (Murphy and Lugo 1986; Viani et al. 2014).

Alternatively, it may be the case that important traits were not included in the analysis (Cadotte et al. 2013), as already mentioned here. The fact that cerrado and seasonal forest differed in the traits we measured strengthens this possibility because, if these were the only traits of importance, we would have found more evidence for environmental filtering in the cerrado than we actually found. For example, we did not consider what was happening below ground, where competition for nutrients can be very strong, and many traits are linked to nutrient use, and, thus, could have a large effect on species coexistence (Casper and Jackson 1997). In the cerrado, in particular (often described as an ‘upside-down forest’), the below-ground system is perhaps highly important for community functioning but its functional traits are still under-explored (Durigan et al. 2012; Loiola et al. 2015; Ribeiro et al. 2011). Notwithstanding, it is an uncertain issue in terms of phylogenetic patterns, since different root traits tend to differ in their degree of variation and phylogenetic conservatism (Kong et al. 2014), especially because they are subject to trade-offs between resource acquisition and conservation along environmental gradients (Pietro et al. 2015).

Cerrado sites had more impoverished soils, with lower variation in their features than the seasonal forest. As a matter of fact, Miatto et al. (2016) assessed whether these cerrado and seasonal forest communities were different in terms of soil properties and found that cerrado sites are constrained towards soils with lower pH, lower concentrations of clay and organic matter, and lower cation exchange capacity. Thereby, the low-nutrient soil in the cerrado selected for species with the most advantageous traits to succeed there (Miatto et al. 2016; Ruggiero et al. 2002). However, there were no differences in soil total nitrogen and available phosphorus (see Miatto et al. 2016), contrary to what has been found for other sites in south-eastern Brazil (Viani et al. 2011). As a consequence, soil nitrogen and phosphorus did not account for the variation in the functional-phylogenetic distances. Conversely, organic matter, sum of bases, cation exchange capacity and, more importantly, clay content were related to the functional-phylogenetic distances by driving the supply of soluble nutrients available to the plants (Park 2001). Even so, a low percentage of the variation in the functional-phylogenetic distances was explained. This result was likely related to the fact that there was a wide range of pairwise functional-phylogenetic distances in the cerrado, as showed in linear model graphs, even though the soils were equally poor across cerrado communities. This reinforces our evidence that limiting similarity and environmental filtering are both structuring cerrado communities and that niche partitioning is occurring, even though conservative strategies prevail in its low-nutrient soil (Mayfield and Levine 2010).

The cerrado and the seasonal forest are functionally different (Loiola et al. 2015; Viani et al. 2014) but not necessarily phylogenetically different because phylogenetic information alone did not detect differences between these environments. Nevertheless, it did not hinder better predictions on assemblies of cerrado and forest communities when combined with the functional information. Soil was an important factor contributing to the differences in both environments, but it appears that soil nutrient-status is not the only ecological force acting to maintain the cerrado-forest boundary. Limiting similarity also appears to be structuring this vegetation type. Thus, accounting for several important traits simultaneously along with phylogenetic distances, we found largely similar sorting mechanisms occurring in the cerrado and in the seasonal forest, despite past studies finding evidence for abiotic-environmental filtering in the cerrado versus biotic-interaction filtering in the seasonal forest when a trait by trait approach was used (Viani et al. 2011; Vourlitis et al. 2014). Even with evidence of a biotic-interaction filter structuring both cerrado and seasonal forest, our results support the theory that soils have an important role in maintaining the functional distinctiveness of the two vegetation types, and suggest that shifts in the cerrado-forest boundaries can occur under the predicted scenario of eutrophication in the cerrado (Hunke et al. 2015).
SUPPLEMENTARY MATERIAL

Supplementary material is available at Journal of Plant Ecology online.

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