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Resource availability shapes fire-filtered savannas

Vinícius de L. Dantas, Marco A. Batalha, Helena França & Juli G. Pausas

Keywords
Cerrado; community assembly; fire regimes; fire-filtered landscapes; functional traits; intraspecific variability; phylogenetic turnover; savanna; soil texture; spatial structure

Abbreviations
CT = compositional turnover; PT = phylogenetic turnover; FT = species-based functional turnover; iFT = individual-based functional turnover.

Nomenclature
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Dantas, V.L. (corresponding author, viniciusldantas@gmail.com)[1],
Batalha, M.A. (marcobat@fastmail.fm)[2],
França, H. (helena.franca@ufabc.edu.br)[3],
Pausas, J.G. (juli.g.pausas@uv.es)[4]

[1]Departament of Plant Biology, University of Campinas, Campinas, SP 13083-970, Brazil;
[2]Department of Botany, Federal University of São Carlos,PO Box 676, São Carlos, SP 13565-905, Brazil;
[3]Center for Engineering, Modelling, and Social Sciences, Federal University of ABC,166 Santa Adélia, Santo André, 09210-170, Brazil;
[4]CIDE-CSIC, Ctra. Naquera Km. 4.5 (IVIA), Montcada, Valencia 46113, Spain

Abstract

Questions: Humid savannas can be considered fire-filtered landscapes because fire is very frequent (<10 yr return intervals) and only fire-resistant species can occur. This flammable vegetation can be functionally heterogeneous, structurally and floristically patchy. We hypothesized that resource availability (mainly water and nutrient availabilities) accounted for most of the functional and phylogenetic spatial structure of communities across these savanna landscapes.

Location: Emas National Park, central Brazil.

Methods: We used individual-based functional trait, phylogenetic and environmental data combined with spatial information to assess the main drivers and mechanisms of community functional change (turnover) in a large fire-filtered savanna landscape. We used Mantel correlograms and a maximum rank correlation approach to assess the spatial structure and the subset of landscape factors that best predict compositional, phylogenetic, species-based and individual-based functional community turnovers and the mechanism by which they do operate.

Results: Communities were spatially structured across the landscape, presenting functional convergence at shorter distances and divergence at larger distances. All of the turnover metrics presented unique spatial structures and were correlated with a unique set of landscape predictors. Soil texture accounted for the largest fraction of the spatial structure, but soil N availability, pH, altitude and fire frequency were also important.

Conclusions: Our results support the idea that the patchy distribution of water and nutrients mediated by clay content shape community membership in fire-filtered savannas, whereas current variations in fire frequency interact with resource availability to shift community attributes from species average trait values (intraspecific variability).

Introduction

Understanding how biotic interactions and abiotic drivers synergistically shape species co-existence across spatial scales is a central issue in ecology. In the last decade, information on phylogenies and functional traits has been combined with information on resource availability gradients and disturbance regimes to provide a deep understanding of the mechanisms by which species are assembled within communities (e.g. Webb et al. 2002; Kraft et al. 2008; Pausas & Verdú 2010). Using such information to understand the structure of communities within landscapes (i.e. variation in β-diversity) is currently emerging as a prominent tool for linking ecological, historical and biogeographic patterns (Bryant et al. 2008; Graham & Fine 2008; Hardy et al. 2012; Swenson et al. 2012).

In tropical landscapes, stabilizing feedbacks between tree cover and fire drive major functional shifts maintaining two stable states: a state in which fires are uncommon and of very low intensity (forest communities), and a state maintained by frequent fires (shrub, tree and woodland savannas). In highly flammable landscapes, this process often results in heterogeneous savanna matrices with frequent fires that are spotted with infrequently burned forest patches (Dantas et al. 2013a). In the flammable savanna matrix, fire acts as an environmental filter, allowing only

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species with fire resistance traits to survive (Simon et al. 2009; Hoffmann et al. 2012; Dantas et al. 2013a). In these savannas, the functional trait dissimilarities among local communities are seldom explained by differences in fire frequency (Dantas et al. 2013b). We define as fire-filtered savannas those in which fire frequency is high and its range is not sufficiently large to promote important differences in species composition among communities (mean fire interval <10 yr).

These patchy savannas are particularly well represented in the humid tropics, where the most species-rich and structurally heterogeneous savannas occur (Simon et al. 2009; Murphy & Bowman 2012). In these humid savannas, tree density and species composition can be spatially structured and such fine-grained structure is not related to climate differences (Goodland & Pollard 1973; Hoffmann et al. 2005). Many authors have suggested that soil fertility, water availability and fire frequency are important factors shaping these mosaics (Goodland & Pollard 1973; Kellman 1984; Ferreira et al. 2007; Batalha et al. 2011; Hoffmann et al. 2012). However, there is little mechanistic understanding on how they synergistically interact to influence the spatial heterogeneity of savanna landscapes (Bond 2010; Hoffmann et al. 2012; February et al. 2013; Viani et al. 2014). Moreover, most of the field studies on these savannas have investigated the role of a single predictor in explaining woody plant densities, species richness or basal areas, and are often conducted at small spatial scales (Goodland & Pollard 1973; Ruggiero et al. 2002; Ferreira et al. 2007; Dantas & Batalha 2011). Such approaches can ignore important sources of variability and miss the spatial scale at which predictors operate, possibly leading to conflicting conclusions. A multivariate functional and phylogenetic approach might help to provide an important step forward towards an understanding of the mechanisms by which landscape predictors interact with functional attributes of plants to shape the assembly of these communities.

We explored the relationships among spatial changes (turnovers) in floristic, phylogenetic and functional compositions across fire-filtered savanna communities and spatially structured environmental gradients. We aimed to answer the following questions: (1) Is community functional composition spatially patchy in fire-filtered savannas? (2) What are the main predictors shaping the spatial structure of savanna communities within these landscapes? (3) What mechanisms do these predictors operate by to shape community assembly? And (4) what are the spatial scales at which these predictors operate? To answer these questions, we studied 99 plots, 0.019–54 km apart, distributed across the heterogeneous landscapes of Emas National Park, a 132 000 ha Neotropical reserve in central Brazil, in which most of the physiognomies are savannas, but forest patches also occur (but were not considered in this study). Here, we depict savanna from forest communities using the threshold criterion described in Dantas et al. (2013a). In tropical savannas, the patchy distribution of resource availability interacts with fire events of variable frequencies to influence both the outcome of tree–grass competition and the fire escape probability of young woody individuals, exerting both recruitment and establishment bottlenecks (Kellman 1984; Bond 2008; Hoffmann et al. 2012; February et al. 2013). Thus, we hypothesized that by creating different opportunities of fire escape and affecting tree–grass competitive outcomes, variations in resource availability should explain the functional composition of fire-filtered savannas (Sankaran et al. 2005; Ojeda et al. 2010). Consequently, we predicted a patchy distribution for functional, phylogenetic and floristic composition that would match the spatial distribution of water and nutrient supplies. Because soil texture is an important predictor of water and nutrient availability, we expected this factor to account for an important fraction of community assembly in humid savannas (Haridasan 1992). Moreover, because these communities are fire-filtered (mean fire return intervals between 2 and 8 yr; Dantas et al. 2013a), we expected variations in fire frequency within the current ranges of tropical savannas to drive intraspecific trait shifts instead of changes in community membership (Higgins et al. 2007; Dantas et al. 2013b). We also expected the effects of fire to be resource-dependent, as high resource availability increase fire-escape probabilities in savannas (Bond 2008; Hoffmann et al. 2012). Finally, we expected resource-related predictors to explain the phylogenetic community structure of communities because of the diverse ancestral habitats from which Neotropical savanna lineages evolved (both dry and rain forests with variable nutrient availability to plants; Simon et al. 2009), and because resource-related traits are the most evolutionarily conserved traits among Neotropical savanna woody plant lineages (Cianciaruso et al. 2012).

Methods

Study site

We used the same data set as that used by Batalha et al. (2011), which was sampled in Emas National Park (ENP), a large Cerrado (i.e. a Neotropical grassland-savanna–forest system) reserve located on the Brazilian Central Plateau (17°49′–18°28′ S, 52°39′–53°10′ W). The climate of ENP is tropical and humid, and the area experiences a wet summer and a dry winter (Aw following Köppen 1931). Open Cerrado physiognomies prevail (grasslands and savannas of varying tree densities) in the landscape, covering 68.1% of the total area, whereas woodlands cover 25.1% of the reserve (Ramos-Neto & Pivello 2000). Small forest frag-

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ments also occur scattered across the landscape, but cover only ca. 1.2% of the park (Ramos-Neto & Pivello 2000; Dantas et al. 2013a); they were not considered in the present study because their distributions are strongly linked to very low fire activity (Dantas et al. 2013a). The soils are usually acidic, nutrient-poor oxisols, with textures varying from clayey to sandy (Batalha et al. 2011). The mean fire intervals within the park ranges from 2 to 8 yr, except for forest patches, in which high-intensity fires can be absent for several decades (Dantas et al. 2013a).

We arranged 100 5-m × 5-m plots along ENP's network of firebreaks and small roads (see Batalha et al. 2011 for a map and plot locations). The pair-wise distances between plots ranged from 19 m to 54 km (mean = 20.8 ± 10.7 km, ±SD; median = 20.1 km). The savanna landscapes of the park were classified into ten strata according to time since the last fire, and ten plots were placed haphazardly in the network of small roads within each stratum using a GIS. Plots were set 20 m from the firebreaks, and we defined that the plots should contain at least two woody species with stem perimeter at soil level ≥10 cm, to avoid locating the plot in sites where woody species were nearly absent. One plot with a fire age of 1 yr had to be discarded because it did not fulfil the inclusion criterion, and thus the final number of plots considered was 99. This sampling allowed the inclusion of communities that were highly variable in vegetation structure, species composition, topography, soil features, soil texture and mean fire interval (Batalha et al. 2011).

Field sampling

In the rainy season of 2009/2010, we tagged all woody individuals, identified them to species, measured the functional traits, and collected plant and soil samples, as well as topographic information of all plots. Specifically, we measured plant height, stem perimeter at ground level, bark thickness, leaf toughness and topographic features (altitude and slope) in the field, and collected wood, leaf and soil material for laboratory analysis. The depth to which a knife penetrated five haphazardly selected points on the main stem (50 cm from the ground) was measured using calipers to determine bark thickness. We measured leaf toughness using a gauge penetrometer equipped with a cone tip (Chatillon DFE 010; AMETEK, Berwyn, PA, US) on five haphazardly selected (fully expanded and hardened) leaves per individual. Leaves were penetrated on both sides of the midrib for a total of ten measurements per individual (five measurements at each side of the midrib). We collected five top soil subsamples (depth of 5 cm) in each plot, one at each corner of the plot and one at the centre; the subsamples were then combined into a single sample to estimate the soil chemical and physical properties. In the Cerrado most of the differences in soil features occur in the top soil layers, whereas deeper layers tend to be more homogeneous (Ruggiero et al. 2002). Top soil fertility is expected to be particularly important to the establishment of shallow-rooted seedlings. Moreover, fine root biomass occurs mostly in surface soils in the Cerrado (Castro & Kauffman 1998). The topographic features considered were altitude and slope, and were expected to be related to groundwater depth. In most Cerrados of central Brazil, the topography varies smoothly and is characterized by seasonally waterlogged areas downslope near rivers and by deep groundwater levels upslope (Rossatto et al. 2012).

Laboratory analyses

The samples and the information collected in the field were analysed in the laboratory to determine tree basal area, mean bark thickness, mean leaf toughness, wood density, leaf size, specific leaf area, and leaf nitrogen (N), phosphorus (P) and potassium (K) concentrations for each individual. We determined leaf size and specific leaf area based on five haphazardly collected expanded and hardened leaves per individual, and wood density based on a single cylindrical sample of wood per individual. We determined leaf size by scanning the leaves while fresh and calculating their areas (see Batalha et al. 2011). We obtained specific leaf area by dividing the area of the fresh leaf by its oven-dried weight (80°C for 72 h). We submitted leaf samples to the University of São Paulo for leaf N, P and K determination. The traits considered in this study are expected to reflect important resource and fire-escape strategies among Cerrado woody species (Dantas et al. 2013a,b).

The soil samples were analysed for pH, organic matter, total N concentration, available P, exchangeable K, exchangeable Ca, exchangeable magnesium (Mg), exchangeable aluminium (Al), sum of bases, cation exchange capacity, base saturation and Al saturation, which are considered important indicators of the fertility status of Cerrado soils (Goodland & Pollard 1973). Moreover, the percentages of sand, silt and clay (soil texture) were also determined. The soil texture was expected to relate to water retention, with soils containing more sand (larger particles) retaining less water than soils containing more clay (Salisbury & Ross 1992). Moreover, we also expected soil texture to relate to nutrient availability because clay particles, which have negatively charged surfaces, attract both water and cations (Salisbury & Ross 1992). Because regular differences in rainfall incidence among communities are not expected to occur, soil texture is expected to be an important indicator of the effective water availability for plants. For a detailed description of the soil methods used, see Dantas & Batalha (2011). We also determined time since the last fire and the mean interval between consecutive fires for each plot based on images from the Landsat 5 and 7 satellites (TM and ETM; 30-m resolution) for the years between 1984 and 2009, using the inverse of fire frequency, as described in Dantas et al. (2013a).

Functional, phylogenetic and compositional turnovers

Most studies on how environmental predictors affect species assembly have focused on comparisons of trait variability within communities with null communities generated from random selection of species from a regional species pool (e.g. Kraft et al. 2008). Whereas this approach may provide important insights into community assembly, its focus on within-community variation prevents the detection of patterns associated with community composition (see Swenson et al. 2012). Thus, two communities whose species present very dissimilar resource and fire-escape strategies may be considered identical from this perspective (Swenson et al. 2012). A β-community assembly approach focuses on how environmental gradients sort the species, generating patches of trait convergence (lower turnover than expected by chance) and trait divergence (higher turnover than expected by chance; see Graham & Fine 2008; Swenson et al. 2012 for details).

We calculated four among-community dissimilarity matrices using: (1) Sørensen's compositional turnover (CT; Sørensen 1948), (2) phylogenetic turnover (PT; Bryant et al. 2008), (3) species-based (FT) and (4) individual-based functional turnovers (iFT). To calculate phylogenetic turnover, we constructed a phylogenetic tree for all of the sampled species using the Phylomatic software (Webb & Donoghue 2005). We began by estimating the phylogenetic relatedness among all of the species sampled, based on the current Phylomatic tree (R20091110; APG 2009). We improved tree resolution using recent phylogenies for Fabaceae (Simon et al. 2009), Malpighiales (Korotkova et al. 2009; Bell et al. 2010) and Myrtaceae (Costa 2009), and dated the nodes based on Simon et al. (2009) and Bell et al. (2010). Undated nodes were placed evenly between dated nodes using the 'branch length adjustment' algorithm of Phylocom (Webb et al. 2008). We calculated PT as the one complement of the branch length shared by the taxa of two communities, using a phylogenetic tree and a community presence–absence matrix (Bryant et al. 2008). We calculated FT in the same way as PT, but using a functional dendrogram instead of a phylogenetic tree. To construct the functional dendrogram, we calculated mean trait values for each species and for all ten traits, and computed hierarchical clustering using the unweighted pair group method from the species-by-trait matrix. We used a similar procedure to calculate iFT, but considering the individual data rather than species means, subsequently controlling for the effects of FT as describe below (see Statistical analyses). Although many studies have investigated trait variation using isolated traits, a multivariate approach is preferred because the environmental effects on particular traits are not independent from those on other traits due to evolutionary trade-offs. This approach allowed us to capture how environmental predictors shape the assembly of communities through their effects on individual plants instead of particular traits, which provides a much more realistic view of the plant phenotype that interacts with the environment (Ricklefs & Travis 1980). Thus, this approach should provide a better assessment of the patterns of community assembly (Pausas & Verdú 2008).

Statistical analyses

We first evaluated whether each of the variables considered (soil-, landscape- and fire-related variables) were spatially structured using the Moran's I spatial autocorrelation index. Then, we explored whether communities were spatially structured in the landscape with respect to the four community turnover metrics (CT, PT, FT and iFT) using Mantel correlograms (1,000 randomizations). Simulation studies have demonstrated the power of this method for detecting spatial structures from multivariate data (Borcard & Legendre 2012). This approach allowed us to evaluate whether, for a given distance class, communities were more similar (spatial convergence) or more dissimilar (spatial divergence) than expected by chance, and to assess the spatial resolution of these spatial signals (Borcard & Legendre 2012). We then selected the best subset of landscape predictors explaining variations in CT, PT, FT and iFT using maximum rank correlation as implemented by the function 'bioenv' of the R package 'vegan' (Clarke & Ainsworth 1993; Bryant et al. 2008; R Foundation for Statistical Computing, Vienna, AT). This function searches for the combination of environmental predictors that maximize the Pearson correlation coefficient between the turnover matrix and the distance matrices generated from every possible combination of environmental predictors (standardized from 0 to 1). Landscape predictors were log-transformed prior to the analysis. The significance of the selected model was assessed using a Mantel test (1,000 randomizations). To determine which traits exerted the strongest influence on the FT and iFT matrices, we also used a maximum rank correlation approach using combinations of trait as predictors, instead of environmental features, as explanatory variables for the functional turnover matrices. For FT, we used a trait matrix in which plot mean values were calculated for each trait after assigning the overall species mean trait values to all individuals within the plot (interspecific trait variability only). For iFT, we used the residuals of the correlation of this matrix with a

Table 1. The framework used to interpret relationships between the turnover metrics and hypothetical environmental predictors (A–F).

Environmental Predictor	Community Turnover Index			Functional Changes Driven By	Traits Being Affected
	iFT	FT	PT		
A	x			Intraspecific variability only	Phenotypically plastic traits
B		x		Changes in species composition	Species-specific evolutionary labile traits
C			x	Changes in species composition	Evolutionary conserved unmeasured traits
D	x	x		Intraspecific variability and changes in species composition	Species-specific evolutionary labile and plastic traits
E		x	x	Changes in species composition	Species-specific evolutionary conserved traits
F	x		x	Intraspecific variability and changes in species composition	Phenotypically plastic and unmeasured evolutionary conserved traits

iFT, individual-based functional turnover; FT, species-based functional turnover; PT, phylogenetic turnover.

matrix of means calculated using the actual individual values. Moreover, in all analyses including iFT, we partitioned out the effects of an analogous matrix in which species average values were assigned to all individuals within the plots. This approach allowed disaggregation of the drivers of functional changes (turnover) resulting from changes in species composition (FT) from those exclusively related to intraspecific trait variability (iFT).

To understand the mechanisms by which these predictors shape community assembly, we followed the framework summarized in Table 1, which allowed us to infer the level of organization (species or individual) at which the predictors operate and whether they operate on evolutionarily conserved, evolutionarily labile or unmeasured evolutionarily conserved traits. For instance, the variables predicting the individual-based (iFT) but not the species-based (FT) functional turnover statistics operate mainly on intraspecific trait variability, i.e. they drive shifts away from the species average phenotype rather than species turnover. When an environmental predictor is related to both species-based functional (FT) and phylogenetic (PT) turnovers, it indicates that this predictor drives changes in species composition and interacts with measured evolutionarily conserved traits (see Table 1 for more cases). Finally, we constructed partial Mantel correlograms for CT, PT, FT and iFT, including the environmental predictors obtained during model selection (maximum rank correlation above) as covariates (partial). This allowed us to assess the spatial scale at which landscape predictors operate and whether any spatial structure remained in CT, PT, FT and iFT after considering the effects of the environmental predictors. For the analyses using Mantel correlograms, we only considered the first two-thirds of the distance classes because at longer distances, the significance becomes less reliable due to the low number of plots available for comparison (Fortin & Dale 2005). We conducted all of the analyses in R (v 2.15; R Foundation for Statistical Computing) using the 'betapart', 'ecodist', 'picante' and 'vegan' libraries.

Results

We sampled 531 individuals belonging to 55 species from 26 taxonomic families. The most species-rich families were Fabaceae and Myrtaceae (nine species each), followed by Erythroxylaceae and Malpighiaceae (three species each). The remaining 22 families were represented by either one or two species each. Most of the predictor variables considered were spatially structured across the landscape (see results for Moran's I test for spatial autocorrelation; Table S1 in App. S1). For all turnover metrics, the dissimilarity increased with geographic distance (Fig. 1, Table S2 in App. S1). Specifically, plots were more similar than expected by chance (spatial convergence) in floristic and phylogenetic compositions at shorter distances (<5 km) and were more dissimilar than expected by chance (spatial divergence) at larger distances (>15 km). For functional turnover (both FT and iFT), the spatial grain was larger, with plots more similar between 10 and 20 km and more dissimilar between 30 and 40 km (Fig. 1, Table S2 in App. S1).

All four turnover indicators were related to one or more environmental predictors (Table 2): CT was only related to clay content; PT was related to altitude, soil N and clay content; FT was related only to clay content; and iFT was related to pH, soil N, clay and fire recurrence. Thus, soil clay content was the most important factor explaining among-community turnover across the landscape (Table 2). The main traits accounting for the structure in FT were basal area, plant height, wood density, leaf toughness, leaf size, and leaf N and P concentrations ($r = 0.52$, $P = 0.001$), whereas the main traits expressed in iFT were basal area, wood density, and leaf N, P and K concentrations ($r = 0.28$, $P = 0.001$). Most of the previously detected spatial signals (nine out of 11) disappeared after the effects of landscape predictors were accounted for, further validating the significance of previous Mantel test results. These results showed at which spatial scale different landscape predictors drove major community turnovers (see Fig. 1).

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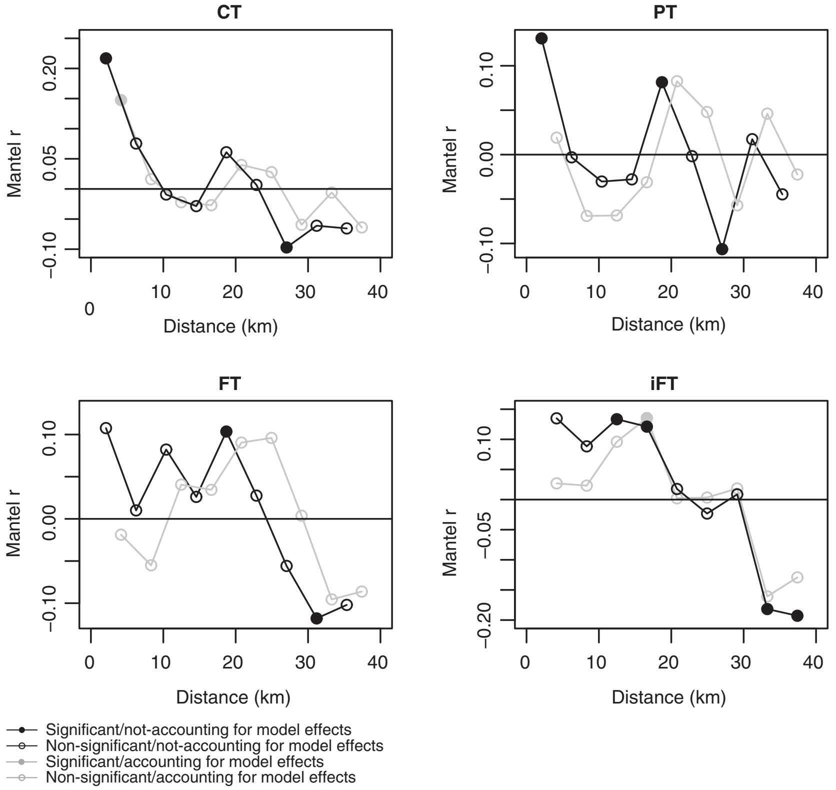

Fig. 1. The spatial structure (Mantel correlograms) of compositional (CT), phylogenetic (PT), species-based (FT) and individual-based (iFT) functional turnovers before (black) and after (grey) accounting for model effects (see Table 2), across a fire-filtered Neotropical savanna landscape. Positive and negative *r*-values indicate plots more similar and more dissimilar than expected by chance, respectively. Significant spatial structures are indicated by filled symbols. For further details, see Tables S2 and S3 in App. 1.

Discussion

Community turnover varies spatially following a non-random pattern in fire-filtered tropical savannas. All turnover indicators were spatially structured and exhibited phenotypic convergence or divergence depending on the spatial scale. Thus, we showed that local communities were spatially structured in the landscape and provided the proportion of the functional variability explained by species' niche. This outcome complements previous results of Batalha et al. (2011), reporting that species within communities present lower trait diversity than expected by random selection of species from the regional species pool. Phylogenetic and functional community metrics (PT, FT and iFT) presented different spatial structures, and were not related to the same subset of environmental predictors. Moreover, although the spatial structure of CT was somewhat similar to the structure of PT, the latter presented more and stronger signals and was associated with more predictors than CT, which was only related to clay content. This showed the small redundancy among the functional and phylogenetic estimators of community composition. None of them alone captured the entire functional spatial structure of the communities, providing evidence of an uncoupling among different aspects of community composition in fire-filtered savannas. Because most of the spatial signals disappeared after considering model effects (nine out of 11 initial signals; Fig. 1), our results indicated that the landscape predictors included in this study account for most of the spatially structured functional heterogeneity in

Table 2. Pearson coefficients (r_M) for the best subset of environmental predictors of functional, phylogenetic and compositional turnover, which were selected using maximum rank correlation. The *P*-values were obtained from a two-sided Mantel test (1,000 permutations) between the turnover matrix and the distance matrix from the variables in the selected models for each index (standardized from 0 to 1).

	Best Model	r_M	*P*
CT	Clay	0.15	0.001
PT	Altitude, N and Clay	0.20	0.001
FT	Clay	0.28	0.001
iFT	pH, N, Clay, Fire Recurrence	0.23	0.001

CT, turnover in species composition; PT, phylogenetic turnover; FT, species-based functional turnover (excluding intraspecific trait variability); iFT, individual-based functional turnover (excluding the effects of species composition).

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these savannas. Overall, our results supported the idea that even in landscapes where fire is very recurrent and exerts a strong filtering effect, spatially structured environmental predictors operate at different levels of organization, spatial scales and functional traits to shape community assembly.

Soil clay content was the most important predictor of community structures because it was related to all metrics of community dissimilarity, despite their different spatial structures. These results match those found for woody cover in African savannas at larger spatial scales (Sankaran et al. 2005), and thus they point towards a general role of soil texture in assembling fire-filtered savannas. We demonstrated that soil texture simultaneously shapes functional, phylogenetic and floristic aspects of savannas at different spatial scales, affecting both composition and intraspecific variation. Soil texture is a key factor influencing the soil water retention capacity. In fine-grained clay soils, water is lost to gravitational forces more slowly than in coarse-grained sandy soils (Salisbury & Ross 1992). Moreover, fine clay particles have negatively charged hydrophilic surfaces that attract both water and exchangeable cations, thus affecting not only the water content but also the actual nutrient status of soils (Salisbury & Ross 1992). Available moisture may be negatively related to fire frequency in some savannas (Lehmann et al. 2014); however, such a pattern was not observed in the studied site (Batalha et al. 2011), suggesting a rather direct effect of soil moisture in community composition instead of a fire-mediated effect. In fact, moisture tends to much less related to fire frequency in Neotropical than in other savannas (Lehmann et al. 2014). This idea is further supported by the fact that the main traits trading-off behind FT were size-related and resource-related (Borchert 1994; Bucci et al. 2004), instead of fire-related. Thus, our results suggest that community composition and structure are influenced by interactions between resource availability and the growth, nutrient and water uptake strategies of the fire-resistant woody flora, instead of indirect effects mediated by fire.

Phylogenetic turnovers were related to altitude, soil acidity and N content. In the savannas of central Brazil, the smooth variations in altitude are closely related to groundwater depth, with seasonally waterlogged areas downslope close to rivers and deep aquifers upslope (Batalha et al. 2011; Rossatto et al. 2012). Some woody species in the Cerrado have deep taproots that allow them to exploit water at great depths (Oliveira et al. 2005; Goldstein et al. 2008). Although we did not measure important traits related to the depth of water uptake, the association between phylogenetic turnover and altitude suggests that these traits might be evolutionarily conserved (as is specific root length in North American trees; Comas & Eisenstat 2009). However, further studies would be necessary to corroborate this postulate. Variations in pH are expected to affect biotic activity and macronutrient mobilization (Salisbury & Ross 1992), whereas N has been identified as an important factor influencing plant growth and hydraulic patterns in Neotropical savanna species (Bucci et al. 2006). Our results suggest that by interacting with phylogenetic conserved traits, pH and N also influence the spatial structure of community membership in fire-filtered landscapes (see Table 1).

After clay content, the most important landscape predictors of iFT were fire recurrence, N content and soil acidity. These results are consistent with Dantas et al. (2013b), who showed that the effects of fire in humid savannas occur mostly at the intraspecific level. In Neotropical savannas, plants are often fully burned or scorched for protracted periods, and staying in this ‘fire trap’ for a long time results in intraspecific shifts in both structural and physiological traits (Dantas et al. 2013b). The present results further suggest that intraspecific fire effects are resource-dependent, which is consistent with the escape hypothesis, according to which factors that enhance plant growth interact with factors that prevent it (disturbance events such as fire) to shape the vegetation structure in savannas (Kellman 1984; Higgins et al. 2000; Bond 2008; Hoffmann et al. 2012). Patches of resource availability may influence the fire interval necessary for plants escaping such effects and transitioning to a fire-independent adult state (Hoffmann et al. 2012).

In tropical savanna landscapes, the functional structure of communities is primarily driven by feedbacks between tree cover and fire that create mosaics of high- and low-fire frequency communities (savanna and forest, respectively; Hoffmann et al. 2012; Murphy & Bowman 2012; Dantas et al. 2013a). Here, we showed that within the fire-filtered savanna matrix, there are structural and functional mosaics that primarily depend on soil resource status, particularly on soil texture. This supports the idea that fire-filtered savanna communities are deterministically assembled by mosaics of resources availability, resulting in communities inhabited by species with different resource and growth strategies. Moreover, we present evidence that in these fire-filtered landscapes, the variation in fire frequency interacts with resource availability to shift attributes away from the average values that characterize species. Overall, our results suggest that resource availability is a fundamental factor in assembling fire-filtered savanna communities at landscape-to-regional scales.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Tests for spatial autocorrelation in the landscape predictors and Mantel correlogram results of Fig. 1.