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ECOLOGY OF FLOODPLAIN *CAMPOS DE MURUNDUS* SAVANNA IN SOUTHERN AMAZONIA

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Premise of research. This represents one of the first studies of the ecology, diversity, and structure of *campos de murundus* termite savannas in the vast seasonal wetlands of southern Amazonia. We aimed to improve understanding of this threatened system by assessing species richness, abundance, and co-occurrence among trees and herbs of *murundus* (earth mounds), investigating the environmental and biological mechanisms underlying these patterns, and discussing implications for biodiversity conservation.

Methodology. We identified every tree, shrub, subshrub, and herb on 373 *murundus* across 11 ha at Araguaia State Park, southern Amazonia. We constructed species abundance distributions of trees and herbs, assessed best-fit models, and tested for nonrandom patterns of species co-occurrence using checkerboard scores. Using detrended correspondence analysis (DCA), we assessed the affinities among tree species and their positions in *murundus*.

Pivotal results. A total of 166 species, 123 genera, and 49 families occupied the *murundus*. The species abundance distribution of trees followed a lognormal distribution, whereas that of herbs was best described by a Mandelbrot distribution. Observed *C*-score indices for trees and herbs were significantly larger than expected by chance, indicating nonrandom distributions and species segregation among *murundus*. DCA revealed a strong gradient in species occurrence within *murundus*, suggesting that internal structuring may be hydrologically based (e.g., variation in mound microrelief).

Conclusions. Environmental (e.g., flooding) and biological (e.g., competition between plants) factors are important for controlling the occurrence of tree and herb species on the *murundus*. The *murundus* function as critical bases for the maintenance of species diversity in this extensive floodplain, thereby deserving recognition among ecosystems with high conservation priorities.

Keywords: cattle grazing, Cerrado, flooding, termites, topography.

Online enhancement: appendix table.

Introduction

The Cerrado biome originally occupied ~21% of Brazilian territory, being the only Neotropical savanna classified as a biodiversity hotspot (Myers et al. 2000; Klink and Machado 2005). However, the Cerrado is highly threatened by agricultural expansion, with 40% of its area having been transformed by anthropogenic uses (Ferreira et al. 2012). It has a strongly seasonal climate with a pronounced dry season, and the predominant soils in the Cerrado (Oxisols) are acidic, nutrient-poor soils with low cation exchange capacity and high levels of aluminum (Lopes and Cox 1977; Coutinho 1990). Fire is an important feature of the Cerrado, and wildfires have occurred since at least ~6000 yr BP (Vernet et al. 1994). Native species are fire tolerant and sometimes fire dependent (Coutinho 1990; Miranda et al. 2002). Some studies (Moreira 2000; Durigan and Ratter 2006) have reported important changes in Cerrado physiognomies following fire suppression.

The Cerrado has one of the world's richest floras, surpassing 10,000 species of trees, shrubs, herbs, and lianas (Mendonça et al. 2008), of which almost half are endemic (Klink and Machado 2005). Comparison between trees and herbs is important because Rossatto et al. (2014) observed that both woody and herbaceous species are plastic regarding their water use strategy, which can determine niche partitioning across

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topographic gradients. However, the flora of the Cerrado is heterogeneous and distributed in mosaics, with more than half of its woody species restricted to phytogeographic groups (Ratter et al. 2003). The coexistence of so many species in the Cerrado appears to be due to the high variability of horizontal landscapes, comparable to the predominantly vertical variability that structures neighboring Amazonian forests (Colli et al. 2002).

The Cerrado has different savanna and forest vegetation types, which may be partly controlled as much by the occurrence (or absence) of flooding and waterlogging as by fire (Eiten 1975; Ratter et al. 2003; Durigan and Ratter 2006; Ribeiro and Walter 2008). Among the vegetation physiognomies typical of Cerrado are the *campos de murundus* (Furley 1986; Oliveira-Filho 1992*b*), also known as *parque de cerrado* (Ribeiro and Walter 2008) or termite savanna (Ratter et al. 1973). *Murundu* is a vernacular Brazilian name of African origin that refers to predominantly rounded mounds of earth 0.3–20 m in diameter and 0.2–2 m in height, usually spread over grassy fields (Oliveira-Filho 1992*a*). The physiognomy known as *campos de murundus* (literally "fields of earth mounds") usually occurs where the water table reaches the surface during the wet season. When the field is flooded, the *murundu* acts as an island that shelters Cerrado species and termite nests, usually intolerant of hydromorphic soils and flooding (Araújo Neto et al. 1986; Oliveira-Filho and Martins 1991; Oliveira-Filho 1992*a*, 1992*b*).

Despite their ecological importance, the *murundus* remain both poorly studied and controversial in origin (Midgley 2010). Some authors have proposed a termite-origin hypothesis (Eiten 1975; Mathews 1977; Prance and Schaller 1982), others suggest that *murundus* are residual geomorphological features formed by differential erosion and that the mounds were simply occupied by termites rather than formed by them (Araújo Neto et al. 1986; Furley 1986; Silva et al. 2010). Based on extensive observations, Oliveira-Filho and Furley (1990) proposed that both abiotic and biotic factors contribute to the formation of this vegetation type in Central Brazil. In coastal French Guiana, *murundu*-type mounds were reportedly formed by pre-Columbian raised-field farmers (Iriarte et al. 2012). Regardless of their origin, irregularities in the field provide vital variation in elevation and, hence, potentially more suitable microenvironments for Cerrado plant species to invade wet grasslands (Ponce and Cunha 1993).

As early as 1975, Eiten (1975) observed that a "type of pantanal is common in the northeast Mato Grosso . . . [that] is not marked as such on any known vegetation map" (p. 124). At the height of the rainy season, the swollen Rio Araguaia and Rio das Mortes together shallowly flood an area of more than 90,000 km^2 for 4–5 mo (Eiten 1985; Latrubesse et al. 1999). This represents the largest continuous flooded area of Brazil (Martini 2006) and is three times larger than the Serengeti-Mara ecosystem in Tanzania and Kenya (Sinclair et al. 2007). In spite of the worldwide awareness of the ecological significance of wetlands and floodplains, the vast floodplain of the Araguaia Pantanal, which covers an area larger than many European countries, remains little studied and, in particular, lacks any analysis of the patterns and controls of species distributions across its extensive *campos de murundus* vegetation. To date, only general descriptions and floristic surveys have been conducted on the vegetation of the region (Eiten 1985; Ratter 1987; Marimon and Lima 2001; Marimon et al. 2012).

Across the southern Amazon region and into the neighboring Cerrado, the frequency and severity of drought events has recently been increasing (Marengo et al. 2011), with largely unknown impacts on the regional vegetation. It is of particular importance to understand the diversity and structural patterns of plant communities that occur in areas subject to seasonal flooding, because these will be among the first to be affected by changing climate (Parmesan 2006). Climate change may have its most pronounced effect on wetlands through alterations in hydrological regimes, specifically the nature and variability of the hydroperiod and the number and severity of extreme events (Erwin 2009); a warming and drying climate change may also complicate future efforts to restore and manage wetlands. As observed by Franco et al. (2014) and Silva (2014), in the Cerrado there are many aspects affected by changes in climate and rising atmospheric CO_2 levels, including species performance, distribution and biodiversity, the competitive balance between trees and grasses, and soil proprieties. All of these changes can also affect the vegetation across the *campos de murundus*.

To understand the ecological significance and diversity of plant communities of wetlands and floodplains, one simple and rapid approach is to quantify species richness (Magurran 2004). This metric is the basis of many conservation studies (May 1988). Another important tool for the study of communities is the investigation of the patterns of distribution and species abundance and their comparison with predictions from mathematical models (Cielo-Filho et al. 2002). For example, the spatial and statistical patterning of the species diversity of communities may help explain whether they are shaped by biotic interactions or are randomly assembled (Weiher and Keddy 1999; Gotelli and McCabe 2002). Species typically co-occur rather less than expected by chance when evaluated for different taxa in different spatial scales (Gotelli and McCabe 2002), indicating that biotic interactions must play a role in community assembly. However, species dispersal can also shape patterns of species co-occurrence (Zalewski and Ulrich 2006), and if species differ in their ability to occupy new areas, they will also differ in their distribution patterns (Meyer and Kalko 2008). The understanding of how species are distributed has been recognized as a crucial step for conservation planning (Marques et al. 2011).

In summary, the largest wetland in Brazil remains essentially unstudied scientifically, with little notion of how species distribution and communities vary across its extent. Here we seek to describe the vegetation structure of a key feature of this globally important wetland, the *campos de murundus*, and elucidate procedures necessary for their conservation. The specific goals of this article are thus to (1) compare species richness and abundance patterns among trees and herbs that occur on *murundus* in a floodplain of central Brazil and (2) explore whether co-occurrence among tree and herb species on *murundus* is random or environmentally controlled. Considering that a lognormal abundance distribution is expected for communities with a large number of species influenced by many independent factors (May 1975; Oliveira and Batalha 2005), we tested the hypothesis that the abundance distribution of trees and herbs fits the lognormal model. In accordance with the predictions of Diamond (1975) and the meta-analysis of Gotelli and McCabe (2002), who concluded that in most natural plant communities there is less species co-occurrence than expected by chance, we tested the hypothesis that the species distributions on *murundus* reflect a nonrandom structure. Finally, we evaluated possible mechanisms underlying the observed distribution patterns of trees and shrubs in *murundus*.

Material and Methods

Study Area

We conducted this study at Araguaia State Park (ASP), which occupies 224,000 ha of northeastern Mato Grosso state, Central Brazil, between lat. 11°43′S, long. 50°43′W and lat. 12°38′S, long. 50°49′W (fig. 1). ASP includes several savanna and forest vegetation types typical of the Cerrado (Marimon and Lima 2001; Marimon et al. 2008, 2012), and more than 80% of its area is occupied by *campos de murundus* (fig. 2; Marimon et al. 2008). The climate is classified as Köppen's savanna subtype *Aw*, with rainy summer (November–April) and dry winter (May–October). The mean annual rainfall is 1600 mm, and the mean temperature is ~25°C (Marimon and Lima 2001). The altitude of the floodplain ranges from 190 m to 220 m, with Gleysols and Plinthosols predominating, both with impediments to drainage and seasonal flooding and originating from recent Holocene sediments (Barbosa et al. 1966; Marimon et al. 2012). The soils of *campos de murundus* have high acidity, low nutrient concentration (especially P, K, and Ca), and high organic matter (OM) levels; there are differences between the soils of *murundus* and the grassy field, especially in values of P, K, and OM, whose concentrations are higher in the *murundus*, and texture, which is sandier in grassland (Marimon et al. 2008). ASP was created in 2001, but some families still reside within the park and raise cattle in a very low-intensity system.

Field Sampling and Data Analysis

We demarcated 11 plots of 100 × 100 m, totaling 11 ha, in which we measured and inventoried every *murundu*. We identified and counted all angiosperms (trees, shrubs, subshrubs, and herbs), except grasses (Poaceae) and sedges (Cyperaceae). For the analyses, we separated trees and shrubs with diameters of 30 cm ($D_{30\,\mathrm{cm}}$) ≥ 3 cm (hereafter trees) from subshrubs and herbs with $D_{30\,\mathrm{cm}} < 3$ cm (hereafter herbs), all classified by species. We visited all the plots over a 24-mo period to make botanical collections, covering both the dry and rainy seasons. We identified sampled species by comparison with vouchers deposited in the Herbarium NX (Universidade do Estado de Mato Grosso, Campus de Nova Xavantina) and Herbarium UB (Universidade de Brasília) and with the aid of specialized literature and taxonomists. We grouped species into families following APG III (2009) and cataloged and deposited them in the Herbarium NX. The complete list of families and species is available at Marimon et al. (2012).

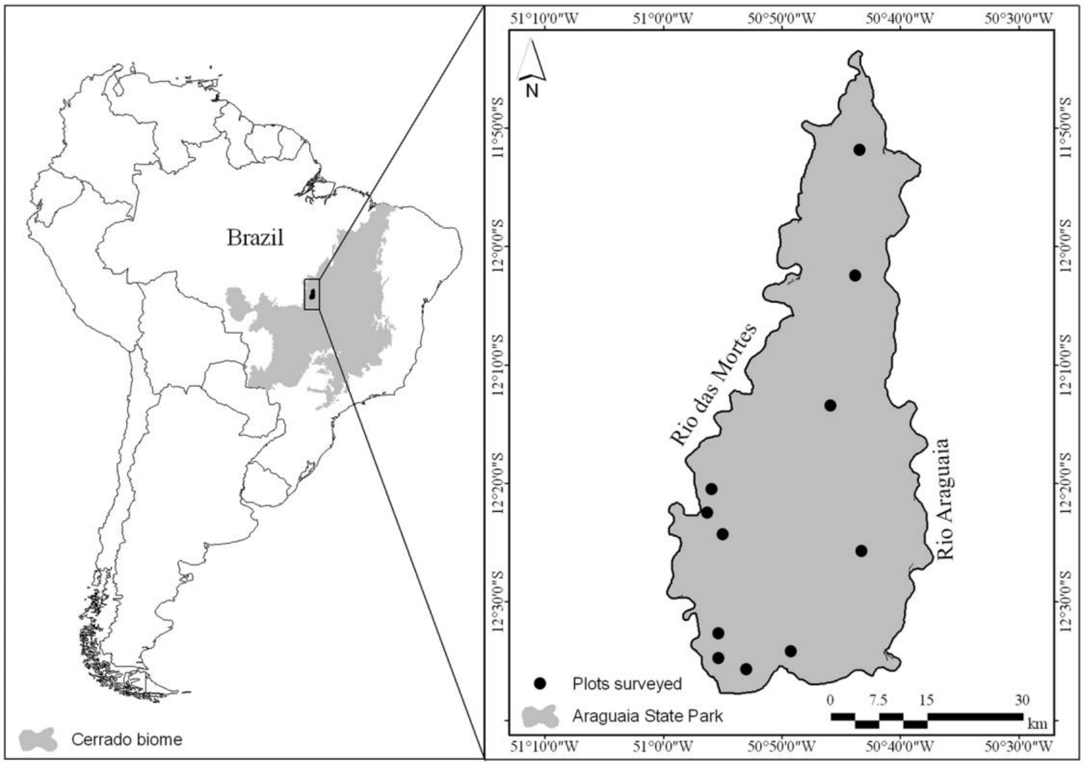

Fig. 1 Study area and plots sampled at Araguaia State Park in Mato Grosso, Brazil.

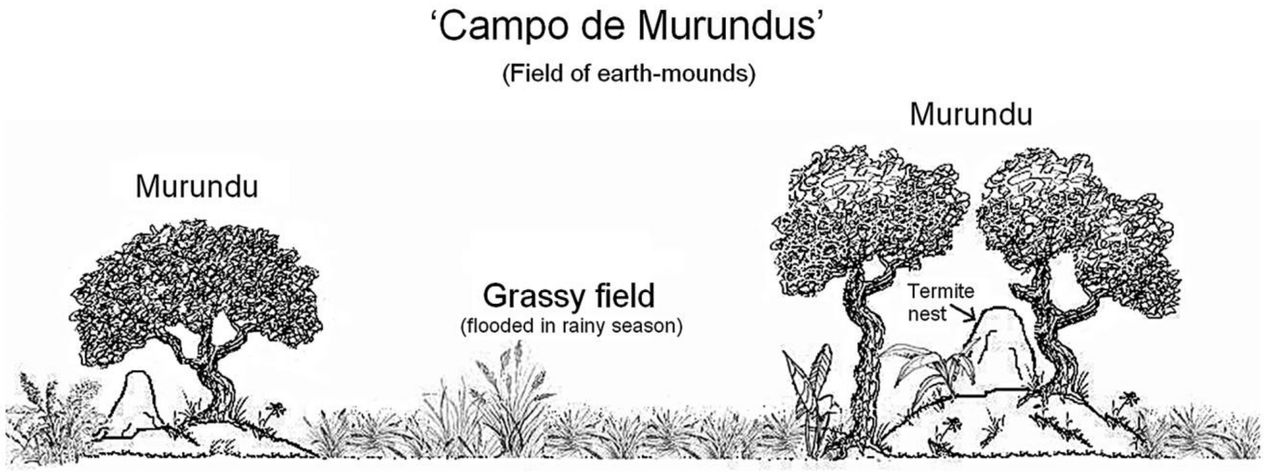

Fig. 2 Schematic profile of the floodplain *campos de murundus* savanna.

For each guild (trees and herbs), we used sample-based rarefaction curves (S_{obs}) to evaluate the adequacy of sampling by assessing whether the cumulative number of species has reached an asymptote and comparing the S_{obs} to species richness estimators (Colwell and Coddington 1994; Gotelli and Colwell 2001). We derived rarefaction curves from 1000 randomizations, without replacement, using EstimateS (Colwell 2009). We evaluated the performance of some estimators (ICE, Chao 2, jackknife 1, jackknife 2, bootstrap, and Michaelis-Menten) by regressing the estimated mean with observed values, evaluating estimator precision from the regression r^2 values, and measuring estimator bias as scaled mean error (SME; Walther and Moore 2005). We performed regression analyses with R (R Development Core Team 2011) and built a rarefaction curve for the estimator with the most accurate performance.

We also used a model of species accumulation (Soberón and Llorente 1993; Díaz-Francés and Soberón 2005) to evaluate the effectiveness and completeness of inventories and to estimate species richness for the two guilds. To determine the best-fitting model for the species richness data in each guild, we calculated parameters for the exponential, logarithmic, and Clench models, where the best estimator was the one with the lowest residual sum of squares (RSS). We used equations (exponential, logarithmic, and Clench) in Soberón and Llorente (1993).

We computed species relative abundance distributions (RAD) of trees and herbs using the RAD package (Dunstan and Foster 2012), based on a least squares statistic for finding the best solution, using the vegan package (Oksanen et al. 2012). The RAD program computes and fits many stochastic, deterministic, and semideterministic models and returns a number of additional statistics. We compared models using Akaike's information criterion (AIC; Burnham and Anderson 2002).

To test for nonrandom patterns of species co-occurrence among *murundus*, we used presence in each *murundu* to calculate the checkerboard score (*C*-score; Stone and Roberts 1990). The *C*-score is a quantitative index of co-occurrence that reveals patterns of high and low overlap of species within a guild; the minimum value is zero, when no species in the guild cooccur, while the more plots that contain two or more species, the larger the index (Gotelli et al. 1997). The arrangement formed by two species that do not co-occur in two areas is called a checkerboard unit, and the *C*-score is the mean number of checkerboard units per species pair in the community (Stone and Roberts 1990). The *C*-score is a measure of the number of mutually exclusive species in two plots. If this index is higher than expected by chance, the local community is significantly structured (nonrandomly) in relation to habitat use, with mutual exclusion being determined by ecological or historical interactions (Gotelli and Graves 1996; Nogueira et al. 2009). The *C*-score is superior to other indexes with respect to type I and type II error rates, and it measures the extent to which species are segregated across plots without requiring perfect checkerboard distributions (Gotelli 2000). We compared the calculated *C*-score to those of 5000 randomly assembled communities using EcoSim 7 (Gotelli and Entsminger 2009). We also calculated a standardized effect size (SES), which indicates the number of standard deviations that the observed index is above or below the mean of simulated matrices (Gotelli and McCabe 2002).

To illustrate and check for the affinities among tree species and their respective position on *murundus* (from edge to center), we performed two ordination analyses (nonmetric multidimensional scaling [NMS] and detrended correspondence analysis [DCA]; McCune and Grace 2002). Based on field observations, we defined five classes of position from edge (3 m $<$ position 1, 3 m $\geq$ position 2 $>$ 2.25 m, 2.25 m $\geq$ position 3 $>$ 1.5 m, 1.5 m $\geq$ position 4 $>$ 0.75 m, and 0.75 $\geq$ position 5 $>$ 0 m), which composed the descriptors of the ordination analyses (species were the objects). We excluded species that occurred on only one *murundu*. Despite recommendations (McCune and Grace 2002), we chose DCA over NMS because of the greater congruency of the former with our field visualization. This same procedure was performed by Santos et al. (2012), who suggested a more pragmatic choice of an ordination method "instead of following any line of methodological reasoning" (p. 142). In DCA, we downweighted "rare" species, that is, those restricted to few position classes, because the χ^2 distance used in DCA is sensitive to rarity. As a measure of the turnover along each DCA axis, we obtained the length

Table 1

Numbers of Individuals, Species, Genera, Families, *Murundus* Occupied by Species (No. *Murundus*), and Species per *Murundu* (Species/*Murundu*) Recorded on 373 *Murundus* at Araguaia State Park in Mato Grosso, Brazil

Parameters	Trees	Herbs
No. individuals	18,643	4413
No. species	94	78
No. genera	71	63
No. families	37	33
No. *murundus*	373	358
Species/*murundu*	1–21	1–18
Murundus occupied with one species	67	34
Species occupying only one *murundu*	17	8

of the gradient, in standard deviation (SD) units (Hill and Gauch 1980). Since the detrended and rescaling procedures preclude the decomposition of variation in DCA, we used the R^2 adjustment between the distances in original n-dimensional space and the χ^2 distances in the ordination as a proxy of the explanatory information represented by each axis. We conducted NMS and DCA in PC-ORD 6.0 (McCune and Mefford 2011) with transformed data (arcsine square root).

Results

Patterns in Floristic Composition, Species Richness, and Abundance Distributions

We sampled a total of 23,056 individuals. When data were pooled, the 373 *murundus* supported a total of 166 species, 123 genera, and 49 families (table A1, available online). There were slightly more species, genera, and families of trees than of herbs (table 1). The 10 most abundant species of trees accounted for 57% of all individuals, and the 10 most abundant species of herbs accounted for 75% of all herbs; the rarest species (1 individual each) accounted for 15% of total richness and for only 0.3% of total abundance for trees, and only 1% and 0.006% for herbs, respectively (table A1).

The most species-rich families were Fabaceae (13 tree and 13 herb species), Myrtaceae (7 trees and 2 herbs), Malpighiaceae (6 trees and 3 herbs), Rubiaceae (2 trees and 6 herbs), Apocynaceae (5 trees and 3 herbs), Bignoniaceae (6 trees and 1 herb), Asteraceae (1 tree and 6 herbs), and Euphorbiaceae (2 trees and 5 herbs). Among Lamiaceae, there were five species of herbs but no trees, while Vochysiaceae had five species of trees but no herbs. There were 17 monospecific tree families and 16 monospecific herb families in our sample. The most species-rich genera were *Byrsonima* (5 trees and 1 herb), *Eugenia* (3 trees and 2 herbs), *Myrcia* (4 trees), and *Hyptis* (3 herbs; table A1).

Among trees, the most abundant were *Erythroxylum suberosum*, *Curatella americana*, and *Qualea parviflora*; among herbs, the most abundant were *Melochia splendens*, *Anacardium humile*, and *Copaifera martii* (table A1). The most frequent tree species were *E. suberosum* (59% of *murundus* occupied) and *C. americana* (57%). Among herbs, *M. splendens* (51%) and *Bauhinia rufa* (42%) had the greatest abundance (table A1).

We found significant positive relationships between observed and estimated richness values for trees and herbs (table 2), and the best estimator (bootstrap) returned values similar to the observed richness. Although both curves were nonasymptotic, comparing species richness at a standardized level of abundance ($S_{\text{Mao Tau}}$) indicated that richness values for trees increased more rapidly than for herbs (fig. 3). Even if the curve is nonasymptotic, the recorded species comprised 94% (trees) and 92% (herbs) of estimated species richness (bootstrap), respectively. Based on the lower residual sum of square values, the cumulative species richness of trees and herbs against number of individuals was best described by a logarithmic regression (table 3).

The species abundance distributions of trees followed a lognormal distribution, while that of herbs was best described by a Mandelbrot distribution (table 4; fig. 4).

Species Co-occurrence

The co-occurrence analysis of species richness for trees revealed that the largest numbers of checkerboard units were between *Byrsonima cydoniifolia* and *Q. parviflora* (8881), *C. americana* and *Q. parviflora* (8437), *Tabebuia aurea* and *Q. parviflora* (7725), *T. aurea* and *E. suberosum* (7425), and *C. americana* and *E. suberosum* (7209). For herbs, this value was maximal for *Melochia splendens* and *Attalea geraensis* (12,096), *M. splendens* and *Annona aurantiaca* (9828), *M. splendens* and *Sabicea brasiliensis* (6850), *Melochia splendens* and *Smilax cognata* (6688), and *M. splendens* and *B. rufa* (6566). The observed C-score index for trees (269.16) was higher than expected by chance (mean of simulated C-score = 261.32, $P < 0.0001$), as it was for herbs (observed C-score of 328.53 vs. simulated C-score of 319.99, $P < 0.0001$). This indicates a strongly negative pattern of species co-occurrence, such that

Table 2

Precision (r^2) and Bias (Scaled Mean Error [SME]) of the Nonparametric Richness Estimators, Based on 1000 Randomizations of Original Data in Estimates 8.2.0

Species, estimator	Precision (r^2)	P	SME
Trees:			
ICE	.9957	<.001	.2001
Chao 2	.9988	<.001	.2227
Jackknife 1	.9995	<.001	.1972
Jackknife 2	.9992	<.001	.3088
Bootstrap	.9999	<.001	.0876
Michaelis-Menten	.7458	<.001	.0908
Herbs:			
ICE	.9913	<.001	.1411
Chao 2	.9947	<.001	.1341
Jackknife 1	.9977	<.001	.1633
Jackknife 2	.9943	<.001	.2251
Bootstrap	.9995	<.001	.0788
Michaelis-Menten	.8335	<.001	.1046

Note. ICE = incidence-based coverage estimator; jackknife 1 and 2 = first- and second-order jackknife estimators, respectively.

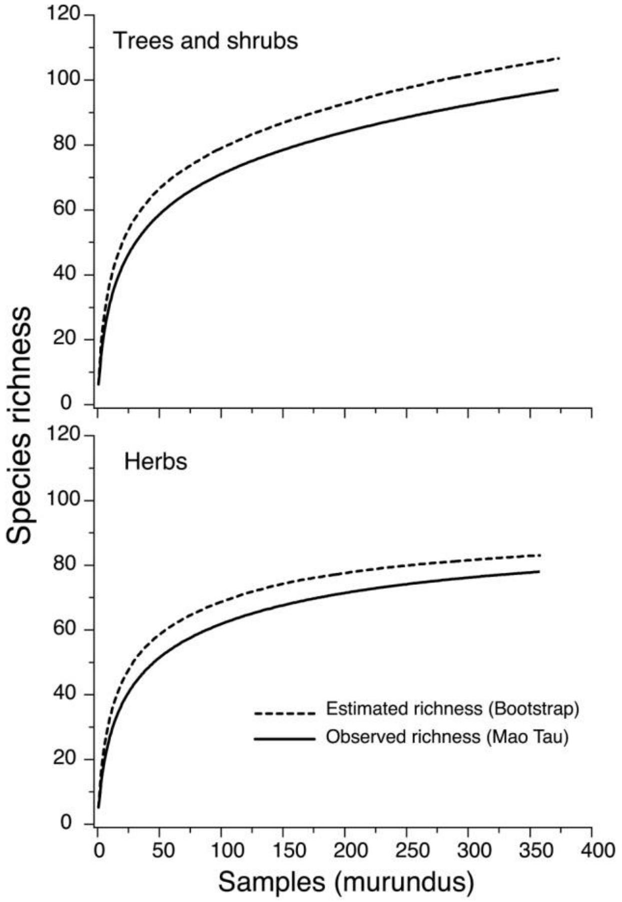

Fig. 3 Sample-based rarefaction curves ($S_{\text{Mao Tau}}$) for trees, shrubs, and herbs sampled in 373 *murundus* at Araguaia State Park in Mato Grosso, Brazil. Black lines = observed values; dashed lines = estimated values.

among both trees and herbs, plant species distributions in *murundus* are highly nonrandom and tend to segregate.

Mechanisms Underlying Spatial Distribution Patterns

Species assemblages varied substantially according to position relative to the border of *murundus* (fig. 5; length of gradient = 2.56 SD). Species occurring at and close to the border, for example, *C. americana*, *Vochysia rufa*, and *B. cydoniifolia*, are subject to more intense flooding effects and differ from those located at the summit, for example, *Magonia pubescens*, *C. martii*, and *Alchornea discolor*. The other species were distributed in a strong gradient, from the greatest to the least flooding influence (fig. 5). Even the axes 2 (2.44 SD) and 3 (1.96 SD) confirmed a moderate to high gradient, and the three axes explained 87.2% (axis 1 = 44%, axis 2 = 32.4%, and axis 3 = 10.8%) of variation in relation to ordination in the original *n*-dimensional space.

Discussion

Floristic Composition and Species Richness

Our study shows that the vegetation that occurs on earth mounds in the little-studied *campos de murundus* of ASP is rather typical of Cerrado savannas, a global hotspot of diversity and land-use change, suggesting that this neglected ecosystem deserves special attention for conservation. All of the flora we recorded are known to occur in Cerrado, according to a checklist of the vascular flora of the biome that covers 12,356 species (Mendonça et al. 2008). The tree species with the greatest number of individuals were also noted as being widely distributed in Cerrado by Ratter et al. (2003). In the study area, several species known to tolerate seasonal soil saturation, such as *Curatella americana* and *Byrsonima cydoniifolia* (Prance and Schaller 1982; Oliveira-Filho 1992*b*; Ponce and Cunha 1993; Mendonça et al. 2008), tend to predominate. In floristic surveys of savanna vegetation, the number of herb species typically exceeds that of woody species (Felfili et al. 1994; Marimon et al. 2012). This was not observed in our study, but as we evaluated only species occurring in *murundus* and excluded grasses and sedges, we likely overlooked some herbaceous species.

Another issue that indicates the importance of conserving the *campos de murundus* is that our sample was extremely diverse, with neither tree nor herb taxa reaching an asymptote in their species accumulation curves, despite an inventory spanning 11 ha and 373 *murundus*. This is reminiscent of large tropical forest plots sampled in Panama, Malaysia, and India, where species accumulation curves have still not reached an asymptote after sampling 50 ha (Condit et al. 1996). In this

Table 3

Estimated Parameters for Logarithmic, Exponential, and Clench Models for Trees and Herbs in Araguaia State Park, Mato Grosso, Brazil

Species, model	*a*	*t*	*P*	*b*	*t*	*P*	RSS
Trees:							
Logarithmic	7.5634	230.3	<.001	.0532	735.9	<.001	44
Exponential	1.7349	48.81	<.001	.0194	43.26	<.001	12,461
Clench	.7559	60.06	<.001	−.0019	−69.35	<.001	63,787
Herbs:							
Logarithmic	9.2291	65.76	<.001	.0706	232.56	<.001	268
Exponential	1.7539	53.34	<.001	.0239	48.43	<.001	5802
Clench	.6826	58.64	<.001	−.0021	−72.80	<.001	46,298

Note. *a* and *b* are fitted parameters, the effort is represented by *t*, and RSS is the residual sum of square.

Table 4

Relative Abundance Distribution Models and Parameter for Trees and Herbs in Araguaia State Park, Mato Grosso, Brazil

Species, RAD model	log μ	log σ	c	γ	β	AIC
Trees:						
Lognormal	2.56	1.60	…	…	…	545.1
Mandelbrot	…	…	20.3	−2.2	8.7	680.3
Zipf	.21	−1.06	…	…	…	1087.8
Herbs:						
Lognormal	4.00	1.79	…	…	…	2384.3
Mandelbrot	…	…	1098.4	−3.4	12.3	958.3
Zipf	.28	−1.18	…	…	…	5058.4

Note. c, γ, and β are fitted parameters; AIC = Akaike's information criterion.

case, species with limited ranges will always be rare, and this condition guarantees that a species accumulation curve will continue to increase at all scales (Condit et al. 1996).

The logarithmic model of species accumulation, observed in our study, may be reasonable in cases in which the sampled region is large, is heterogeneous, or the taxa is poorly known and includes many rare species; thus, the probability of finding a new species never reaches zero (Soberón and Llorente 1993). This information should help lend rigor to future inventories in *campos de murundus* of ASP, as it shows that simply reporting numbers and lists of species is likely to be misleading without careful documentation of sampling effort.

Species Abundance Distributions

Since the first geometric model, where species are considered energetically equivalent and this relationship is proportional to the abundance of species (Motomura 1932), ecologists have tried to describe the species abundance distribution (Preston 1948). For example, Fisher et al. (1943) developed the log series, which resembles a hyperbole, decreasing as the number of individuals of the species increases; Preston (1948) proposed the lognormal distribution, where few species are very common and most species are very rare. MacArthur (1957) suggested the broken-stick model, where species present continuous and nonoverlapping niches, and May (1975) observed that the lognormal model is a consequence of the central limit theorem (CLT). Species abundance distribution patterns may have important implications for biological conservation, as we point out below.

The lognormal abundance distribution model that fit the tree distribution patterns in the studied *campos de murundus* can derive from the interaction of a large number of multiplicative effects and, as stated by May (1975), be a consequence of the CLT. In this context, Oliveira and Batalha (2005) observed a lognormal abundance distribution of woody species in a Cerrado fragment and postulated that this occurred because it is rich in species and influenced by many environmental factors (water stress, fire, flooding, soil aluminum toxicity, etc.), features that also occur in the *campos de murundus* of Araguaia State Park (Marimon et al. 2008, 2012).

By contrast, the herbs of the *campos de murundus* fit best a Mandelbrot distribution model. According to Wilson (1991), the presence of a species depends on the initial physical conditions and the other species present—the costs. In this context, pioneer species require few prior conditions and have low cost, while late successional species have a high cost (e.g,. energy, time, and organization of the ecosystem) before they

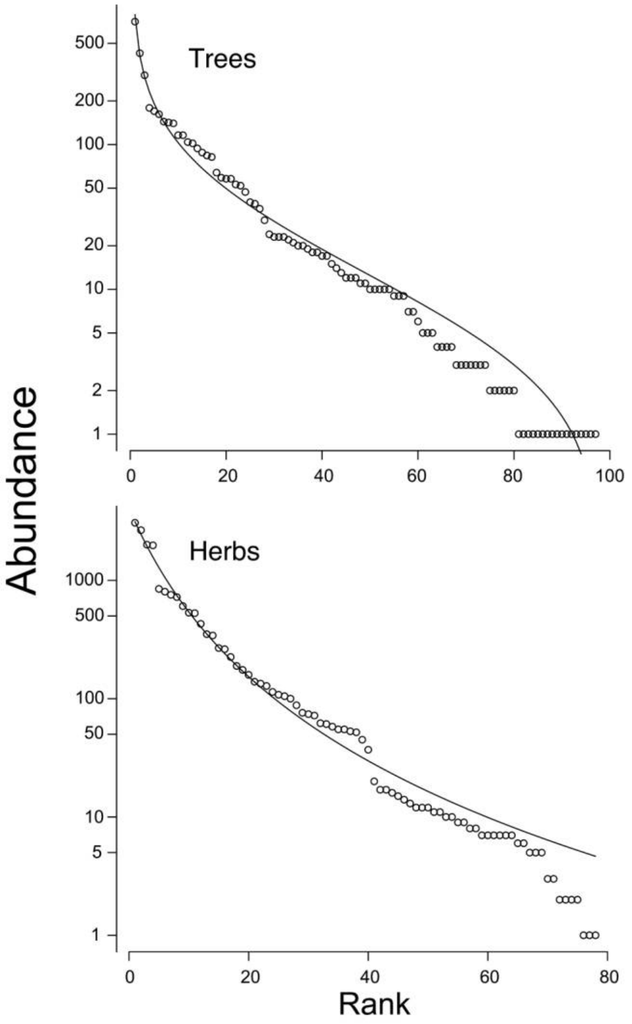

Fig. 4 Species relative abundance distributions as observed (circles) and modeled by lognormal (line) for trees (*A*) and by Mandelbrot for herbs (*B*).

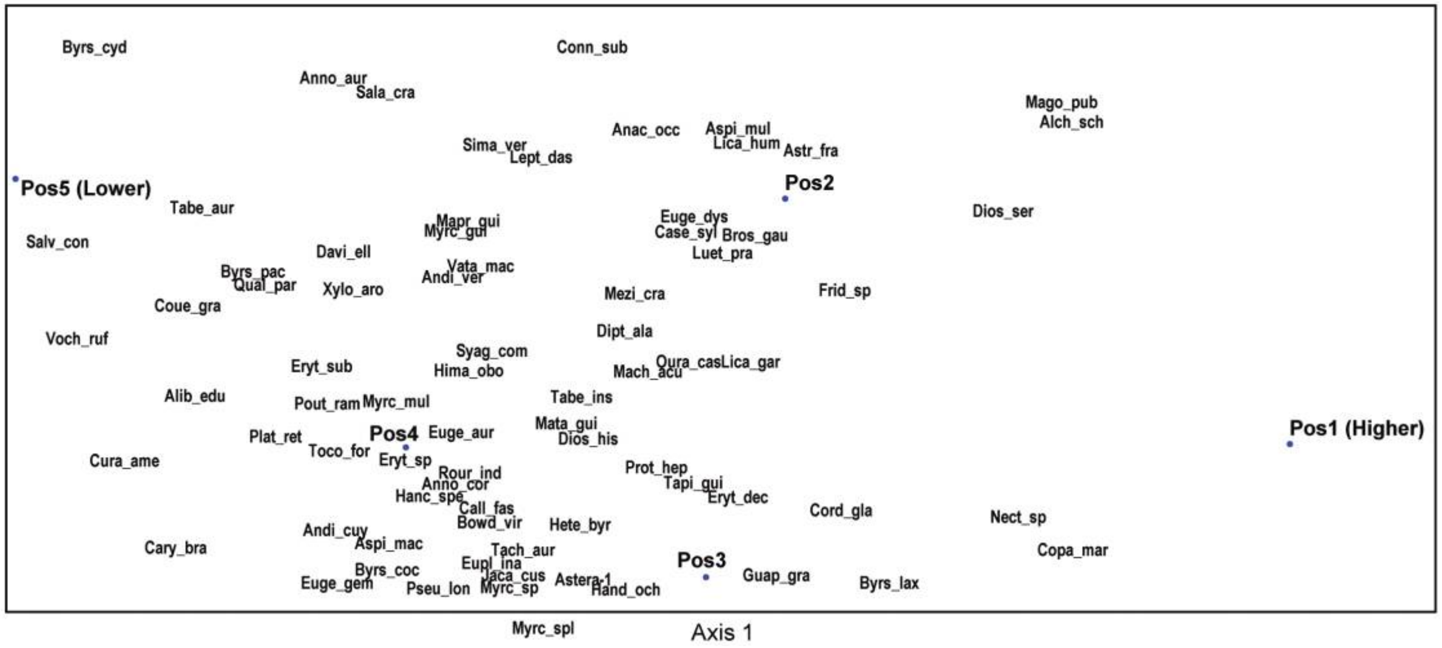

Fig. 5 Ordination by detrended correspondence analysis of trees and shrubs species in 373 *murundus*. For the full species names, see table A1 (available online). Axis 1 predominantly represents the gradient from the edge to the center of the *murundus* (from the most to the least flooding influence).

can invade. These time-dependent differences between species produce a Mandelbrot distribution (Frontier 1985). Thus, whereas species abundances that approximate the lognormal model may result from many factors acting simultaneously, a good fit to the Mandelbrot model is indicative of many factors acting sequentially (Wilson 1991). Both situations may be used as powerful tools for conservation planning, because knowing how the environment influences biological patterns can help to optimize allocation of financial resources for efficient biodiversity preservation (Margules and Pressey 2000; Peterson et al. 2003). However, modeling vegetation patterns in an uncertain world scenario requires that studies regarding the biotic responses to environmental factors be continuously updated, including forecasts related to climate change (Peterson et al. 2003).

Differences in the fitted abundance distribution models between trees and herbs of ASP may also indicate different levels of stability in their composition. Thus, in equilibrium communities, abundance distributions have the appearance of a symmetrical lognormal curve (Ugland and Gray 1982). This model can provide a workable and reliable diagnostic tool for evaluating stress on biological communities, with communities submitted to stress-induced changes typically having a nonlognormal model of species abundance and biodiversity (Kevan et al. 1997). Direct measurements of stress and competition as well as productivity are necessary to provide definitive answers about the role of environmental stressors acting in the *campos de murundus*. In our case, the differences between the abundance distribution patterns of trees and herbs may be related to fire, which in Cerrado usually affect tree species less severely than herbs. Among Cerrado woody plants, the predominant adaptations to fire, such as strong suberization of trunks and branches (cork formation), protect living tissues from dangerously high temperatures (Miranda et al. 1993; Hoffmann et al. 2012). Thus, fire may be preferentially altering the composition and species richness of herbs, perhaps especially by disturbing their phenological cycles (Pivello and Coutinho 1996). These different patterns of fitted abundance distribution models also suggest that different conservation strategies should be applied to maintain the biodiversity of herbs and trees.

Species Co-occurrence and Spatial Distribution Patterns

Our co-occurrence analysis indicated that species composition of trees and herbs on the earth mounds of the floodplain *campos de murundus* is highly structured by negative ecological interactions such as interspecific competition or competition for habitats in the past (Diamond 1975; Connor and Simberloff 1979; Gotelli et al. 1997; Meyer and Kalko 2008). Gotelli and McCabe (2002) observed that plant communities are structured because they compete for nutrients, light, and water. These environmental factors can also act on the vegetation of floodplain *murundus*, as our results indicate that tree and herb assemblages are shaped by species' differential colonization ability. Contrary to a nonflooded Cerrado area sampled in São Paulo, where Silva and Batalha (2009) did not find any effect of phylogenetic relatedness and functional similarity on tree species co-occurrence, the plants of our floodplain *murundus* are characterized by habitat specialists, with differences among earth mounds resulting in low species overlap and a structured pattern of local distribution. The implication of this result for conservation is clear: all habitats of *campos de murundus* are essential and should be preserved.

According to Gotelli and Entsminger (2009), even if the null hypothesis (i.e., that the species distributions reflect random colonization) is rejected—as in our case—we may not be able to conclude that it is competition that has led to less co-occurrence than expected by chance. We need to consider that the pattern may reflect habitat checkerboards, such that species are associated with different abiotic features of the sites, and that historical or phylogenetic effects have led to less coexistence. Here, considering also that Silva and Batalha (2009) observed that species phylogenetic relatedness did not constrain tree co-occurrence in Cerrado vegetation, it may be more likely that the pattern observed in trees and herbs in floodplain *murundus* is a consequence of abiotic features. Thus, one species' preference for wetter sites and another's for drier conditions would result in a perfect checkerboard. That habitat heterogeneity is a source for nonrandom spatial distributions of species is often observed (Bell 2001). A parallel example to our system may be the observation that grasses (Poaceae) grow preferentially on earth mounds in floodplains in French Guiana, whereas sedges (Cyperaceae) occupy the intervening periodically inundated spaces (Iriarte et al. 2012). However, the hypotheses for explaining nonrandom co-occurrence are not mutually exclusive (Gotelli and Entsminger 2009). For example, competitive interactions may lead to the evolution of distinct habitat preferences and thereby over time reduce niche overlap. Despite these difficulties, a first important step toward sorting out these ideas is to at least establish whether the patterns are random.

Thus, we suggest that tree and herb populations in floodplain *murundus* are highly structured both because limited resources (i.e., nutrients and space in the earth mound) would increase species competition (Tilman 1982) and because species presence is related to habitat specificity (Connor and Simberloff 1979), in this case, degree of tolerance to seasonal waterlogging, the severity of which will vary among mounds. Moreno et al. (2006) and Meyer and Kalko (2008) observed that in studies conducted over large areas, heterogeneous landscapes can prevent competitive interactions from inducing detectable deterministic structure. In our study, the floodplain *murundus* do cover a large area and substantial variability in environmental and seasonal conditions. Nevertheless, we detected significant nonrandom patterns, indicating that interspecific interactions may to some degree structure both woody and herbaceous assemblages (Meyer and Kalko 2008).

Other biota, aside from trees and herbs, probably play a key role in defining the structure and ecology of this vegetation. Across the seasonally humid tropics, termites can act as ecosystem engineers (Jouquet et al. 2011), both creating and maintaining habitats, a role that has been observed in southern Africa (Okavango Delta) as well as east Africa (Bloesch 2008; Mosepele et al. 2009; Joseph et al. 2014). The *murundus* at our study sites may be formed in a process involving at least five different species of termites and by mammals (anteaters and armadillos) that feed on termites in a process of construction, destruction, and reconstruction of nests. This culminates in the formation of larger earth mounds that are occupied by Cerrado plants that provide shelter and resources for termites and other animals (Mathews 1977; Oliveira-Filho and Furley 1990). This is in contrast to man-made raised beds and mounds reported for other regions of South America (e.g., Rostain 2010; Iriarte et al. 2012). The uniform pattern of spatial distribution of *murundus* observed by Mathews (1977), Oliveira-Filho (1992*a*), and Marimon et al. (2008) probably reflects the division of foraging territories of termite colonies that are hostile, as observed by Korb and Linsenmair (2001).

We observed species subcommunities on *murundus*, organized in associations corresponding to topographic belts (Oliveira-Filho 1992*b*) in a gradient of flooding level and indicated by their segregation along the DCA axes. This strong association appears to confirm that Cerrado species are not equally intolerant of waterlogging, with some adapted to a seasonally superficial water table (Oliveira-Filho et al. 1989). Thus, species such as *C. americana* growing at the border of *murundus* are more tolerant of seasonal soil saturation (Ratter et al. 1973; Prance and Schaller 1982; Oliveira-Filho 1992*b*) than those occurring mainly at the summit of the *murundus* (e.g., *Dipteryx alata*).

This study also highlights the importance of conserving taxa and landscape features that control large-scale vegetation structure and pattern. Throughout much of Central Brazil, especially in pastures, *murundus* and termite nests have been destroyed and removed. However, the removal of *murundus* or, as reported by Jones (1990), Pringle et al. (2010), and Bonachela et al. (2015), the removal of termite nests may reduce the productivity of the whole landscape or affect the robustness of dryland ecosystems to climatic changes. This has provoked local extinctions of several termite populations, while other termite species have become pests (Brandão and Fernandes de Souza 1998). Furthermore, some studies have shown that recovery initiatives of degraded areas may be more effective when trees act as nucleating agents in otherwise uniform landscapes (Tucker and Murphy 1997; Reis et al. 2003). For example, in a distinct type of coastal tropical moist forest (*restinga*) in Brazil, Scarano (2000) observed that “nurse plant” species are able to promote the growth of other species. In our case, *murundus* function as important bases for species nucleation in this extensive floodplain. From a management perspective, when cattle ranching occurs in areas of *campos de murundus*, it would therefore be beneficial to vegetation to maintain the largest possible number of *murundus* in the landscape.

We suggest that in the extensive *campos de murundus* of Central Brazil, environmental (principally flooding) and biological (competition between plants and termite activity) parameters are important controls of the occurrence of species of trees and herbs on *murundus*. However, their interactions with fire disturbance, soil nutrient status, and functional groups remain to be investigated. From an ecosystem conservation viewpoint, *murundus* persistence and functional connectivity plays a vital role in enhancing the biodiversity of floodplain savanna vegetation.

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