Biota Neotropica 23(1): e20221401, 2023
www.scielo.br/bn

biotaneotropica
ISSN 1676-0611 (online edition)

Article

The neglected tropical grasslands: first record of *campo com murundus* and its plant communities in the state of São Paulo, Brazil

Bruna Helena Campos*[1], Natashi Aparecida Lima Pilon*[1]*, Lucas Gonçalves*[1]*,***

***Natalia Macedo Ivanauskas*[2]* & Giselda Durigan*[1,2]**

[1]*Universidade Estadual de Campinas, Instituto de Biologia, P.O. Box 6109, 13083-865, Campinas, SP, Brasil.*
[2]*Instituto de Pesquisas Ambientais, São Paulo, SP, Brasil.*
**Corresponding author: brunahel92@gmail.com*

CAMPOS, B.H., PILON, N.A.L., GONÇALVES, L., IVANAUSKAS, N.M., DURIGAN, G. **The neglected tropical grasslands: first record of *campo com murundus* and its plant communities in the state of São Paulo, Brazil**. Biota Neotropica 23(1): e20221401. https://doi.org/10.1590/1676-0611-BN-2022-1401

Abstract: Tropical grasslands have been systematically neglected worldwide in maps, conservation policies, and ecological studies. After eradicating invasive pine trees from a Cerrado reserve in southeastern Brazil, an unprecedented grassy ecosystem arose in recent satellite images. In the field, we confirmed the first record of wet grasslands with termite mounds – locally named *campo com murundus* - beyond 21°S in the São Paulo state. Besides reporting this occurrence, we sampled the two plant communities forming this peculiar vegetation type (the mounds and the waterlogged matrix around them) to investigate if they are floristically and functionally distinct. We also explored how these two communities relate to those of the surrounding open vegetation types (savanna, dry and wet grassland). Woody plants were recorded on the mounds but not in the matrix, although the two communities share some ground layer species. Compared to the adjacent vegetation types, the mounds were floristically distinct and functionally more balanced in growth forms, dispersal syndrome, and tolerance to waterlogging. We hope this borderline record of *campo com murundus* can stimulate the search for other unnoticed remnants out of their known occurrence region, triggering efforts for their conservation and studies to improve comprehension of these iconic ecosystems.

Keywords: *Earth mounds; termite savanna; wet grassland; wetland; Cerrado; floristic similarity.*

Campos tropicais negligenciados: primeiro registro de campo com murundus e suas comunidades vegetais no estado de São Paulo, Brasil

Resumo: Os campos naturais tropicais têm sido sistematicamente negligenciados em todo o planeta, seja nos mapas, nas políticas de conservação ou em estudos ecológicos. Após controle da invasão por *Pinus* em unidade de conservação do Cerrado no sudeste do Brasil, um ecossistema graminoso sem registro regional surgiu nas imagens de satélite recentes. Observação em campo resultou no primeiro registro de campo com murundus em latitude superior a 21°S, no estado de São Paulo. Além de relatar essa ocorrência, amostramos as duas comunidades vegetais que formam esse tipo de vegetação peculiar (ocorrendo sobre os murundus e na matriz alagadiça ao redor deles) para investigar se são florística e funcionalmente distintas. Também exploramos como essas duas comunidades estão relacionadas com os tipos de vegetação aberta circundantes (savana, campo seco e campo úmido). Plantas lenhosas foram registradas nos murundus, mas não na matriz, embora as duas comunidades compartilhem algumas espécies do estrato rasteiro. Em comparação com os outros tipos de vegetação adjacentes, os murundus se mostraram floristicamente distintos e funcionalmente mais equilibrados em relação às formas de crescimento, síndrome de dispersão e tolerância ao encharcamento. Esperamos que esse registro limítrofe de campo com murundus possa estimular a busca por outros remanescentes despercebidos fora da região de ocorrência já conhecida, desencadeando esforços para sua conservação e estudos que possam melhorar a compreensão desses ecossistemas icônicos.

Palavras-chave: *Murundu; covoal; campo úmido; área úmida; Cerrado; similaridade florística.*

Introduction

The knowledge about the structure and functioning of tropical grasslands and savannas is scarce compared to forests (Parr et al. 2014). Besides that, these open ecosystems have been highly threatened by land conversion, biological invasions, suppression of natural disturbances (*e.g.* fire and herbivory), and afforestation (Veldman *et al*. 2015a, b, Durigan & Ratter 2016). Although grasslands and savannas are neglected when compared to forest vegetation (Silveira et al. 2021), they are considered of significant environmental, economic, and cultural importance once they are responsible for essential ecosystem services such as water provisioning, carbon storage, and shelter for pollinators and wildlife animals (Scholes & Archer 1997, Van Der Werf et al. 2010, Bardgett et al. 2021).

Among the wide variety of tropical grassland types worldwide (Dixon et al. 2014), vast portions of land are dominated by intriguing earth mounds, primarily associated with termites, thus named termite savannas. The dotted-like landscape of termite savannas is widely distributed, with records in North America (Mima-mounds) and Africa (*heuweltjies*), with similar appearance and ecological drivers (Hlongwane 2009, Midgley 2010). In Brazil, this vegetation type is represented by the so-called *campo com murundus*, one of the many phytophysiognomic types of the Cerrado (Furley 1986, Oliveira-Filho 1992, Overbeck et al. 2022), also known as *parque de cerrado* (Ribeiro & Walter 2008), *savana parque* (IBGE 2012), termite savanna (Ratter et al. 1973), or hyperseasonal termite savanna (Eiten 1983). Apparently, *campo com murundus* is ecologically equivalent to the thicket clumps found in the Kagera savanna landscape, which occupy a large portion of East Africa, as observed by Bloesch (2008).

Cerrado – the Brazilian savanna – is a vast region dominated by savannas forming a landscape mosaic with distinct vegetation types conditioned by complex relationships between environmental and disturbance factors. The *campo com murundus* are characterised by the occurrence of earth mounds covered by woody plants, sometimes inconspicuous, but often regularly spread over large tracts of the landscape, invariably associated with termites and seasonally waterlogged grasslands, being included among the Brazilian wetlands (Junk et al. 2014; Durigan et al. 2022). In Brazil, this vegetation type has been recorded so far in several states: Amazonas, Bahia, Distrito Federal, Goiás, Mato Grosso, Minas Gerais, Rondônia, Roraima (Eiten 1975, Araujo Neto et al. 1986, Barbosa et al. 2005, Cianciaruso et al. 2005, Antunes et al. 2012, Marimon et al. 2012, Paêlo 2013, Morais et al. 2014, Oliveira et al. 2014, Maricato et al. 2018, Souza et al. 2020).

The earth mounds function as well-drained islands, harbouring endemic Cerrado species which are not flood-tolerant (Araújo Neto et al. 1986, Oliveira-Filho & Martins 1991, Oliveira-Filho 1992). The plant species found on top of the *murundus* and those found in the matrix around are reported to belong to different guilds (Ribeiro & Walter 2008), whose floristic and structural differences and relationships with other vegetation types in the landscape have rarely been explored. Compared to other vegetation types, grasslands have been poorly studied in the Cerrado (Walter et al. 2015). Those in wetlands are practically unknown, likely due to the difficulty of performing samplings in flooded areas. Marimon et al. (2012, 2015) found waterlogging as the main factor influencing the occurrence of both woody and non-woody species on top of the *murundus.* Cianciaruso et al. (2005) investigated the influence of hyperseasonality on plant communities in the Cerrado and demonstrated waterlogging as a significant environmental filter, restricting plant diversity of hyperseasonal *cerrado*.

The origin of termite mounds is still controversial (Hlongwane 2009, Midgley 2010, Silva et al. 2010), and two main hypotheses have been considered. The first hypothesis states that termite nests raised the microtopography above the grassland vegetation (Mathews 1977, Eiten 1984, 1990, Prance & Schaller 1982, Oliveira-Filho 1992, Ponce & Cunha 1993, Hlongwane 2009). The relationship between thicket clumps on earth mounds and termites in seasonally waterlogged flat land is well known (Walter 1973, Pomeroy 1976, Barbosa et al. 2005). Despite that, there is a second hypothesis proposing that the microtopography of the termite savannas is a consequence of differential erosion, suggesting that the earth mounds are remnants from a previous relief that were just occupied by termites and not formed by them (Araujo Neto et al. 1986, Furley 1986, Silva et al. 2010). Either way, the ecological importance of the *campo com murundus* in promoting habitat diversification and faunal refugia is undeniable.

The occurrence of termite savannas in South America has been mostly recorded in tropical regions, in latitudes smaller than 15 degrees. We here report the existence of a patch of *campo com murundus* at 22°47'22" S, which is the first record of this vegetation type beyond 21° S, in the state of São Paulo, Brazil. In addition to reporting this first occurrence, we aimed to investigate to which extent the plant communities of the termite savanna are floristically and functionally related to the plant communities occupying the surrounding open vegetation types. We expected the well-drained mounds to resemble savanna plant communities in well-drained soils (savanna and dry grassland) and the surrounding waterlogged matrix resembling the composition of a wet grassland without mounds due to the species filtering imposed by soil water saturation (Ribeiro et al. 2021). Although we primarily aimed at floristically describing the *campo com murundus* and their relationships with other vegetation types to increase basic knowledge, we considered that applying this knowledge is crucial to support biodiversity conservation and the species selection for ecological restoration of these ecosystems.

Material and Methods

1. *Study area*

Santa Bárbara Ecological Station (SBES) hosts a mosaic of vegetation types, including forests, savannas, and grasslands (dry and wet) near the southern edge of the Cerrado region in the state of São Paulo. The patch of *campo com murundus* studied occupies an area of 3.5 ha within SBES, located by the central coordinates 22°47'22"S to 49°14'40"W (Figure 1). The regional climate is classified as Köppen Cwa-type, with rainy summers and dry winters lasting for five months (Alvares et al. 2013). The mean annual precipitation is 1332 mm, the average daily minimum temperature is 10.1 °C in July, and the average daily maximum reaches 28.7 °C in January. Despite being almost flat, the altitude is 634 m in the centre of the studied patch and 635 m in its border, creating a long-lasting waterlogged condition during the rainy season. Being flooded in the summer and overdried in the winter, the fluctuation of the groundwater level allowed the formation of plinthosols, often associated with *campos com murundus* (Curi et al. 2017). Monitoring the groundwater level close

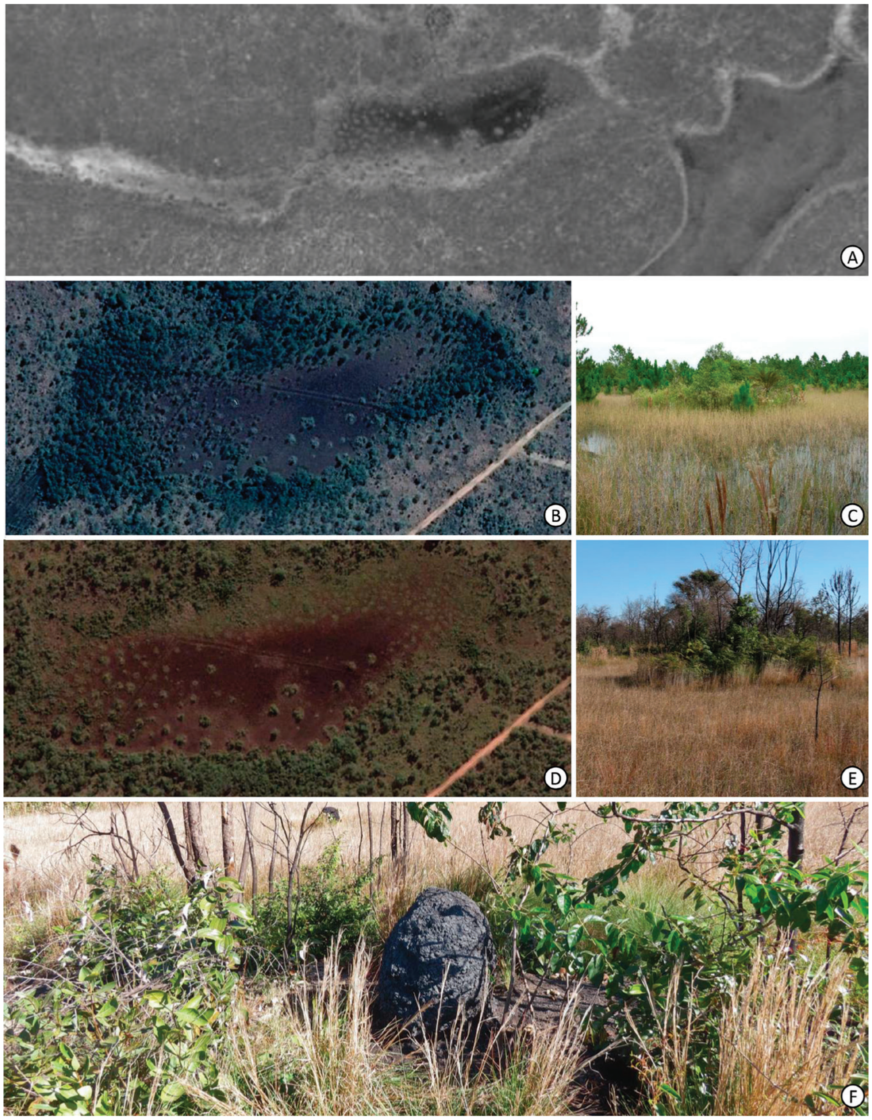

Figure 1. Views of the termite savanna studied at Santa Bárbara Ecological Station (SBES, Águas de Santa Bárbara, state of São Paulo, Brazil). A) The termite savanna patch in 1962, before pine invasion and without roads around (aerial photograph). B) In 2013, after the invasion by *Pinus elliottii* and before the invasion control (Google Earth image). C) A termite mound surrounded by *Pinus elliottii* (2010). D) In 2017, after clearcutting pines and burning, exposing the termite mounds (Google Earth image). E) A termite mound after pine eradication (2020). F) A termite nest surrounded by woody species on top of the mound (2020).

to the studied patch showed it ranging over the year from +10 cm to –210 cm (Manzione 2018), evidencing the hyperseasonal environment expected for *campo com murundus* (Eiten 1983).

The small patch of *campo com murundus* studied was already shown by aerial photographs taken in 1962 (Figure 1a), before the cattle farm became a governmental reserve (1964) and pine plantations replaced native grasslands around. For more than five decades, however, the peculiar feature of that vegetation was never noticed as a distinct ecosystem by the managers of SBES. *Pinus elliottii* Engelm slowly invaded this termite savanna, with some sparse founders arriving from the plantations around in 1994, massively colonising the whole patch and completely mischaracterising the landscape 19 years later (Brandes et al. 2020). The invasion process made it impossible to observe the earth mounds over a long period (Figure 1b-c). In 2013, there was an intervention to control the invasion by clearcutting the adult trees and applying a prescribed fire (2016) to burn pine needles and kill young invaders. The restoration intervention was successful, and the woody plants on top of the *murundus* and the grassy ground cover around them were quickly recovered, re-establishing the dotted landscape (Figure 1d-e). Not even a single pine individual was observed in the *campo com murundus* by the sampling occasion. When sampling, we observed at least one termite nest per mound (Figure 1f). The average height of the *murundus* (measured from the ground level of the wet grassland around to the top of the mound) was 93.8 cm (ranging from 73 cm to 113 cm).

2. *Experimental design and data collection*

To characterise the two plant communities of this termite savanna, in August 2020, we assessed 10 pairs of sampling units, each formed by a *murundu* (from now on referred to as mound) and a paired area of equivalent size in the wet grassland around the mound (from now on referred to as surrounding matrix), systematically positioned in the west from the termite mound. In the analyses, all plots on top of the mounds represented one plant community that is predominantly woody and associated with the well-drained condition. Those plots in the matrix represented another plant community, exclusively herbaceous, associated with seasonally waterlogged soils.

On top of each mound and in its paired area in the surrounding matrix, we sampled five circular 1-m² subplots in quincunx, totalling 100 1-m² subplots (50 on top of the mounds and 50 in the surrounding matrix). In each subplot we assessed plant richness and species composition. All individuals from the seedling stage were identified at the species level. When the identification was not possible in the field, we collected botanical material for later identification based on the literature (Durigan et al. 2004, 2018) or by comparison with material deposited in herbaria.

We investigated whether the plant community on top of the mounds and that in the surrounding matrix were floristically or functionally similar to the plant communities occupying three open vegetation types in the neighbourhood, according to the nomenclature proposed by Ribeiro & Walter (2008): savanna (*cerrado sentido restrito*), dry grassland (*campo limpo seco*), and wet grassland (*campo limpo úmido* without mounds, the groundwater close but never above the surface). Distance from the termite savanna was 1,400 m to the savanna, 400 m to the dry grassland, and 900 m to the wet grassland. We used the species composition sampled in randomly distributed 1-m² circular plots in patches of savanna (40 plots), dry grassland (30 plots), and wet grassland (10 plots). To explore the functional composition (relative abundance of functional guilds) of the five plant communities being compared, we categorised each species in functional guilds as follows: growth form (woody, forb, grass or sedge, following Durigan et al. 2004; 2018); dispersal syndrome (zoochory, anemochory or barochory, according to Peres 2016); and tolerance to waterlogging (yes or no, based upon Tannus & Assis 2004, and Pilon et al. 2017, 2018). In this case, tolerance to waterlogging refers to plants being able to survive and grow in habitats where the soil is fully water-saturated, at least in the rainy season, no matter if the groundwater rises above the surface. We expected differences related to waterlogging since it limits tree establishment (Ribeiro et al. 2021) and favours sedges (Pilon et al. 2017). We also explored the dispersal syndrome because the termite savannas resemble well-drained islands isolated by a waterlogged matrix. Therefore, their colonisation could depend on long-distance dispersal agents (volant animals or wind able to cross the waterlogged matrix) to bring diaspores of species able to survive in dry environments (the mounds).

3. *Data analysis*

To verify if plant species richness (number of species in 1 m²) differs between the community on the mounds and the other four communities sampled, we calculated the mean effect size using the log response ratio approach by mean values per plot of each community (Hedges et al. 1999). We constructed 95% confidence intervals for each community to determine whether the mean effect size differed from zero. Thus, we considered that the richness of each community differed from the mounds if 95% confidence intervals did not include zero (Zar 1999).

Differences in species composition (presence/absence) between sampled communities were explored using non-metric multidimensional scaling (NMDS), based upon a Bray-Curtis dissimilarity matrix, and calculating 95% confidence ellipses to check for overlapping of the confidence intervals. At first, we explored the floristic composition between the mounds and the matrix within the termite savanna. In the second step, besides the mound and the matrix, we included the plant communities representing each of the surrounding open vegetation types – dry grassland, savanna, and wet grassland – in the NMDS (all plant species and communities are presented in Table S1).

To verify a possible functional bias in the assembly of the studied communities, we adopted a guild proportionality approach, as recommended by Götzenberger et al. (2012). We used chi-square analysis ($\alpha = 0.05$). We applied Yates correction for $n < 5$ to investigate if the frequency of each functional guild within the group of species of each community differed from the expected. We considered as the expected values the proportion of each functional guild within the whole set of species sampled in all communities together (representative of the global species pool). If there was no difference between the observed value in a particular community and the regional pool, that attribute was not decisive for the composition of that community.

Results

A total of 64 plant species were recorded in the termite savanna, 59 on top of the mounds, and 22 in paired areas of the surrounding matrix. In the dry grassland, savanna, and wet grassland, 131, 121, and 27 species were recorded, respectively. Richness per square meter was distinct between communities (Figure 2). It was higher in dry grassland (19 species) and savanna (13 species) patches than on the mounds (7 species), and lower in the matrix (5 species) than on the mounds. The wet grassland without mounds did not differ from the mounds (both with 7 species). Of the 64 species sampled in the termite savanna, 17 species were common to

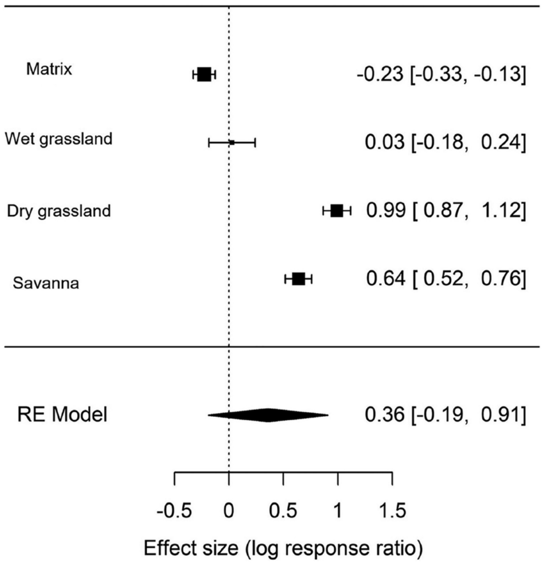

Figure 2. Effect size (distance from zero along the bar) of different plant communities in plant species richness related to that recorded on top of the mounds. Boxplots represent the mean effect size with 95% confidence interval. The dashed vertical line represents the mean richness recorded on top of the mounds. Values following each boxplot represent the mean and [confidence interval] in a logarithmic scale for each community. Richness of each community differs from the mounds if 95% confidence interval does not include zero.

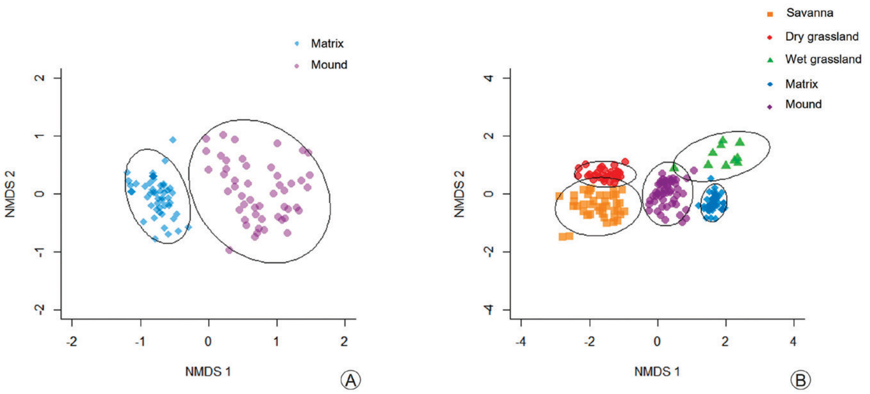

Figure 3. Nonmetric multidimensional scaling (NMDS) ordination across plots and community types based on Bray-Curtis distances. A) Floristic composition of mounds and matrix (wet grassland around the mounds). The best ordination solution was two-dimensional with final stress of 0,15. B) Floristic composition of different communities: on the mounds (purple), waterlogged matrix (blue), wet grassland without mounds (green), dry grassland (red), and savanna (orange). The best ordination solution was two-dimensional with final stress of 0,09. Ellipses represent 95% confidence intervals for the standard deviation.

mound and matrix, 42 species occurred only on top of the mounds, and 4 were exclusive of the matrix. When all communities were considered, the mounds shared 10 species with the wet, 15 with the dry grassland, and 19 with the savanna (Table S1).

Regarding the floristic composition, the NMDS ordination analysis showed a clear separation of the mound and the matrix (Figure 3a). When the species composition of the mounds and matrix of the termite savanna were compared to savanna, dry grassland, and wet grassland without termite mounds, neither the mound nor the matrix matched the other communities around (Figure 3b).

We found associations between functional guilds and plant communities, with differences related to tolerance to waterlogging (Figure 4a), growth form (Figure 4b), and dispersal syndrome (Figure 4c). Functional relationships between communities generally follow the taxonomic relationships, with the termite mounds occupying an intermediate position between dry (grassland and savanna) and waterlogged (wet grasslands and matrix) environments. The frequency of tolerant or intolerant species to waterlogging differed from the expected in all communities (Figure 4a, Table S2). The proportion of forbs was higher than expected only in the wet grassland (Figure 4b, Table S2). Dominant plants in the wet matrix around the mounds were grasses, followed by sedges, and both growth forms occurred in higher proportions than expected (Figure 4b). Compared to the regional pool, woody species were less frequent in the wet environments, not differing between dry grassland and the mounds. Regarding dispersal syndrome, the frequency of anemochory in all five communities did not differ from the regional pool (Figure 4c). Seed dispersal by gravity was more frequent than expected in both wet environments, while seed dispersal by animals was more frequent in the savanna.

Discussion

Termite savannas are peculiar ecosystems recorded in tropical regions worldwide, still not fully understood (Davies et al. 2014). Their microtopography creates a mosaic of two distinct habitats due to soil conditions (Hlongwane 2009), increasing patchiness, and heterogeneity of savanna vegetation (Moe et al. 2009). Our study indicated a bimodal floristic composition, resulting in distinct plant communities on the well-drained mounds and the waterlogged matrix, corroborating previous studies from Brazilian and African termite savannas showing distinct communities occupying the mounds and the surrounding matrix (Erpenbach et al. 2013, 2017, Van der Plas et al. 2013, Seymour et al. 2016, Muvengwi et al. 2017). This bimodality has important implications for the conservation and ecological restoration of these ecosystems. These permanently-dry ‘islands’ – the *murundus*, merged in seasonally flooded grasslands, are extremely important as refuges for terrestrial organisms and play relevant roles in maintaining biodiversity cycles, functions, and processes (Junk et al. 2014). By sampling only the woody plants on the mounds, which are mainly intolerant to waterlogging (Araujo Neto et al. 1986, Oliveira-Filho & Martins 1991), the biodiversity of the whole ecosystem will be underestimated for plants and likely also for animals and microorganisms (Leitner et al. 2020). If mounds and matrix have distinct biota, restoring the native vegetation of termite savannas will require separate sets of species to reintroduce in each microhabitat (Moe et al. 2009, Cuma Mushagalusa et al. 2018).

Besides creating well-drained islands, termites act as “ecosystem engineers” by promoting soil transformations (Dangerfield et al. 1998). Organic matter and mineral particles can be collected and deposited in the mounds by termites, increasing the content of organic C, clay, and nutrients (Sarcinelli et al. 2009). As in the hyperseasonal cerrado (Cianciaruso et al. 2005, Cianciaruso & Batalha 2009), seedlings of woody species are likely unable to survive the seasonal flooded conditions around the mounds. In our study areas, we expected the plant community on the well-drained mounds to resemble that of open Cerrado physiognomies on dry land. However, this was true only for woody plants, a subset of the surrounding dry areas. Since the herbaceous layer on the mounds is predominantly composed of a subset of species that occur in both the seasonally flooded matrix and the wet grasslands without mounds, the whole plant community on the mounds is floristically distinct from all other communities, being a mixture of the flora of humid and dry environments, as also observed by Sileshi et al. (2010) and Joseph et al. (2013). Despite the low species richness, the mounds presented a more balanced distribution among

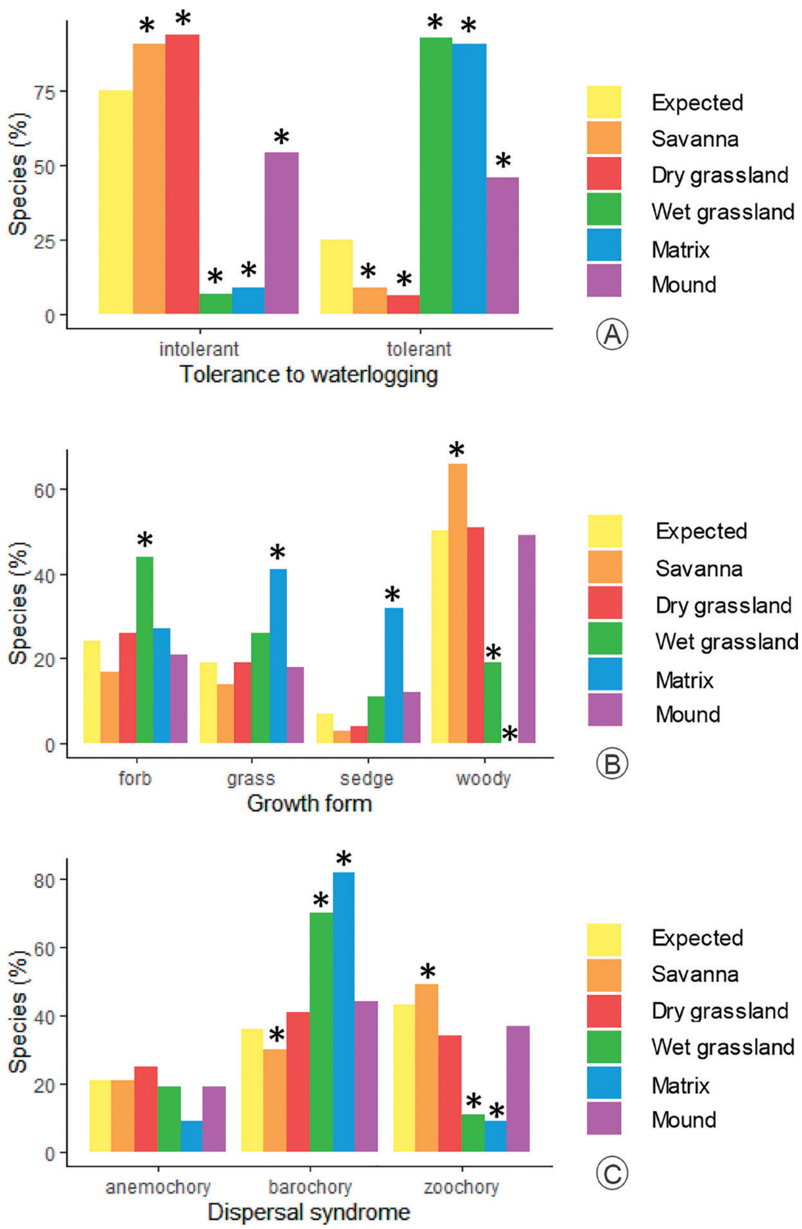

Figure 4. Proportion of functional guilds in the total species pool (Expected frequencies) and within each of the five community types (Observed frequencies): savanna, dry grassland, wet grassland without mounds, matrix (around the mounds), and on the mounds, at Santa Bárbara Ecological Station (SBES, Águas de Santa Bárbara, state of São Paulo, Brazil). A) Tolerance to waterlogging (tolerant or intolerant); B) Growth form (forb, grass, sedge, woody); C) Dispersal syndrome (anemochory, barochory, zoochory). Asterisks (*) mean the frequency of that guild in that community significantly differs from the expected frequency on the basis of the total species pool (α = 0.05).

functional guilds, either for tolerance to waterlogging, growth forms, or dispersal syndrome, in comparison with the matrix or even with the other communities compared. This functional redundancy may make the mound plant communities more resilient than the others analysed to abiotic or biotic changes, which cause species loss (Biggs et al. 2020). Even without exclusive flora, the plant community of the grassy and humid matrix around the mounds differed from all other communities, including the wet grassland, moreover due to the absence of species which are frequent in the other communities. In addition to the absence of woody plants, the forbs and part of the grasses and sedges recorded in the wet grasslands without mounds seem vulnerable to the long dry period that characterises the hyperseasonal environment around the mounds. On the other hand, some common grasses of dry land (*e.g., Andropogon leucostachyus* Kunth) take advantage of drought periods and colonise the matrix around the mounds.

The double environmental filtering (flooding and drought) likely resulted in the matrix around the mounds having the lowest richness (average number of species per square metre) among the five communities compared. We do not disregard that the legacy effects of about two decades of pine invasion can have contributed to the low richness in the matrix around the termite mounds. These plant communities can have suffered more intensively the negative effects of the needles layer and changes in the hydrological regime (Abreu & Durigan 2011). However, the mounds were also under pine invasion and presented higher richness. Batalha et al. (2005) also found lower richness in hyperseasonal savanna when compared to seasonal savanna, probably because most woody species are unable to survive this alternating double environmental filter, which enhances the anaerobic activity during the wet season, and then plants quickly dry after ceasing the waterlogging (Sarmiento & Monasterio 1975). Low species richness has been observed in *campos com murundus* in other regions, such as Roraima (Barbosa et al. 2005).

In addition to environmental filters, limitations on seed dispersal may explain the absence, on the mounds, of many species from the surrounding dry environments since barochoric species or even species whose seeds are windblown close to the ground (like many Poaceae) may have difficulties in transposing the seasonally flooded matrix. The influence of hyperseasonality on the efficiency of dispersal syndromes and the phenology of cerrado plants has been previously reported by Silva et al. (2009).

There are previous records of termite savannas throughout the tropical regions in Brazil, in the states of Goiás (Cianciaruso et al. 2005, Maricato et al. 2018), Mato Grosso (Eiten 1975, Marimon et al. 2012, Morais et al. 2014), Bahia (Oliveira et al. 2014, Souza et al. 2020), Distrito Federal (Araujo Neto et al. 1986), Roraima (Barbosa et al. 2005), and northern Minas Gerais (Antunes et al. 2012). However, none of these records was beyond 21°S, indicating a clear association with warm climates. The record of a remnant of *campo com murundus* in the state of São Paulo, at 22°47’22” S, considerably distant from the known records of this vegetation type in Brazil, demonstrates the climatic, hydrological, and edaphic conditions that allow their existence are broader than previously thought. Thus, it is possible that other patches still exist in the state of São Paulo or marginal regions elsewhere without having been noticed. It is also possible that they existed in the past, but the termite mounds were destroyed by the widespread perception of landowners that termites are an agricultural pest to be combated, besides blocking mechanisation.

Despite their great importance in maintaining biodiversity cycles, functions, and processes (Junk et al. 2014), the *campos com murundus*, like other vegetation types that cover Cerrado wetlands, have not been properly protected by law in Brazil (Durigan et al. 2022), being not even mentioned in Federal Law # 12651. The state of Goiás has a specific law declaring *campos com murundus* as Permanently Preservation Areas (State Law # 16153), but that is an isolated solution. Their protection depends, therefore, on a broad interpretation of the term ‘vereda’ as it is the federal law: “savanna vegetation occurring in hydromorphic soils, usually with sparse palms (*buritis*) over an herb-shrub layer” (Law # 12651, Art. 4°, XI). Alternatively, *campos com murundus* can be understood as wetlands and thus treated as restricted use areas (Law # 12651, Art. 10). Ideally, to effectively protect these iconic ecosystems, they should be one of the many different vegetation types internationally recognised as wetlands and subjected to a single legal treatment, as proposed by Junk et al. (2014).

The *campos com murundus* and most natural grasslands in Brazil appear on the maps of the remaining natural vegetation only when they occupy large extensions. That makes it even more difficult to preserve these ecosystems since they usually occupy small areas, such as the 3.5-ha patch of *campo com murundus* recorded in this study. Absent in the maps and neglected by conservation policies, these ecosystems have also been forgotten by scientists and thus misunderstood or unknown.

Supplementary Material

The following online material is available for this article:

Table S1 - List of species sampled in the study, with their growth form, dispersal syndrome, waterlogging tolerance, the vegetation type where each species was sampled, and the frequency of each species in the matrix and in the mound. Disp. Syn.: Dispersal syndrome; Wat. Tol.: water tolerance; Ane = anemochory; Bar = barochory; Zoo = zoochory. Veg. type = vegetation type; Dry grass. = Dry grassland; Wet grass. = Wet grassland. Freq. Matrix = frequency of the species in the matrix; Freq. mound = frequency of the species in the mound.

Table S2 - Chi-square analysis of the frequency of functional traits among six groups of species: Expected (all species recorded in the five vegetation types), Savanna, Dry grassland, Wet grassland, matrix and mound. The species attributes were tolerance to waterlogging (yes or no), growth form (forb, grass, sedge or woody) and dispersal syndrome (anemochory, barochory or zoochory). χ^2: chi-square values, df: degrees of freedom; *p*: p-value; ns: p-value non-significant ($\alpha = 0.05$).

Acknowledgments

This study was sponsored by São Paulo Research Foundation (FAPESP, grants #2020/01378-0, #2019/03463-8; # 20/09257-8) and, in part, by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (Capes) – Finance code 001. We thank also the National Council for Scientific and Technological Development (CNPq) for the scholarships (B.H.C., L.N.G., grants #140954/2019-8 and #155859/2019-6, respectively), and productivity grant (G.D., #309709/2020-2).

Associate Editor

Carlos Joly

Author Contributions

Bruna Helena Campos: contributed to data collection, data analysis and interpretation, and manuscript preparation.

Natashi Aparecida Lima Pilon: contributed to data collection, data analysis and interpretation, and manuscript preparation.

Lucas Gonçalves: contributed to manuscript preparation.

Natalia Macedo Ivanauskas: contributed to manuscript preparation.

Giselda Durigan: was responsible for conceptualizing and designing the study; contributed to data collection, data analysis and interpretation, and manuscript preparation.

Conflicts of Interest

The author(s) declare(s) that they have no conflict of interest related to the publication of this manuscript.

Ethics

This study did not involve human beings and/or clinical trials that should be approved by one Institutional Committee.

Data Availability

Data is available from the Biota Neotropica Dataverse: <https://doi.org/10.48331/scielodata.2MFNQW>.

References

ABREU, R.C.R. & DURIGAN, G. 2011. Changes in the plant community of a Brazilian grassland savannah after 22 years of invasion by *Pinus elliottii* engelm. Plant Ecol. Divers. 4(2-3):269–278.

ALVARES, C.A., STAPE, J.L., SENTELHAS, P.C., GONÇALVES, J.L.M. & SPAROVEK, G. 2013. Köppen's climate classification map for Brazil. Meteorol. Zeitschrift 22(6):711–728.

ANTUNES, P.D., HENRIQUE, L., FIGUEIREDO, A., SILVA, J.F., KONDO, M.K., AUGUSTO, J., AUXILIADORA, M. & FIGUEIREDO, P. 2012. Caracterização físico-química de micro-relevo de montículos "murundus" na região de Janaúba no norte de Minas Gerais. Geonomos 20(1):81–85.

ARAUJO NETO, M.D., FURLEY, P.A., HARIDASAN, M. & JOHNSON, C.E. 1986. The murundus of the cerrado region of Central Brazil. J. Trop. Ecol. 2(1):17–35.

BARBOSA, R.I., NASCIMENTO, S.P., AMORIM, P.A.F. & DA SILVA, R.F. 2005. Notas sobre a composição arbóreo-arbustiva de uma fisionomia das savanas de Roraima, Amazônia Brasileira. Acta Bot. Brasilica 19(2):323–329.

BARDGETT, R.D., BULLOCK, J.M., LAVOREL, S., MANNING, P., SCHAFFNER, U., OSTLE, N., CHOMEL, M., DURIGAN, G., FRY, E.L., JOHNSON, D., LAVALLEE, J.M., LE PROVOST, G., LUO, S., PNG, K., SANKARAN, M., HOU, X., ZHOU, H., MA, L., REN, W., LI, X., DING, Y., LI, Y., SHI, H. 2021. Combatting global grassland degradation. Nat. Rev. Earth Environ. 2(10):720–735.

BATALHA, M.A., CIANCIARUSO, M.V., SILVA, I.A. & DELITTI, W.B. 2005. Hyperseasonal cerrado, a new Brazilian vegetation form. Braz. J. Biol. 65(4):735–738.

BIGGS, C.R., YEAGER, L.A., BOLSER, D.G., BONSELL, C., DICHIERA, A.M., HOU, Z., KEYSER, S.R., KHURSIGARA, A.J., LU, K., MUTH, A.F., NEGRETE, B. & ERISMAN, B.E. 2020. Does functional redundancy affect ecological stability and resilience? A review and meta-analysis. Ecosphere 11(7):e03184.

BLOESCH, U. 2008. Thicket clumps: A characteristic feature of the Kagera savanna landscape, East Africa. J. Veg. Sci. 19(1):31–44.

BRANDES, A.F. das N., ALBUQUERQUE, R.P., DOMINGUES, G. de A.F., BARROS, C.F., DURIGAN, G. & ABREU, R.C.R. 2020. Dendroecology of *Pinus elliottii* Engelm. reveals waves of invasion in a neotropical savanna. Biol. Invasions 22(2):403–419.

CIANCIARUSO, M.V. & BATALHA, M.A. 2009. Short-term community dynamics in seasonal and hyperseasonal cerrados. Brazilian J. Biol. 69(2):231–240.

CIANCIARUSO, M.V., BATALHA, M.A. & SILVA, I.A. 2005. Seasonal variation of a hyperseasonal cerrado in Emas National Park, central Brazil. Flora Morphol. Distrib. Funct. Ecol. Plants 200(4):345–353.

CUMA MUSHAGALUSA, F., BAUMAN, D., MUJINYA BAZIRAKE, B., MLECI, Y., KALENGA, M., NGOY SHUTCHA, M. & MEERTS, P. 2018. Edaphic specialization in relation to termite mounds in Katanga (DR Congo): A reciprocal transplant experiment with congeneric tree species. J. Veg. Sci. 29(5):921–932.

CURI, N., KER, J.C., NOVAIS, R.F., VIDAL-TORRADO, P., SCHAEFER, C.E.G.R. 2017. Pedologia: solos dos biomas brasileiros. Sociedade Brasileira de Ciência do Solo, Viçosa.

DANGERFIELD, J.M., MCCARTHY, T.S. & ELLERY, W.N. 1998. The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. J. Trop. Ecol. 14(4):507–520.

DAVIES, A.B., LEVICK, S.R., ASNER, G.P., ROBERTSON, M.P., VAN RENSBURG, B.J. & PARR, C.L. 2014. Spatial variability and abiotic determinants of termite mounds throughout a savanna catchment. Ecography (Cop.). 37(9):852–862.

DIXON, A.P., FABER-LANGENDOEN, D., JOSSE, C., MORRISON, J. & LOUCKS, C.J. 2014. Distribution mapping of world grassland types. J. Biogeogr. 41(11):2003–2019.

DURIGAN, G., BAITELLO, J.B., FRANCO, G.A.D.C., SIQUEIRA, M.F. 2004. Plantas do Cerrado Paulista: imagens de uma paisagem ameaçada. Páginas & Letras, São Paulo.

DURIGAN, G. & RATTER, J.A. 2016. The need for a consistent fire policy for Cerrado conservation. J. Appl. Ecol. 53(1):11–15.

DURIGAN, G. PILON, N.A.L., ASSIS, B.G., SOUZA, F.M., BAITELLO, J.B. 2018. Plantas pequenas do cerrado: biodiversidade negligenciada. Governo do Estado de São Paulo, Secretaria do Meio Ambiente, Instituto Florestal, São Paulo.

DURIGAN, G., MUNHOZ, C.B., ZAKIA, M.J.B., OLIVEIRA, R.S., PILON, N.A.L., VALLE, R.S.T. do, WALTER, B.M.T., HONDA, E.A. & POTT, A. 2022. Cerrado wetlands: multiple ecosystems deserving legal protection as a unique and irreplaceable treasure. Perspect. Ecol. Conserv. 20(3):185–196.

EITEN, G. 1975. The Vegetation of the Serra do Roncador. Biotropica 7(2):112–135.

EITEN, G. 1983. Classificação da vegetação do Brasil. Conselho Nacional de Desenvolvimento Científico e Tecnológico- CNPq, Coordenação Editorial, Brasília.

EITEN, G. 1984. Vegetation of Brasilia. Phytocoenologia 12: 271–292.

EITEN, G. 1990. Vegetação do Cerrado. In: PINTO, M.N. Cerrado: caracterização, ocupação e perspectivas. SEMATEC, UnB, Brasília.

ERPENBACH, A., BERNHARDT-RÖMERMANN, M., WITTIG, R. & HAHN, K. 2017. The contribution of termite mounds to landscape-scale variation in vegetation in a West African national park. J. Veg. Sci. 28(1):105–116.

ERPENBACH, A., BERNHARDT-RÖMERMANN, M., WITTIG, R., THIOMBIANO, A. & HAHN, K. 2013. The influence of termite-induced heterogeneity on savanna vegetation along a climatic gradient in West Africa. J. Trop. Ecol. 29(1):11–23.

FURLEY, P.A. 1986. Classification and distribution of Murundus in the Cerrado of Central Brazil. J. Biogeogr. 13(3):265–268.

GÖTZENBERGER, L., DE BELLO, F., BRÅTHEN, K.A., DAVISON, J., DUBUIS, A., GUISAN, A., LEPŠ, J., LINDBORG, R., MOORA, M., PÄRTEL, M., PELLISSIER, L., POTTIER, J., VITTOZ, P., ZOBEL, K. & ZOBEL, M. 2012. Ecological assembly rules in plant communities-approaches, patterns and prospects. Biol. Rev. 87(1):111–127.

HEDGES, L. V., GUREVITCH, J. & CURTIS, P.S. 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80(4):1150–1156.

HLONGWANE, Z. 2009. The origin and geomorphological significance of earth mounds in the Mkhuze wetlands, KwaZulu-Natal. PHD thesis, University of KwaZulu-Natal, South Africa.

IBGE - Instituto Brasileiro de Geografia e Estatística. 2012. Manual Técnico da Vegetação Brasileira. 2nd. ed. Rio de Janeiro, Brazil.

JOSEPH, G.S., SEYMOUR, C.L., CUMMING, G.S., CUMMING, D.H.M. & MAHLANGU, Z. 2013. Termite mounds as islands: woody plant assemblages relative to termitarium size and soil properties. J. Veg. Sci. 24(4):702–711.

JUNK, W.J., PIEDADE, M.T.F., LOURIVAL, R., WITTMANN, F., KANDUS, P., LACERDA, L.D., BOZELLI, R.L., ESTEVES, F.A., NUNES DA CUNHA, C., MALTCHIK, L., SCHÖNGART, J., SCHAEFFER-NOVELLI, Y. & AGOSTINHO, A.A. 2014. Brazilian wetlands: their definition, delineation, and classification for research, sustainable management, and protection. Aquat. Conserv. Mar. Freshw. Ecosyst. 24(1):5–22.

LEITNER, M., DAVIES, A.B., ROBERTSON, M.P., PARR, C.L. & VAN RENSBURG, B.J. 2020. Termite mounds create heterogeneity in invertebrate communities across a savanna rainfall gradient. Biodivers. Conserv. 29(4):1427–1441.

MANZIONE, R.L. 2018. Water table depths trends identification from climatological anomalies ocurred between 2014 and 2016 in a Cerrado conservation area in the median Paranapanema Hydrographic region/SP - Brazil. Bol. Goiano Geogr. 38(1):68–85.

MARICATO, H.S., AUGUSTO, F., GUILHERME, G. & GOMES, D.C. 2018. Aspectos físicos e estrutura da vegetação lenhosa em três campos de murundus no sudoeste goiano. Rev. Bras. Biociencias 15(4):169–177.

MARIMON, B.S., MARIMON-JUNIOR, B.H., MEWS, H.A., JANCOSKI, H.S., FRANCZAK, D.D., LIMA, H.S., LENZA, E., NAZARETH, A. & CRISTINA, M. 2012. Florística dos campos de murundus do Pantanal do Araguaia, Mato Grosso, Brasil. Acta Bot. Brasilica 26(1):181–196.

MARIMON, B.S., COLLI, G.R., MARIMON-JUNIOR, B.H., MEWS, H.A., EISENLOHR, P. V., FELDPAUSCH, T.R. & PHILLIPS, O.L. 2015. Ecology of floodplain campos de murundus savanna in southern Amazonia. Int. J. Plant Sci. 176(7):670–681.

MATHEWS, A.G.A. 1977. Studies on termites from the Mato Grosso State, Brazil. Academia Brasileira de Ciências, Rio de Janeiro.

MIDGLEY, J.J. 2010. More mysterious mounds: Origins of the Brazilian campos de murundus. Plant Soil 336(1):1–2.

MOE, S.R., MOBÆK, R. & NARMO, A.K. 2009. Mound building termites contribute to savanna vegetation heterogeneity. Plant Ecol. 202(1):31–40.

MORAIS, R.F., MORAIS, F.F. & DE LIMA, J.F. 2014. Composição e estrutura da comunidade arbórea e arbustiva em murundus no Pantanal de Poconé, Mato Grosso. Rev. Arvore 38(3):443–451.

MUVENGWI, J., WITKOWSKI, E.T.F., DAVIES, A.B. & PARRINI, F. 2017. Termite mounds vary in their importance as sources of vegetation heterogeneity across savanna landscapes. J. Veg. Sci. 28(5):1008–1017.

OLIVEIRA-FILHO, A.T. 1992. Floodplain “Murundus” of Central Brazil: Evidence for the termite-origin hypothesis. J. Trop. Ecol. 8(1):1–19.

OLIVEIRA-FILHO, A.T. & MARTINS, F.R. 1991. A comparative study of five Cerrado areas in southern Mato Grosso, Brazil. Edinburgh J. Bot. 48(3):307–332.

OLIVEIRA, P.P., FUNCH, R.R. & DOS SANTOS, F. de A.R. 2014. First pollen survey of murundus in the Chapada Diamantina region of the state of Bahia, Brazil. Acta Bot. Brasilica 28(4):638–640.

OVERBECK, G.E., VÉLEZ-MARTIN, E., MENEZES, L.S., ANAND, M., BAEZA, S., CARLUCCI, M.B., DECHOUM, M.S., DURIGAN, G., FIDELIS, A., GUIDO, A., MORO, M.F., MUNHOZ, C.B.R., REGINATO, M., RODRIGUES, R.S., ROSENFIELD, M.F., SAMPAIO, A.B., SILVA, H.B., SILVEIRA, F.A.O., SOSINSKI, E.E., STAUDE, I.R., TEMPERTON, V.M., TURCHETTO, C., VELDMAN, J.W., VIANA, P.L., ZAPPI, D.C., MÜLLER, S.C. 2022. Placing Brazil’s grasslands and savannas on the map of science and conservation. Perspect. Plant Ecol. Evol. Syst. 56:125687.

PAÊLO, M.G. 2013. Estrutura e relações florísticas entre campos de murundus do Vale do Guaporé, Rondônia e Brasil Central. MSc thesis (Mestrado em Ecologia e Conservação da Biodiversidade) - Federal University of Mato Grosso, Brazil.

PARR, C.L., LEHMANN, C.E.R., BOND, W.J., HOFFMANN, W.A. & ANDERSEN, A.N. 2014. Tropical grassy biomes: Misunderstood, neglected, and under threat. Trends Ecol. Evol. 29(4):205–213.

PERES, M.K. 2016. Estratégias de dispersão de sementes no Bioma Cerrado: considerações ecológicas e filogenéticas. PhD thesis, University of Brasília, Brazil.

PILON, N.A.L., CAVA, M.G.B., NALON, M.A., ZIMBACK, L. & DURIGAN, G. 2017. Riqueza, relevância e estratégias para a conservação de fisionomias campestres do Cerrado no Horto Florestal de Botucatu, SP, Brasil. Rev. do Inst. Florest. 29(1):19–37.

PILON, N.A.L., BUISSON, E. & DURIGAN, G. 2018. Restoring Brazilian savanna ground layer vegetation by topsoil and hay transfer. Restor. Ecol. 26(1):73–81.

VAN DER PLAS, F., HOWISON, R., REINDERS, J., FOKKEMA, W. & OLFF, H. 2013. Functional traits of trees on and off termite mounds: Understanding the origin of biotically-driven heterogeneity in savannas. J. Veg. Sci. 24(2):227–238.

POMEROY, D.E. 1976. Studies on a population of large termite mounds in Uganda. Ecol. Entomol. 1:49–61.

PONCE, V.M. & CUNHA, C.N. 1993. Vegetated earthmounds in tropical tavannas of Central Brazil: a synthesis with special reference to the Pantanal do Mato Grosso. J. Biogeogr. 20(2):219.

PRANCE, G.T. & SCHALLER, G.B. 1982. Preliminary study of some vegetation types of the Pantanal, Mato Grosso, Brazil. Brittonia 34(2):228–251.

RATTER, J.A., RICHARDS, P.W., ARGENT, G., GIFFORD, G.R. 1973. Observations on the vegetation of the northeastern Mato Grosso: I. The woody vegetation types of the Xavantina-Cachimbo expedition area. Philos. Trans. R. Soc. 266: 449–492.

RIBEIRO, J.F. & WALTER, B.M.T. 2008. As principais fitofisionomias do bioma Cerrado. In: SANO, S.M., ALMEIDA, S.P., RIBEIRO, J.F. (ed.). Cerrado: ecologia e flora. p. 152–212.

RIBEIRO, J.W.F., PILON, N.A.L., ROSSATTO, D.R., DURIGAN, G. & KOLB, R.M. 2021. The distinct roles of water table depth and soil properties in controlling alternative woodland-grassland states in the Cerrado. Oecologia 195:641–653.

SARCINELLI, T.S., SCHAEFER, C.E.G.R., LYNCH, L. de S., ARATO, H.D., VIANA, J.H.M., FILHO, M.R. de A. & GONÇALVES, T.T. 2009. Chemical, physical and micromorphological properties of termite mounds and adjacent soils along a toposequence in Zona da Mata, Minas Gerais State, Brazil. Catena 76(2):107–113.

SARMIENTO, G. & MONASTERIO, M. 1975. A critical consideration of the environmental conditions associated with the occurrence of savanna ecosystems in tropical America (F.B. Golley, E. Media,eds), Tropical Ecological Systems, Springer, New York p. 223–250.

SCHOLES, R.J. & ARCHER, S.R. 1997. Tree-Grass Interactions in Savannas. Annu. Rev. Ecol. Syst. 28(1):517–544.

SEYMOUR, C.L., JOSEPH, G.S., MAKUMBE, M., CUMMING, G.S., MAHLANGU, Z. & CUMMING, D.H.M. 2016. Woody species composition in an African savanna: determined by centuries of termite activity but modulated by 50 years of ungulate herbivory. J. Veg. Sci. 27(4):824–833.

SILESHI, G.W., ARSHAD, M.A., KONATÉ, S. & NKUNIKA, P.O.Y. 2010. Termite-induced heterogeneity in African savanna vegetation: Mechanisms and patterns. J. Veg. Sci. 21(5):923–937.

SILVA, I.A., CIANCIARUSO, M.V. & BATALHA, M.A. 2009. Dispersal modes and fruiting periods in hyperseasonal and seasonal savannas, central Brazil. Rev. Bras. Bot. 32(1):155–163.

SILVA, L.C.R., VALE, G.D., HAIDAR, R.F. & DA STERNBERG, L.S.L. 2010. Deciphering earth mound origins in central Brazil. Plant Soil 336(1):3–14.

SILVEIRA, F.A.O., ORDÓÑEZ-PARRA, S.C.A., MOURA, L.C., SCHMIDT, I.B., ANDERSEN, A.N., BOND, W., BUISSON, E., DURIGAN, G., FIDELIS, A. & OLIVEIRA, R.S. 2021. Biome Awareness Disparity is BAD for tropical ecosystem conservation and restoration. J. Appl. Ecol. 59(8):1967–1975.

SOUZA, H.J., DELABIE, J.H.C. & SODRÉ, G.A. 2020. Termite participation in the soil-forming processes of “murundus” structures in the semi-arid region of Brazil. Rev. Bras. Cienc. do Solo 441–18.

TANNUS, J.L.S. & ASSIS, M.A. 2004. Composição de espécies vasculares de campo sujo e campo úmido em área de cerrado, Itirapina - SP, Brasil. Rev. Bras. Bot. 27(3):489–506.

VAN DER WERF, G.R., RANDERSON, J.T., GIGLIO, L., COLLATZ, G.J., MU, M., KASIBHATLA, P.S., MORTON, D.C., DEFRIES, R.S., JIN, Y. & VAN LEEUWEN, T.T. 2010. Global fire emissions and the contribution of deforestation, savanna, forest, agricultural, and peat fires (1997-2009). Atmos. Chem. Phys. 10(23):11707–11735.

VELDMAN, J.W., BUISSON, E., DURIGAN, G., FERNANDES, G.W., LE STRADIC, S., MAHY, G., NEGREIROS, D., OVERBECK, G.E., VELDMAN, R., ZALOUMIS, N.P., PUTZ, F.E., BOND, W.J. 2015a. Toward an old-growth concept for grasslands, savannas, and woodlands. Front. Ecol. Environ. 13:154–162.

VELDMAN, J.W., OVERBECK, G.E., NEGREIROS, D., MAHY, G., LE STRADIC, S., FERNANDES, G.W., DURIGAN, G., BUISSON, E., PUTZ, F.E., BOND, W.J. 2015b. Tyranny of trees in grassy biomes. Science 347: 484–485.

WALTER, H. 1973. Vegetation of the Earth in relation to climate and the eco-physiological conditions. English Universities Press, London, UK.

WALTER, B.M.T., DURIGAN, G., MUNHOZ, C.B.R., RIBEIRO, J.F. 2015. Fitofisionomias do Cerrado: classificação, métodos e amostragens fitossociológicas. In: Eisenlohr PV, Felfili JM, Melo MMRF, Andrade LA, Meira-Neto JAA (Org.). Fitossociologia no Brasil: métodos e estudos de casos. Editora UFV, Viçosa-MG, v. II.

ZAR, J.H. 1999. Biostatistical analysis. Prentice-Hall, Upper Saddle River, New Jersey.

Received: 20/07/2022
Accepted: 21/02/2023