Time to go home: The temporal threshold in the regeneration of the ant community in the Brazilian savanna

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ABSTRACT

The aim of this study was to evaluate the influence of succession stages of regeneration of the Brazilian savanna (Cerrado) on the richness, diversity, trophic guilds, and community composition of ants looking for taxonomic and functional changes in the community. The areas included an active pasture that had been created within the past six months, areas with several years of abandonment with different degrees of natural Brazilian savanna regeneration (from 2 to 15 years), and two large remnants of native forest that had been preserved for at least 40 years. Collections were carried out in 56 plots using sardine baits and an active search for a period of one hour in each plot. In addition to calculating the regeneration age, we evaluated successional stages by measuring vegetal characteristics in each plot. A total of 60 species was obtained, distributed in 28 genera and 8 sub-families, and these demonstrated a direct association with the regeneration age of the areas, as well as their richness and diversity of ants. Areas with initial regeneration showed a greater proportion of generalist species and, as plant succession increased, generalist species decreased. A temporal threshold of 5–6 years for re-generation age was observed, when the community structure tended to stabilize. We observed that the main-tenance of a minimum quantity of vegetation in areas destined for livestock can efficiently preserve ant diversity.

1. Introduction

The loss of natural habitats causes irreversible changes in biodiversity (Fahrig, 2003; Galetti et al., 2010; Hanski, 2011), affecting the population growth rates (Dobson et al., 2006), species interactions (Komonen et al., 2000), the diversity of the trophic chain (Forero-Medina and Vieira, 2007) and community structure. Thus, habitat loss is considered the greatest threat to biodiversity at all organizational levels (population, community and ecosystem) (Watling and Donnelly, 2006; Barnosky et al., 2011). The Brazilian savanna, known as the 'Cerrado', is one of the most threatened Brazilian biomes (Cardoso Da Silva and Bates, 2006), mainly due to agriculture and livestock activities (Machado et al., 2004). Occupying an area of about 2 million km^2, the Brazilian savanna (Cerrado) is concentrated in the central Brazilian plateau (Ratter et al., 1997), presenting herbaceous and arboreal vegetation components (Coutinho, 2006) with different combinations of distinct phytophysiognomies. (Goodland, 1971). Since the Brazilian savanna is a world hotspot (Myers et al., 2000) that is composed of a phytophysiognomic mosaic (Coutinho, 2006; Batalha, 2011), its conservation is essential. However, losses of ~2.2 million hectares per year threaten the preservation of the Brazilian savanna in the coming decades, making the acquisition of areas for regeneration urgent (Machado et al., 2004). The regeneration of an area is directly related to its structure, richness, species composition, and functioning, and relies on resource availability and the processes that occur after land abandonment or recovery (Neves et al., 2006; Hoffmann et al., 2012).

Matthes and Martins (2006) defined ecological succession as a natural process in which gradual changes occur in the community; these involve the installation of pioneer species that provide conditions for secondary species emergence. In turn, these secondary species provide the conditions for the so-called climax species or species that are the most tolerant and the best competitors (Gonçalves et al., 2005). Efforts towards achieving ecological restoration in Brazil have focused on forest-type environments, while open areas, such as the phytophysiognomies of the Brazilian savanna have received less attention in recent years (Overbeck et al., 2013).

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Biological indicators are species that are closely related to changes in environmental variables, and their presence indicates a positive or negative condition of an ecosystem (Allaby, 1992). Ants (Hymenoptera: Formicidae) have been used as bioindicators (Underwood and Fisher, 2006), due to their fast responses to environmental changes, broad distribution, high diversity and abundance in various niches in an ecosystem, which are easily sampled and identified (Hölldobler and Wilson, 1990; Majer et al., 2007; Silva and Brandão, 1999; Silvestre and Silva, 2001). Therefore, ants have been used to assess various environmental impacts, such as burning, deforestation, logging, mining, and urbanization (Underwood and Fisher, 2006; Philpott et al., 2010). Ecological parameters, such as species richness and frequency are important for community studies (Silveira-Neto et al., 1995), allowing their characterization and the comparison of fauna in different environments (Lutinski et al., 2005; Mariano et al., 2006). Studies have investigated the response of ant communities to forest regeneration after disturbances using bioindication (Vasconcelos, 1999; Neves et al., 2006; Ottonetti et al., 2006; Silva et al., 2007), where most studies that lack areas with different regeneration ages use regeneration stages categorically, usually addressing early, intermediate and advanced stages.

Studies carried out in the Caatinga (Neves et al., 2006; Bestelmeyer, 2006) presented a small temporal scale (regeneration up to 15 years). The same is true for studies carried out in Australian rainforests, American savannas and grasslands, all of which are considered age categories within the temporal range covered. Studies in Savanna-type environments are limited (Lawes et al., 2017) and absent for the Brazilian savanna, with age categories that do not establish a succession threshold for the ant community. In our study, we used the continuous age scale since it was possible to verify the age of the pastures and the period of preservation of these areas. Furthermore, studies that relate richness patterns to the variety of environmental factors that occur during the process of plant succession are needed (Estrada and Fernandez, 1999), since the ant community will respond better to the quality of the environment, making it possible to establish thresholds in the restoration process (Bestelmeyer, 2006; Hobbs et al., 2009; Suding and Hobbs, 2009). On the other hand, the presence of ants, which act as an ecosystem engineers, can promote small-to-large scale changes, such as soil water infiltration rates, erosion reduction and organic material increment (Cammeraat and Risch, 2008; Cerda and Jurgensen, 2008; Cerda et al., 2009), which enable positive interactions with the flora. The role of ants in establishing the plant community can take many forms, from facilitating mycorrhizal colonization with nitrogen and phosphorus enhancement (Dauber et al., 2008) to seed dispersal during the restoration process (Kovář et al., 2013).

Accordingly, we aimed to evaluate the influence of successional stages on the species richness, diversity and composition of the ant fauna and the relationship between the trophic guilds and successional stages of regeneration in an area of Brazilian savanna, focusing on taxonomic and functional changes in the community. We tested the hypotheses that (i) the richness and diversity of ants are higher in areas with advanced successional stages, (ii) vegetation characteristics related to successional stages influence the composition of ant functional groups, with generalist species being more frequent in areas of initial succession and specialists more frequent in areas at advanced successional stages and preserved areas, and (iii) the advance in ecological succession increases the similarity of ant fauna composition, in relation to the preserved native area, and may establish a threshold for community regeneration.

2. Materials and methods

2.1. Study area

The study area (Fig. 1) lies on a rural property used for livestock activities, with 2700 ha located in the municipality of Ribas do Rio Pardo, State of Mato Grosso do Sul (21°4′15.60″S and 53°41′ 11.64″O).

The property presents several successional stages of natural recovery of the Brazilian savanna vegetation, including pasture areas under intense use, moderate use, and following several years of abandonment. The areas used in our study were categorized as follows; areas of initial regeneration, including areas where the livestock activities were abandoned, ranging from two to eight years of natural regeneration; areas of intermediate regeneration where there have been no livestock for at least 12 and 15 years and that are being regenerated naturally; and preserved areas, composed of two large remnants of native vegetation, one of them being a Private Reserve of Natural Patrimony (RPPN) that has been preserved for at least 40 years (Table 1). Using these areas, we covered a large temporal scale of vegetation succession. Pasture ages were obtained from records maintained by the farmers. The maintenance of the pasture consists of plowing the land, removing the vegetation cover, and planting *Paspalum* sp. to form pastures for cattle. Unlike other studies, which have focused on successional stages of regeneration in different biomes, our study presents 13 areas, nine of which have different ages of natural vegetation regeneration.

2.2. Samples and identification

Collections were carried out during April and May 2016, between the end of the rainy season and the beginning of the dry season. The average temperature during the collection months was 24.6 °C and the accumulated rainfall during the period was 19.3 mm (Centro de Monitoramento do Tempo e do Clima de Mato Grosso do Sul – CEMTEC, http://www.cemtec.ms.gov.br). In the sampling areas, a grid with plots of 100×100 m was installed. In each area, we randomly chose a number of plots, corresponding to 30–40% of the total plots, to allow sampling of smaller and representative area (Table 1). In the central region of each plot, an area of 100 m^2 was sampled, where ants were collected using the attractive bait method and an active search, during one hour (Romero and Jaffe, 1989), during which ants were collected in labeled plastic bags. Sardine baits consisted of two cm^3 sardines in oil deposited on paper towel. In each plot, five sardine baits were placed evenly distributed on the soil and five on vegetation, when present (Bestelmeyer et al., 2000). The total sample effort carried out was 560 h/bait and 56 h/active search. The collection was authorized by the MMA and ICMBio (license n° 53,601, April 29th 2016).

The identification of ants at genus level was carried out using classification keys presented by Baccaro et al. (2015). Subsequently, insects were identified at the species level using taxonomic literature (Feitosa et al., 2008; Fisher and Smith, 2008; Cuezzo and Guerrero, 2012). Representatives of the collected species were deposited in the Zoological collection of Universidade Federal de Mato Grosso do Sul (deposit codes ZUFMSHYM0333, ZUFMSHYM00342-580, and ZUFMS-HYM00584-585).

In addition to the age of regeneration, we evaluated the successional stages of each plot using the vegetal characteristics: Number (n) and height (m) of tree and shrub cover (%) and litter depth (cm). The environmental data were accessed locally to ensure that local features, on a fine spatial scale, were responsible for any alterations in the ant community.

2.3. Data analyses

The relative frequency of species collected from the baits varied from 0 (absent) to 1 (present in all baits). Frequencies were determined separately for soil and vegetation. During the active search, the relative frequency of each species was determined as the ratio between the number of specimens of the species and the total number of specimens collected in the plot. In order to combine the active search and bait frequencies, the relative frequency of the two methods, with the variation between soil and vegetation was added, representing the importance of the occupation of the species in each plot.

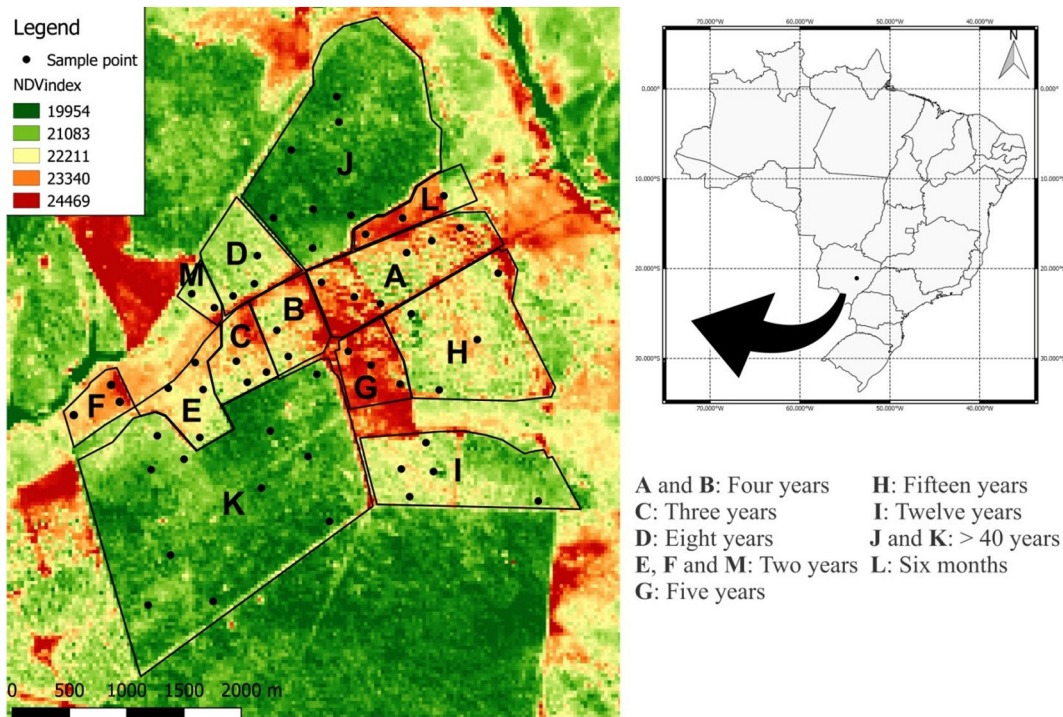Ecological parameters were determined for the plots; namely, the

Fig. 1. Study area located in the municipality of Ribas do Rio Pardo, MS. Vegetation cover of the sampled areas obtained through the normalized difference vegetation index (NDVIndex) during the collection period (green, larger vegetation cover; red, greater soil exposure) and the regeneration ages of each. Black dots correspond to the points of ant fauna sampling. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Characterization of the study area, according to the age of regeneration, size and number of plots.

Area	Age of regeneration	Size	Number of plots	Vegetative characterization of the area
A	4 years	90 ha	6	Undergrowth, grasses, sparse shrubs and low trees
B	4 years	38 ha	2	Undergrowth, grasses and sparse shrubs
C	3 years	31 ha	3	Pasture
D	8 years	47 ha	3	Undergrowth, grasses, sparse shrubs and low trees
E	2 years	36 ha	4	Pasture
F	2 years	22 ha	3	Pasture
G	5 years	35 ha	3	Undergrowth, grasses and sparse shrubs
H	15 years	126 ha	4	Undergrowth, shrubs, medium-sized trees and many lianas
I	12 years	101 ha	5	Undergrowth, shrubs, medium-sized trees and few lianas
J	> 40 years	223 ha	7	RPPN with preserved vegetation, few grasses, shrubs, lianas and tall trees
K	> 40 years	389 ha	11	Few grasses, shrubs, lianas and tall trees
L	6 years	28 ha	3	Pasture
M	2 years	11 ha	2	Pasture
Total		1.177 ha	56	

estimate of richness (JackKnife 2nd order), the Margalef diversity index and equitability, as well as the rarefaction curve of the total area. The data were transformed using a logarithmic scale to remove the effect of the differences between the regeneration ages (> 40 years), in comparison to the others, due to the absence of ages within this interval. The quadratic regression (after initial exploration of the data, this was found to be non-linear, as in other analyzes) between the average richness and total number of ant species, as a function of the area regeneration age, was carried out to verify the effect of the successional stage on ant species richness.

The species collected were classified according to the guild model proposed by Silvestre (2000) as: (I) Large predators; (II) Patrolling; (III) Small opportunists; (IV) Cryptic species of litters; (V) Leaf strippers; (VI) Fungus growers; (VII) Generalized mirmecines; (VIII) Aggressive dolichoderines; (IX) Nomadic species; (X) Minimum specialists; (XI) Cephalotines; and (XII) Nectar-feed dolichoderines. Categories I, II, III, VII, VIII and XI were considered generalist species and categories IV, V,

VI, IX, X and XII was designated as specialist species. Therefore, the set of plots in each area was used as the sampling unit to verify the proportion of generalists/specialists, using the total richness and average richness in each area, and determining the total number of species in each area and the percentage of generalist/specialist in the area. Finally, we performed a quadratic regression analysis between generalist species, as a function of the regeneration ages of the areas.

To evaluate the ant composition, each plot was used as a subsample of the area. Mantel Analysis (999 randomized matrix) was performed using the Euclidean distance between the distance (m) of the plots and the species composition to verify whether plot proximity influenced the community of ants. Principal Component Analysis (PCA) was performed between the environmental variables and the regeneration age of the areas. We performed Canonical Correspondence Analysis (CCA) to evaluate the environmental variables in the composition of ant genera, as well as non-parametric multidimensional scaling (NMDS-Bray-Curtis similarity measure) to visualize the community structure of

different restoration ages, using the Euclidean distance similarity index.

The spatial heterogeneity index (HI) was used to interpret environmental data as a function of age using the environmental variables of the sampled areas (Olivier et al., 2014). The data of the environmental variables were standardized and the frequency of each variable was calculated for each plot. Subsequently, the frequencies per plot were added, which gave weight to each of the variables in each plot, using the following equation:

$$HI = \Sigma_{f\ i}^{\eta}$$

where n = number of variables, f = frequency of the variable and i = variable.

Based on the HI values, we constructed a quadratic regression between HI and the age of regeneration to verify how the value adjusts to age. Furthermore, direct ordering between the environmental heterogeneity and the ant species collected was carried out in order to verify the relationship between the environmental variables and the species composition (Brower and Kyle, 1988). Statistical analyzes were performed using Past® and R® (version 1.1.463, vegan packages) using 0.05 alpha.

3. Results

We obtained a total of 60 species, distributed in 28 genera and 8 subfamilies (Table 2). Considering all the areas sampled, the subfamily that presented the highest richness was Myrmicinae, while the Dorylinae, Paraponerinae and Pseudomyrmecinae subfamilies were demonstrated the lowest richness.

The expected richness was 70 species, according to Jackknife 2nd order. With regard to the richness of the different areas, we found the lowest richness in areas with the youngest regeneration age. The greatest richness was observed in an area that had been preserved for 40 years. The areas with intermediate regeneration ages presented between 21 and 24 species. In relation to the expected richness (Jackknife 2nd order), we found that the area with 6 months of regeneration presented a richness that was 4-fold lower than areas with 4 years of regeneration (Table S1). The observed and expected richness were 60 and 70 species, respectively. With regard to the rarefaction curve (95% CI), the sampling performed in the areas was satisfactory, as demonstrated by growth and the fact that the curve had started to become asymptote, showing that most species (85%) were sampled (Fig. S1).

According to the Margalef index, the area with the highest regeneration age presented a diversity index of 2.24-fold higher than the area with 6 months of regeneration (Table S1). However, the area with 4 years of regeneration presented the highest index and richness (Table S1). The area with the highest regeneration age had the lowest equitability index, with few dominant species, while the areas that were aged 6 months and 4 years presented higher values with more dominant species (Table S1).

The species, *Pheidole* sp.2, presented the highest frequency (30%), followed by *Pheidole radoszkowskii*, *Camponotus* sp.1, *Crematogaster arata*, *Crematogaster nigropilosa* and *Linepithema* sp.2, which had frequencies that were higher than 5%. Twenty species presented a frequency of between 1.1 and 4.9% and most species (34) presented low frequencies (> 1%), being considered rare (Fig. S2), and representing a pattern with few frequent species and numerous rare species.

The species, *Cardiocondyla wroughtonii*, *Cyphomyrmex rimosus* and *Linepithema micans*, were present only in areas with 2 years of regeneration, whereas *Cephalotes persimilis*, *Odontomachus chelifer* and *Neoponera magnifica* were exclusive to areas with 3, 4, and > 40 years of regeneration, respectively. In contrast, *Camponotus* sp.1, *Ectatomma brunneum*, *Pheidole* sp.1 and *Pheidole* sp.2 were distributed in all areas with different ages of regeneration. Additionally, no species was exclusive to areas of up to 15 years of regeneration (Table 2).

We identified a direct relationship between the regeneration age

and the richness of ants ($R^2 = 0.64$, p < .05). From 6 years of regeneration, the species richness began to stabilize, approaching that of the intermediate and advanced regeneration areas (Fig. 2A). When analyzing the ant guilds by calculating the proportion of generalists/specialists, according to the age of regeneration of the areas, we noticed initial areas with a large proportion of generalists and a reduction of generalists that occurred concomitant with increasing of numbers of specialists ($R^2 = 0.35$, p < .05), in association with the increase in regeneration years (Fig. 2B). Dominant species found in areas with recent regeneration were generalists and initial areas of succession showed lower heterogeneity, which increased with vegetation regeneration ($R^2 = 0.72$, p < .05) (Fig. 2C).

Using the Mantel Analysis and considering the distance between the sampled plots, no significant influence of the proximity between the plots on the ant fauna composition was found (R = 0.13, p = .116), ensuring that the samples were spatially independent and indicating that the species occurrence reflects the niche occupied.

The PCA revealed that the number of shrubs (62.45%), trees (16.4%), as well as litter depth (14.16%) explained 93% of the data variance, especially related to areas with intermediate and advanced regeneration. One of the areas with four years of regeneration was also related to these variables. The height of shrubs (0.97%) presented a greater association with the areas undergoing initial regeneration (six months to eight years) (Fig. S3). From the CCA, we observed that the height (50.02%) and the number of trees (25.29%) significantly corresponded to about 75% of the data (p = .009 and p = .04, respectively). Thus, these environmental variables are related to areas with > 40 years of regeneration, since they have a primary structure of vegetation. The variables, depth (cm) and litter cover (%), were also associated with the same ant genera, since more trees were related to greater depth and litter cover. The genera of ants collected in the areas with initial and intermediate regeneration correlated more to the heights of shrubs (Fig. S4).

The NMDS indicated a difference in the community structure, with an overlap in ant fauna composition between areas with recent regeneration (six months to eight years) (stress = 0.1647). However, the areas with four years of regeneration presented a composition that was closer to that found in intermediate and advanced areas. Thus, these areas present differences in species composition, since they do not totally overlap (Fig. 3).

The direct ordering analysis between the environmental heterogeneity and the species collected showed species related to areas with recent regeneration (*Atta sexdens*, *Linepithema micans*, *Pseudomyrmex holmgreni*, *Ectatomma planidens*), which were absent in intermediate and advanced areas. Similarly, species collected in advanced aregas were absent in areas of initial succession, such as *Cephalotes eduarduli*, *Neoponera villosa*, *Trachymyrmex kempfi*, *Hypoponera foreli*. Some species, such as *Nomamyrmex esenbeckii*, *Camponotus* sp.1 and sp.2, *Wasmannia auropunctata*, *Solenopsis* sp.1, *Pheidole radoszkowskii* and *Pheidole* sp.3, *Cephalotes pusillus*, *Pseudomyrmex simplex*, *Crematogaster nigropilosa*, *Linepithema* sp.2, *Ectatomma brunneum* and *Atta saltensis*, were present in areas of succession (Fig. 4).

4. Discussion

4.1. Species richness and composition

The richness of the ant fauna in the Brazilian savanna varies between 32 and 77 species in the fauna inventory of the domain (Silvestre, 2000; Tavares et al., 2008). We, herein, obtained a richness of 60 species. Ant richness was directly proportional to the regeneration age of areas, as observed for ant community in the Brazilian savanna (Pais and Varanda, 2010) and Atlantic Forest (Braga et al., 2010). However, Neves et al. (2006) found no significant difference in the influence of succession stage on the richness of ant species in the Caatinga. A similar increase in species richness at intermediate levels

Table 2
List of ant species collected in the study area.

Subfamily	Species	Age of regeneration								
		1	2	3	4	5	8	12	15	> 40
Dolichoderinae	*Azteca brevis* Forel, 1899				x				x	
	Dorymyrmex brunneus Forel, 1908		x	x	x	x	x			x
	Dorymyrmex goeldii Forel, 1904				x					x
	Dorymyrmex piramicus (Roger, 1863)	x	x	x	x	x	x			x
	Linepithema humile (Forel, 1868)		x			x				x
	Linepithema micans (Mayr, 1908)		x							
	Linepithema sp.2		x		x	x	x	x	x	x
Dorymyrmex	*Nomamyrmex esenbeckii* (Westwood, 1842)							x		
Ectatomminae	*Ectatomma brunneum* Smith, 1958	x	x	x	x	x	x	x	x	x
	Ectatomma edentatum Roger, 1863	x	x		x		x	x	x	x
	Ectatomma opaciventre (Roger, 1861)				x	x				
	Ectatomma planidens Borgmeier, 1939		x		x	x				
	Ectatomma tuberculatum (Olivier, 1792)		x		x					
	Gnamptogenys acuminata (Emery, 1896)		x			x				
Formicinae	*Brachymyrmex aphidicola* Forel, 1909	x	x		x	x			x	x
	Camponotus crassus			x	x					x
	Camponotus sp.1	x	x	x	x	x	x	x	x	x
	Camponotus sp.2		x	x	x			x	x	x
	Camponotus sp.5							x		x
	Myrmelachista sp.1		x			x	x			x
	Myrmelachista sp.2									x
	Nylanderia fulva (Mayr, 1862)				x		x	x	x	x
Myrmicinae	*Acromyrmex rugosus* (Smith, 1858)				x					x
	Atta saltensis Forel, 1913		x		x		x		x	x
	Atta sexdens (Linnaeus, 1758)				x	x			x	
	Cardiocondyla wroughtonii (Forel, 1890)	x								
	Cephalotes atratus (Linnaeus, 1758)								x	x
	Cephalotes eduarduli (Forel, 1921)					x				x
	Cephalotes laminatus (Smith, 1860)				x			x		
	Cephalotes persimilis De Andrade, 1999				x					
	Cephalotes pusillus (Klug, 1824)	x	x	x	x	x	x	x	x	x
	Crematogaster arata Emery, 1906		x						x	x
	Crematogaster brasiliensis Mayr, 1878							x		x
	Crematogaster nigropilosa Mayr, 1870				x		x	x	x	x
	Cyphomyrmex rimosus (Spinola, 1851)		x				x			
	Cyphomyrmex minutus Mayr, 1862		x							
	Mycocepurus goeldii (Forel, 1893)		x			x			x	
	Pheidole oxyops Forel,1908		x		x	x				
	Pheidole radoszkowskii Mayr, 1884	x	x	x	x	x	x	x	x	x
	Pheidole sp.2	x	x	x	x	x	x	x	x	x
	Pheidole sp.3		x				x		x	x
	Pheidole sp.4				x					x
	Pheidole sp.5		x				x			x
	Rogeria ciliosa Kugler, 1994				x					x
	Solenopsis saevissima (Smith, 1855)			x	x	x		x	x	
	Solenopsis sp.1		x	x	x	x		x	x	x
	Trachymyrmex iheringi (Emery, 1888)		x				x	x		
	Trachymyrmex kempfi Fowler, 1982		x				x	x	x	
	Wasmannia auropunctata (Roger, 1863)		x		x				x	x
Paraponerinae	*Paraponera clavata* (Fabricius, 1775)				x			x	x	x
Ponerinae	*Hypoponera foreli* (Mayr, 1887)				x			x	x	x
	Neoponera magnifica (Borgmeier, 1929)									x
	Neoponera villosa (Fabricius, 1804)									x
	Odontomachus chelifer (Latreille, 1802)			x						
	Odontomachus meinerti Forel, 1905						x			x
	Pachycondyla harpax (Fabricius, 1804)		x		x			x		x
Pseudomyrmecinae	*Pseudomyrmex denticollis* (Emery, 1890)	x	x	x	x	x	x	x		x
	Pseudomyrmex gracilis (Fabricius, 1804)							x		x
	Pseudomyrmex holmgreni (Wheeler, 1925)			x	x					x
	Pseudomyrmex simplex (Smith, 1877)		x	x	x	x				x

(> 5 years) has been reported for other environments (Lawes et al., 2017), corroborating the theory of environmental heterogeneity, which states that the richness and diversity of species must increase in complex environments, since the richness and composition of the plant community provides more resources (Pianka, 1994; Ribas et al., 2003; Tews et al., 2003).

Areas with initial regeneration presented species found in all sampled areas, as these display ease of nesting, and these ants are present in both soil and vegetation. Intermediate areas did not present exclusive species. Areas with initial regeneration are composed of grasses, while intermediate areas present greater vegetation succession. We observed that some species, such as *Myrmelachista* sp.1, *Neoponera magnifica* and *N. villosa,* were collected in areas of > 40 years of regeneration, supporting the necessity of plant complexity for the establishment of some ant species (Lassau and Hochuli, 2004). The *N. magnifica* specimen has sparse records with a low number of specimens (Souza et al., 2007), representing the first report of the species in the state of Mato Grosso do Sul (data not published).
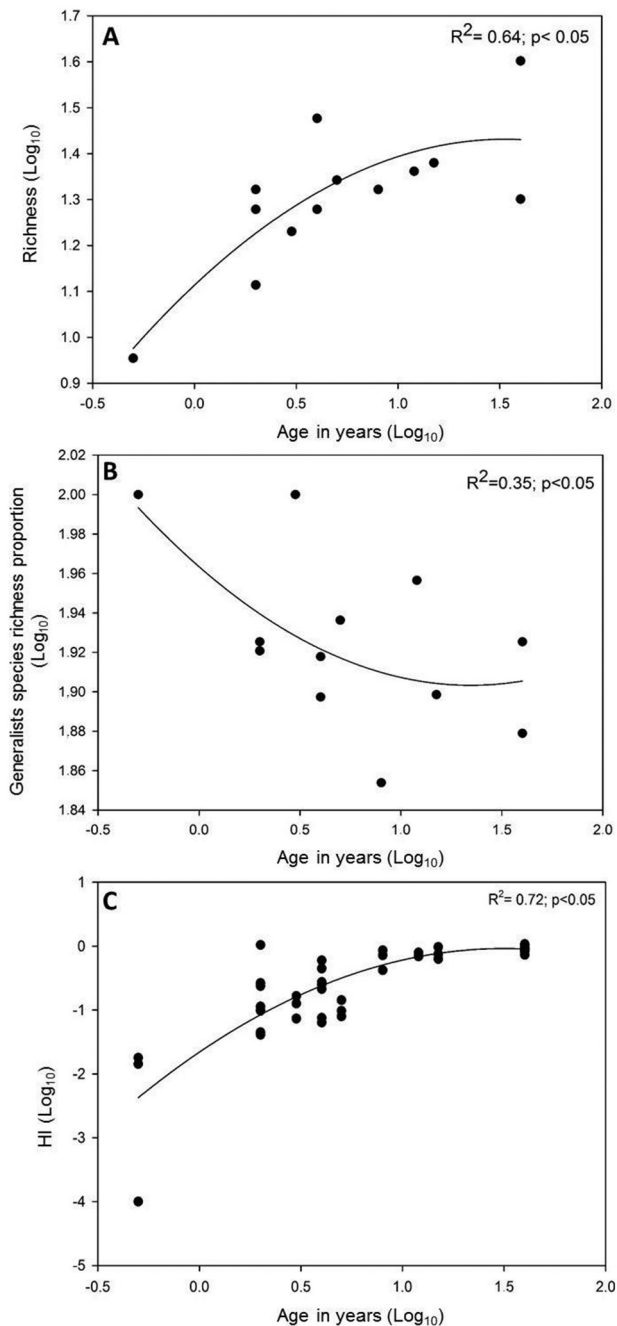
Fig. 2. Quadratic regression between ant richness (A), between generalist species ratio (B) and environmental heterogeneity index (C), as a function of the regeneration age of the areas (axes on a logarithmic scale).

Fig. 3. Non-parametric multidimensional scaling (Bray-Curtis similarity measure) in relation to species composition and areas with different regeneration ages (Stress: 0.16, Axis 1 = 58% and Axis 2 = 26%).

4.2. Spatial-temporal relationship of the ant composition and applications for the conservation of the Brazilian savanna

The richness of ant composition is directly related to the time of regeneration of the area (Ribas et al., 2003; Pais and Varanda, 2010). Areas displaying between six and eight years of regeneration showed the highest richness, since they present both secondary and climatic species, in agreement with the theory of intermediate disturbance (Flöder and Sommer, 1999). The analysis of the richness and composition of species revealed a similar composition in some areas with different regeneration ages. Areas of between five years and > 40 years of regeneration presented greater similarity in composition. The changes in ant species composition from the initial successional stage to the intermediate/late stage indicat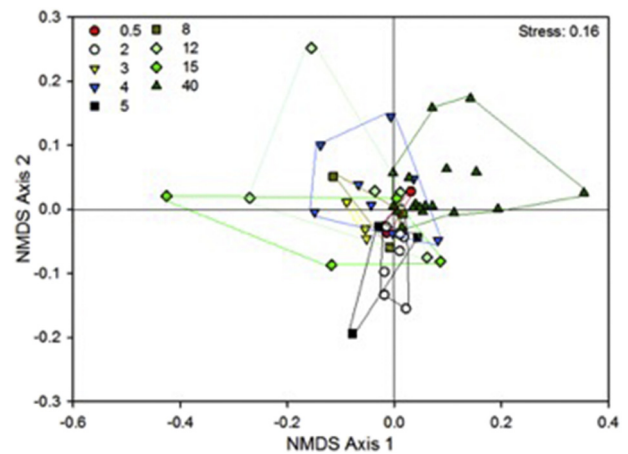e the effect of the age of plant succession on the ant composition (Neves et al., 2006). We found a threshold from five/six years of regeneration, where the community structure tends to stabilize, approaching the richness and composition found in areas with higher regeneration (12 to over 40 years). A similar threshold in regeneration was found by Lawes et al. (2017) in pasture areas.

The areas with initial succession (from six months to five years) showed a greater proportion of generalist species, due to the environmental variables found, such as shortage of shrubs and lack of trees. Areas with higher vegetation (shrubs, lianas, and trees) showed a reduction in generalist ants and an increase in specialist species. The relationship between the trophic guilds (proportion of generalists/specialists) and the index of environmental heterogeneity suggests a threshold in which the community tends to reestablish. Surprisingly, one of the initial areas (four years of regeneration) showed a richness degree that was similar to those of intermediate and preserved areas; this was due to practices used in this area, where the depositing of felled vegetation in corridors called "leiras" (Fig. S1, area A) facilitated this richness. This strategy does not hinder cattle breeding and favors the survival and maintenance of biodiversity. The area with four years of regeneration that contained "leiras" demonstrated vegetation-related variables that were similar to those of intermediate and preserved areas. Although not analyzed, a greater number of animals, such as reptiles (lizards) and birds, were observed in area with "leiras". Furthermore, Godoi et al. (2016) and Godoi and De Souza (2016) reported that areas with different vegetation cover present differences in the richness and composition of birds. The creation of "leiras" is a simple and low-cost practice, cattle-breeding compatible, which increases the environmental heterogeneity and biodiversity and might be used to predict the quality and survival of further groups of animals in addition to ants.

When analyzing the relationship between environmental variables and ant genera, we observed that the number of trees and their height explained > 90% of the results, since *Cardiocondyla*, *Crematogaster*, *Paraponera* and *Wasmannia* are arboreal and nest easily in trees, being directly related to vegetal components. However, no interconnection between tree canopies occurs in the Cerrado, as seen in the Amazon and Atlantic forest. This feature reduces the habitat complexity and makes tree nesting by ants more difficult, when compared to soil nesting. Habitats with higher tree complexity present greater richness of ants foraging on trunks and branches (Campos et al., 2008), corroborating Campos et al. (2008), who related ant richness in association with plant height.

The ant composition differs taxonomically and functionally between areas with different regeneration ages and these insects act as
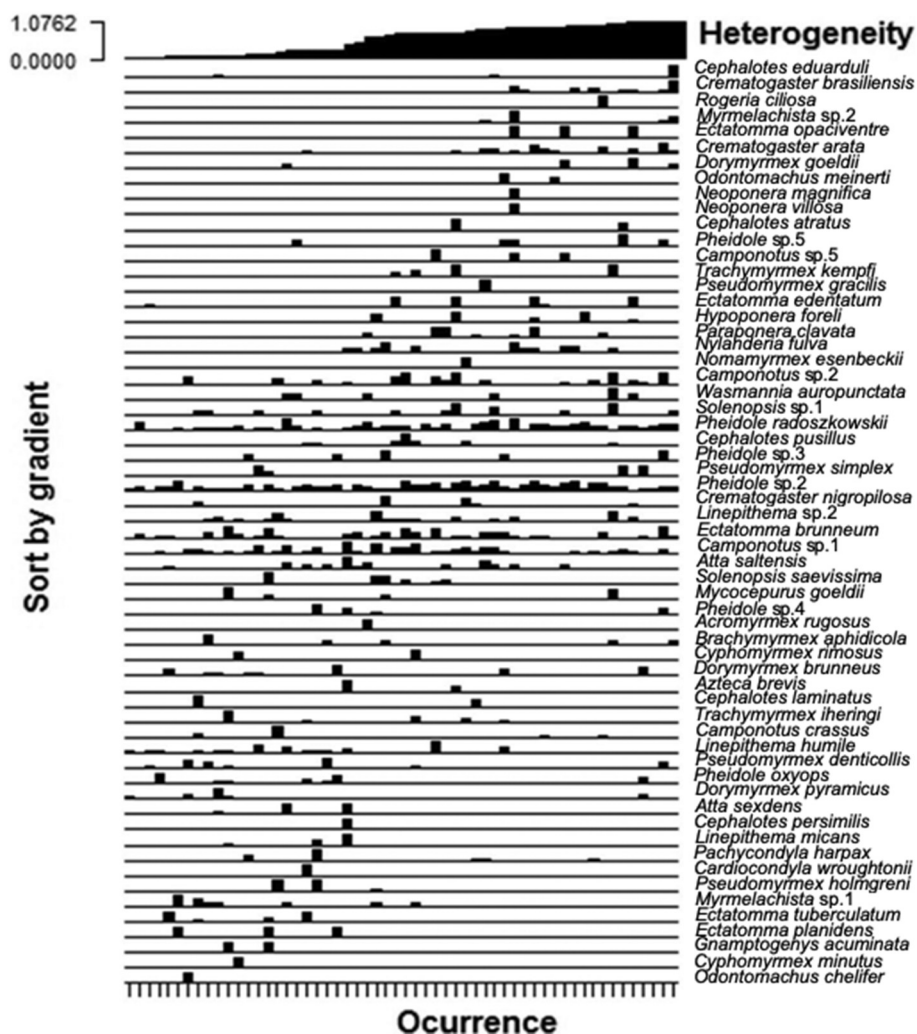
Fig. 4. Direct ordination between the environmental heterogeneity index and the composition of the ant species (height of the bar indicates frequency of occurrence).

ecosystem engineers, favoring regeneration. Although some species, such as *Atta* spp., decrease the nutrient availability in the soil around nests (Meyer et al., 2013), during the early and intermediate stages, the considerable presence of *Pheidole* spp., *Ectatomma* spp. and *Camponotus* spp. may favor soil drainage and fertilization, enabling more efficient seed banking and slowing down the regeneration process (Skoglund, 1992; Cerda and Doer, 2010; Reis et al., 2010; Cerda and Jurgensen, 2011). As the area studied has a low-intensity land use, we can observe taxonomic and functional regeneration in a short time (6 years) with respect to the regeneration process. Diverse soil management practices ensure greater success in regeneration strategies in tropical regions (Vieira et al., 2009).

We found that the maintenance of "leiras" in areas used for livestock is adequate and efficient to preserve the Brazilian savanna's biodiversity, providing a greater richness and composition of ant species, comparable with areas of intermediate and late regeneration. Since livestock is one of the main activities in the region of the Brazilian savanna, such practices can be used as short-term remedies to restore biodiversity. Although it may be difficult to find areas with detailed regeneration histories, we recommend research focused on other biological groups to verify whether a temporal threshold of five/six years is sufficient. Since Sustainable Development Goals from UNESCO Agenda, related to food, health, water, and climate, are central discussions for ensuring efficient productivity strategies (Keesstra et al., 2018), aspects related to soil protection and degradation remains as challenge. We have detected of such a simple and effective practice to ensure

ecosystem services should be encouraged. Therefore, areas with initial regeneration showed greater proportion of generalist species; thus, a temporal threshold for ant community regeneration from 6 years and the maintenance of a minimum amount of vegetation in areas destined for livestock is an adequate and efficient way of preserving the Brazilian savanna's biodiversity.

Declaration of competing interest

The authors of this manuscript declare that we have no conflict of interest in the publication.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://

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