



The Ground-Dwelling Ant Fauna from a Cerrado Reserve in Southeastern Brazil: Vegetation Heterogeneity as a Promoter of Ant Diversity

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Abstract

Ants represent one of the most diverse and ecologically important group of insects in tropical ecosystems, including in highly threatened ones such as the Brazilian Cerrado. Yet, a detailed understanding of the species diversity and composition of local Cerrado ant assemblages is lacking in many cases. Here we present the results of a comprehensive ant inventory performed within a region of the Cerrado (in São Paulo state) where most of the original vegetation has already been lost and where few conservation units exist. We performed consecutive surveys of the ant fauna that forage on the ground in replicated plots established in open savanna (*campo sujo*), dense savanna (*cerrado sensu stricto*), and forest (*cerradão*). Our surveys, with an estimated sample coverage of 99.4%, revealed a total of 219 species of ants from 60 genera, of which 36.1% were found in all the three vegetation types and 29.7% in just one. Rarefied species richness did not differ between vegetation types, but species composition differed markedly, especially between the two savannas in one hand and the forest in the other. Several species (60.1% of the 128 species analyzed) were significant “indicator” species due to their strong association with a given vegetation type. Overall, our findings reinforce the idea that habitat heterogeneity enhances ant diversity and that the mosaic of vegetation types that characterizes the Cerrado biome is one of the main factors explaining the elevated number of species that can be found at relatively small scales.

Keywords Biological inventories · Hymenoptera · Diversity · Indicator species · Fire suppression · Savanna-forest transitions

Introduction

Species inventories play a key role in conservation biology, as they represent the foundation of studies involving the assessment and monitoring of biodiversity (Longino and Colwell 1997; Sodhi 2010). Baseline information about the species richness and composition of local assemblages

is essential to assess changes in biodiversity, such as those expected to occur in regions mostly highly threatened by human activities. Yet, in many cases, such information is lacking, and this is especially true for most insect groups.

Home for the largest and most biodiverse of all tropical savannas, the Brazilian Cerrado has already lost over half its original vegetation, while only 8.2% is protected (Parente et al. 2021). These figures are even worse towards the southern limit of the Cerrado. In São Paulo state, for instance, less than 1% of the Cerrado vegetation (which once covered 14% of the area of the state) remains, and less than 20% of this vegetation is under some level of protection, either in public reserves or in private lands (Fiori and Fioravanti 2001). Furthermore, altered fire regimes are also threatening the conservation of the Cerrado biota, notably the open habitat specialists, which are susceptible to forest encroachment resulting from the suppression of savanna fires (Durigan and Ratter 2016; Abreu et al. 2017; Stevens et al. 2017).

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Ants (Hymenoptera: Formicidae) are a dominant group of insects in the Cerrado savannas, where they play a variety of ecological roles (Andersen and Vasconcelos 2022). The Cerrado ant fauna is highly diverse, containing at least 700 species (Andersen and Vasconcelos 2022). Nonetheless, this diversity is not uniformly distributed across the biome. In fact, contrasting to the usual latitudinal diversity pattern, within the Cerrado, more ant species are found at higher latitudes—where plant primary productivity is also higher—than at lower latitudes (Vasconcelos et al. 2018). Cerrado ant diversity is also sensitive to local variations in the structure of the vegetation. However, while some studies indicate that tree cover has a positive effect on ant diversity (Ribas et al. 2003; Pacheco and Vasconcelos 2012; Rabello et al. 2021), others have found the opposite pattern (Marques and Del-Claro 2006; Neves et al. 2013; Queiroz and Ribas, 2016). Importantly, ant species composition tends to change markedly as the structure of the vegetation changes (e.g., Neves et al. 2013; Rabello et al. 2021), and this has important implications for explaining ant diversity at the landscape scale (Pacheco and Vasconcelos 2012) and to better understand the indirect effects of fire on the Cerrado ant fauna (Maravalhas and Vasconcelos 2014; Andersen and Vasconcelos 2022).

Here we present the results of a structured inventory (Longino and Colwell 1997) of the ant fauna that nest and/or forage on ground, performed within one of the few Cerrado reserves found in São Paulo state (near the southern limit of the biome). Over a 4-year period, we sampled ants in replicated savanna and forest plots that were established at the Santa Bárbara Ecological Station (hereafter SBES). In addition to provide a comprehensive species list of the ants found at SBES, we attempted to answer the following questions: (a) How similar is the ant fauna from the different Cerrado vegetation types present at the SBES? (b) Which are the species most typical from each habitat? Overall, the results of our study point out for the importance of vegetation heterogeneity as a promoter of local ant diversity.

Material and methods

The Santa Bárbara Ecological Station (SBES) is located in Águas de Santa Bárbara, São Paulo, Brazil, within the coordinates 22°46′–22°51′S and 49°10′–49°16′W, at an elevation of 600 to 680 m a.s.l. The local climate is classified as Köppen's Cfa type, characterized by a wet summer and a dry winter (Alvares et al., 2013). The annual rainfall is around 1300 mm and mean monthly temperatures range from 18 to 22 °C (Meira-Neto et al. 2007). The soils are deep oxisols, characterized by high sand and low nutrient content, high saturation of aluminum, and low soil water holding capacity (Abreu et al. 2017).

SBES protects 2715 ha of Cerrado vegetation, including grasslands, savannas, and forests. However, since its creation in 1984 and associated with fire suppression policies, a substantial increase in tree biomass was detected over the entire area of the reserve, resulting in the loss of open habitats, thus threatening the conservation of the species associated with these habitats (Abreu et al. 2017). In 2015, a fire experiment was initiated (Durigan et al. 2020), and ant sampling took place in the plots designed for this experiment. A network of 30 plots (20 × 50 m each) was distributed across three savanna-forest transitions, distant 3 to 5 km from each other (Fig. S1). Twelve plots were established in forest areas (*cerradão* according to Brazilian terminology), 12 in dense savanna (*cerrado sensu stricto*), and six in open savanna (*campo sujo*).

Ant sampling took place in December 2014, in January 2016, in December 2016, and in November 2020, but only the dense savanna plots were sampled in all four sampling years. The open savanna plots were sampled three times (no sampling in the second year) and the forest plots twice, once in the first and once in the last sampling year. Half of the open savanna plots and three-quarters of the dense savanna and forest plots were experimentally burned at least once over the course of the entire sampling period. A preliminary analysis, however, indicated that the experimental fires did not have a significant effect on the ground-dwelling ant fauna, at least not in the short term (Durigan et al. 2020).

Five 2.5-m × 2.5-m grids were established in each sampling plot. The grids were set alongside the borders of each plot, keeping a minimum distance of 20 m between any two sampling grids. Four pitfall traps were set in each grid, totaling 20 traps per plot (over the course of the study we missed the traps installed in 17 grids, so our final sample size is 433 grids sampled rather than 450). Pitfall traps consisted of small plastic cups (250 ml, 8.5 cm high, and 7.8 cm in diameter) buried in the ground and partially filled with water and detergent. Pitfall traps remained in operation for 48 h and their contents were combined within grids. In the lab, ant workers were sorted into morphospecies and a representative specimen from each sample was dry mounted for subsequent identification using available taxonomic keys or by comparison with specimens previously identified by ant taxonomists deposited at the Zoological Collection of the Federal University of Uberlândia (UFU) and the Entomological Collection Padre Jesus Santiago Moure (DZUP) from the Federal University of Paraná (UFPR), where the specimens collected were also deposited. Sources used for species-level identification for each genus were the following: *Acromyrmex* (Gonçalves 1961); *Crematogaster* (Longino 2003); *Ectatomma* (Kugler and Brown 1982); *Gnamptogenys*, *Holcoponera*, and *Poneracatnha* (Camacho et al. 2020); *Labidus* and *Neivamyrmex* (Watkins 1976); *Linepithema* (Wild 2007); *Megalomyrmex* (Brandão 1990); *Odontomachus* (Brown 1976, 1978); *Oxyepoecus* (Albuquerque and

Brandão 2009); *Neoponera* and *Pachycondyla* (Mackay and Mackay 2010); *Pheidole* (Wilson 2003); *Sericomyrmex* (Jesovnik and Schultz 2017); *Wasmannia* (Longino and Fernández 2007). Specimens for which a species-level identification was not possible received a morphospecies code (the same used in UFU's collection).

We compared ant species richness between the three types of vegetation using both sample-based (Gotelli and Colwell 2001) and coverage-based (Chao and Jost 2012) rarefaction curves. Rarefaction curves were built in R version 4.0.5 (R Core Team 2021) using the packages “iNEXT” (Hsieh et al. 2016) and “ggplot2” (Wickham 2016). We compared the level of similarity in ant species composition between the three vegetation types using the Sørensen index for presence or absence data. We used the “betapart” package to calculate the overall dissimilarity between each pair of vegetation types and to partition this dissimilarity into its turnover and nestedness components (Baselga 2010). We also used the “betapart” package to calculate the “abundance-based” overall dissimilarities between vegetation types (Bray–Curtis index). Abundance was calculated as the number of samples in which a species occurred divided by the total number of samples taken in a given vegetation type. By “sample,” we mean the combined contents of four pitfall traps set within each grid of 2.5 × 2.5 m in a given year.

The ant species most characteristic of each type of vegetation were identified using the indicator species analysis (Dufrene and Legendre 1997). For this, we first built a matrix containing information about the average abundance (mean per sampling year) of each ant species in each vegetation type. The analysis was restricted to species present in at least six of the 433 samples taken over the course of this study (in all vegetation types combined), given that the remaining species were too rare for any meaningful analysis of habitat association. The indicator species analysis combines information about the relative abundances (number of samples in which the species was recorded) and relative frequencies (number of plots in which the species occurred) of each species in each habitat to calculate an indicator value (IndVal) for each species in each habitat. Indicator values range from 0 (no indication) to 100% (perfect indication). For each species, the habitat with the largest IndVal was considered the most characteristic habitat. The significance of the largest IndVal of each species was tested using the Monte Carlo test with 4999 permutations. Species which received a significant IndVal were classified as either open savanna, dense savanna, or forest specialists.

Results

Our surveys, with an estimated sample coverage of 99.4% (Fig. 1b), revealed a total of 219 species or morphospecies of ants from 60 genera and eight subfamilies (Table S1).

Species-level identification was possible for 64% of the species collected (Table S1). Despite the comprehensive sampling effort, 41 species (18.7%) were recorded in only one sample and 16 (7.3%) in only two. Among the species collected, three—*Paratrachymyrmex bugnioni* (Forel, 1912), *Pheidole calimana* Wilson, 2003, and *Strumigenys lygatrix* (Bolton, 2000)—were recorded for the first time in São Paulo state. In fact, the occurrence of *P. bugnioni* and *P. calimana* at SBES represents the southernmost record for these species.

Overall, the most abundant species in our surveys were *Pheidole fracticeps* Wilson, 2003 (found in 76% of the samples), followed by *Pheidole oxyops* Forel, 1908 (71.6%), and *Ectatomma permagnum* Forel, 1908 (53.6%). Only five species were present in all the 30 sampling plots, and these were *Brachymyrmex pictus* Mayr, 1887, *Cyphomyrmex rimosus* (Spinola, 1851), *Ectatomma edentatum* Roger, 1863, *Pheidole fracticeps*, and *Pheidole triconstricta* Forel, 1886. The most diverse genera were *Pheidole* (35 species), followed by *Camponotus* (22 species), *Solenopsis* (16 species), *Mycetomoellerius* (10 species), and *Brachymyrmex* (9 species).

More samples were taken in the dense savannas and, consequently, comparatively more species were recorded in this habitat (174 species) than in either the open savannas (137 species) or forests (141 species). However, as revealed by both the sample-based and coverage-based rarefaction/extrapolation curves (Fig. 1), these three vegetation types seem to support a similar diversity of ant species. Rarefied species richness based on sample sizes was only slightly greater in the open and dense savannas than in forest, whereas the reverse was true when comparing the sample coverage rarefied species richness (Fig. 1).

About one-third (36.1%) of the 219 species recorded were found in all the three vegetation types, whereas 29.7% were found in only one (Fig. 2). Ant assemblages in the open savanna shared much more species with assemblages from dense savanna than with those from the forest. Consequently, we found less dissimilarity in species composition between open and dense savanna than between each of the savannas and forest. Furthermore, while turnover accounted for only 54.3% of the overall dissimilarity between open and dense savanna, it accounted for 97.1% of the dissimilarity between open savanna and forest and 75.2% of the dissimilarity between dense savanna and forest.

We found similar levels of overall dissimilarity in species composition between open and dense savanna using either abundance (Bray–Curtis dissimilarity index = 0.280) or presence/absence data (Sørensen dissimilarity index = 0.228). In contrast, dissimilarity was much greater using abundance than presence/absence data when comparing each of the savannas with forest (Fig. 2).

The indicator value analysis revealed that 60.1% of the 128 species analyzed (those present in at least 6 samples)

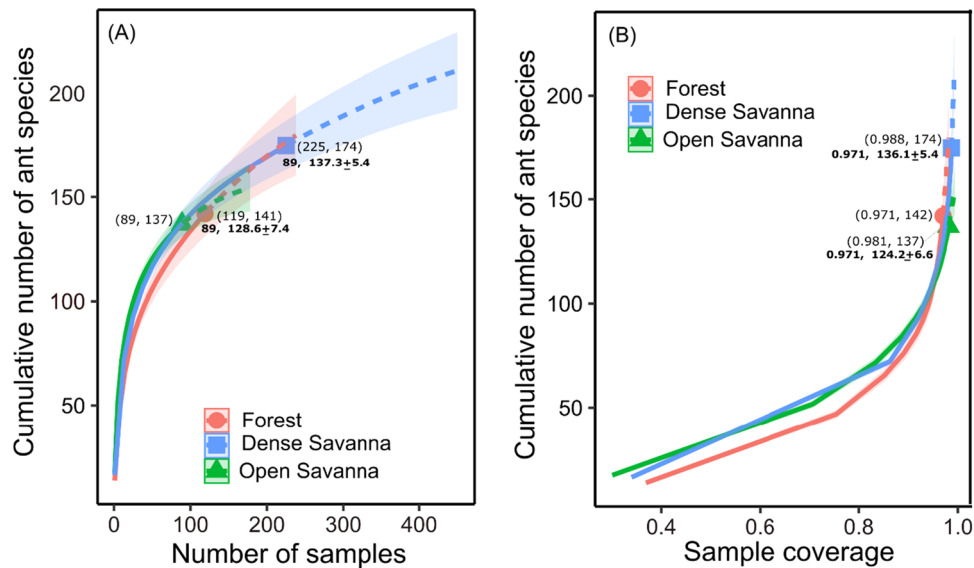


Fig. 1 Rarefaction (solid lines) and extrapolation (dashed lines) curves, showing the cumulative number of ant species recorded in each habitat in relation to **A** the sampling effort (cumulative number of samples) or **B** the sampling completeness (sample coverage estimator). In **A**, numbers within parentheses represent, respectively, the total number of samples taken and the observed species richness in each habitat. In bold is the rarified species richness (and 95% confidence intervals) in the dense savanna and forest habitats for a sam-

ple size = 89 samples, which represents the total number of samples taken in open savanna (the habitat with the lowest sampling effort). Numbers in **B** represent, respectively, the estimated sample coverage and the observed species richness. The rarified species richness in the open and dense savanna habitats, considering the sampling coverage achieved in the forest habitat (the habitat with the lowest sampling coverage), is shown in bold

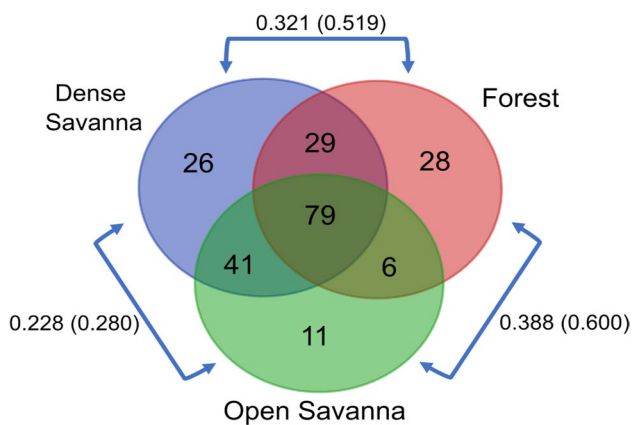


Fig. 2 Venn diagram showing the number of ant species recorded exclusively within a given habitat, and the number of species shared with one or two other habitats. Numbers outside the circles represent two measures of the overall dissimilarity in species composition between ant assemblages in different habitats: the Sørensen index for species presence or absence data, and (within parentheses) the Bray-Curtis index, which took into account the relative abundances of each species in each habitat

presented a significant indicator value (Table 1). Of these, 33 species were primarily associated with the open savanna, 15 with the dense savanna, and 18 with the forest habitat. Another seven species were more characteristic of the savanna habitat in general (primarily found both in open

and dense savannas) and four of the more “closed” habitats (primarily found both in dense savanna and forest) (Table 1).

Discussion

Overall species richness

With an estimated sample coverage of over 99%, our ant inventory at SBES represents one of the most complete inventories of the ground-dwelling ant fauna of a Cerrado locality. In total, we recorded 219 species, of which 174 were found in *cerrado stricto* sensu (dense savanna), which is the most typical and dominant Cerrado vegetation. Comparing the ant diversity found at SBES with other Cerrado areas is difficult given differences in sampling methodology, effort, and/or design between our study and others (e.g., Silva et al. 2004 found much less species at two Cerrado sites in São Paulo than we found at SBES, and this can be attributed to the fact that their sampling was restricted to the ant fauna that visit sardine baits). To our knowledge, only one other study performed ant surveys in multiple types of Cerrado vegetation and in multiple years as was done in here. Interestingly, this study (Camacho and Vasconcelos 2015), which took place in a 400-ha reserve located ca. 500 km north of SBES, revealed a surprisingly similar number of ground-dwelling species (226 species) as in the present study. The

Table 1 List of the ant species with a significant indicator value, together with their indicator values (in %, where zero = no indication and 100 is perfect indication) in each of the three sampled habitats

Species	Open savanna	Dense savanna	Forest
Open savanna indicators			
<i>Acromyrmex balzani</i> Forel, 1893	59	1	0
<i>Atta laevigata</i> Smith, 1858	83	0	0
<i>Camponotus innocens</i> Forel, 1909	49	18	0
<i>Camponotus leydigi</i> Forel, 1866	30	1	0
<i>Camponotus melanoticus</i> Emery, 1894	49	8	4
<i>Camponotus substitutus</i> Forel, 1899	65	27	0
<i>Cyphomyrmex transversus</i> Emery, 1894	61	34	0
<i>Dorymyrmex</i> sp. 6	41	3	0
<i>Ectatomma brunneum</i> Smith, 1858	47	0	0
<i>Ectatomma opaciventre</i> Roger, 1861	67	28	0
<i>Ectatomma planidens</i> Borgmeier, 1939	48	12	0
<i>Ectatomma tuberculatum</i> Olivier, 1792	45	26	1
<i>Forelius brasiliensis</i> (Forel, 1908)	61	2	0
<i>Forelius</i> sp. 9	65	9	0
<i>Gnamptogenys sulcata</i> (Smith, 1858)	50	11	12
<i>Gracilidris pombero</i> Wild & Cuzzo, 2006	30	1	0
<i>Kalathomyrmex emeryi</i> (Forel, 1907)	33	0	0
<i>Mycetagroicus cerradensis</i> Brandão & Mayhé-Nunes, 2001	52	1	1
<i>Mycetomoellerius kempfi</i> (Fowler, 1982)	47	0	0
<i>Myrmicocrypta</i> sp.1	48	17	2
<i>Neoponera verenae</i> Forel, 1922	46	0	1
<i>Pheidole jujuyensis</i> Forel, 1913	30	1	0
<i>Pheidole</i> nr. <i>mapinguar</i>	55	30	11
<i>Pheidole schwarzeieri</i> Borgmeier, 1939	51	11	0
<i>Pheidole</i> sp. 106	41	23	0
<i>Pheidole</i> sp. 70	31	1	0
<i>Pheidole vafra</i> Santschi, 1923	59	33	0
<i>Pogonomyrmex naegelli</i> Emery, 1878	58	5	0
<i>Rogeria</i> sp. 1	37	6	0
<i>Solenopsis</i> nr. <i>frank</i>	57	29	1
<i>Solenopsis</i> nr. <i>goeldii</i>	77	13	0
<i>Solenopsis</i> nr. <i>latastei</i>	58	32	0
<i>Solenopsis substituta</i> Santschi, 1925	53	7	0
Indicators of savanna habitat in general			
<i>Apterostigma</i> sp. 1	49	40	1
<i>Dorymyrmex</i> sp. 10	54	46	0
<i>Ectatomma permagnum</i> Forel, 1908	39	48	1
<i>Linepithema cerradense</i> Wild, 2007	46	44	8
<i>Mycetomoellerius urichii</i> (Forel, 1893)	48	39	0
<i>Myocepurus goeldii</i> (Forel, 1893)	42	46	9
<i>Pheidole</i> nr. <i>germani</i>	44	53	1
Dense savanna indicators			
<i>Dinoponera grandis</i> (Guérin-Méneville, 1838)	19	54	0
<i>Hypoconera</i> sp. 3	0	42	0
<i>Linepithema angulatum</i> Emery, 1894	0	58	0
<i>Linepithema micans</i> Forel, 1908	36	52	7
<i>Mycetomoellerius</i> sp. 15	8	62	15
<i>Mycetomoellerius</i> sp. 36	12	50	1
<i>Oxyepoecus rastratus</i> (Mayr, 1887)	4	49	0

Table 1 (continued)

Species	Open savanna	Dense savanna	Forest
<i>Pachycondyla harpax</i> (Fabricius, 1804)	20	54	20
<i>Pheidole radoszkowskii</i> Mayr, 1884	38	55	2
<i>Pseudomyrmex pallidus</i> (Smith, 1855)	9	62	3
<i>Pseudomyrmex tenuis</i> (Fabricius 1804)	12	47	3
<i>Rogeria</i> sp. 5	0	50	0
<i>Solenopsis loreтана</i> Santschi, 1936	25	54	12
<i>Solenopsis</i> nr. <i>basalis</i>	3	49	19
<i>Wasmannia auropunctata</i> (Roger, 1863)	39	56	2
Indicators of dense savanna and forest			
<i>Atta sexdens</i> Linnaeus, 1758	0	50	34
<i>Nylanderia docilis</i> (Forel, 1908)	10	48	37
<i>Pheidole oxyops</i> Forel, 1908	18	36	43
<i>Pheidole fracticeps</i> Wilson, 2003	26	31	43
Forest indicators			
<i>Acromyrmex subterraneus</i> (Forel, 1893)	0	0	56
<i>Camponotus iheringi</i> Forel, 1908	0	1	46
<i>Camponotus lespesii</i> Forel, 1886	5	7	79
<i>Carebara brevipilosa</i> (Fernández, 2004)	0	3	59
<i>Cyphomyrmex laevigatus</i> Weber, 1938	0	0	58
<i>Hypoponera</i> nr. <i>parva</i>	0	1	38
<i>Hypoponera</i> sp. 7	0	0	73
<i>Hypoponera</i> sp. 13	0	1	79
<i>Linepithema aztecoides</i> Wild, 2007	0	6	54
<i>Nylanderia</i> nr. <i>caeciliae</i>	0	1	54
<i>Odontomachus chelifer</i> (Latreille, 1802)	3	34	56
<i>Pachycondyla striata</i> Smith, 1858	14	11	71
<i>Pheidole calimana</i> Wilson, 2003	0	1	95
<i>Pheidole lovejoyi</i> Wilson, 2003	1	0	71
<i>Pheidole</i> nr. <i>obscurior</i>	13	32	56
<i>Pheidole</i> sp. 136	0	0	42
<i>Solenopsis</i> nr. <i>brevicolis</i>	15	21	62
<i>Solenopsis</i> nr. <i>westwoodi</i>	3	0	35

fact that over 200 ant species can be found within relatively small Cerrado areas (as shown here and in previous studies; Camacho and Vasconcelos 2015; Oliveira and Feitosa 2021) is surprising, notably when considering that current estimates indicate the occurrence of only ca. 700 species in the entire biome (Andersen and Vasconcelos 2022). That local ant diversity is high relative to the regional diversity can be explained, at least in part, because many of the species found within local assemblages are widespread species. This is the case for most of the species that are numerically dominant within local assemblages, such as *P. oxyops* and *E. permagnum*. However, this is not to say that Cerrado ants are of least conservation concern as the rampant rate of habitat destruction in the biome is likely to be reducing the number, size, and level of isolation of the remaining populations. One example is that of *Dinoponera grandis* (Guérin-Méneville, 1838) (Fig. 3), a relatively widespread species

in the southern portion of South America (Dias and Lattke 2021) but whose population recorded at SBES represents one of the last known populations of this remarkable species in São Paulo (R. Feitosa & J. Lattke, unpublished). Furthermore, many Cerrado ant species appear to be naturally rare and, as such, are also of conservation concern. Examples of rare species (currently known from only a very few locations in South America) found at SBES include *Gnamptogenys nana* Kempf, 1960, *Neoponera agilis* Forel, 1901, and *Strumigenys lygatrix* (Fig. 3). Interestingly, none of these three species were recorded in the plots that became forest as result of savanna woody encroachment. Similarly, with a single exception, no *D. grandis* was found in the forest plots. Finally, it is important to mention that most of the species-rich genera of Cerrado ants still require taxonomic revision and/or lack molecular information, and therefore, many of the individual species that we now regard as widespread may

Fig. 3 Species of potential conservation concern recorded at Santa Bárbara Ecological Station. **A** *Dinoponera grandis* (DZUP 549,812, image by Amanda Dias), **B** *Gnamptogenys nana*, **C** *Neoponera agilis*, and **D** *Strumigenys lygatrix*



in fact represent a complex of geographically distinct species (Feitosa et al. 2022).

Species diversity and composition in different vegetation types

Our results indicate a high level of similarity in the overall species richness of ground-dwelling ants between open savanna (*campo sujo*), dense savanna (*cerrado stricto sensu*), and forest (*cerradão*), despite the marked structural and floristic differences between these three vegetation types. Interestingly, our coverage-based rarefaction curves showed that, at an estimated sample coverage of about 80%

or less, ant species richness was lower in forest than in either open or dense savannas, while at higher levels of sample coverage within each habitat this difference disappeared. This points out for the importance of considering differences in sampling completeness when comparing ant diversity in different habitats (cf. Chao and Jost 2012).

In contrast to species richness patterns, we found marked differences in ant species composition between the different Cerrado habitats. There was a large number of species that showed significant habitat associations, even though the three types of vegetation we surveyed were in close proximity to each other (i.e., dispersal limitation was not an issue). These findings reinforce the idea that habitat heterogeneity

enhances ant diversity at the landscape scale (Pacheco and Vasconcelos 2012; Neves et al. 2013). As observed also for plants (Durigan et al. 2003), the mosaic of vegetation types that characterizes the Cerrado seems, therefore, one of the main factors in explaining the high number of ant species that can be found at relatively small spatial scales. Maintaining the mosaic of vegetation types should, therefore, be the target for management interventions aiming at Cerrado biodiversity.

Differences in species composition were particularly pronounced between the forest in one hand and the two savanna habitats in the other, although somewhat greater between open savanna and forest than between dense savanna and forest. In addition to find several species that seem exclusive of the forest or of the savanna habitat, we often found sharp differences in the abundance of those species that were recorded in both types of habitats. In other words, species that were relatively common in forest were relatively rare in the savannas, and vice-versa, suggesting that the former may represent marginal habitats for ant populations that are most typical in savanna (i.e., they are sink populations), while savannas represent marginal habitats for forest ants. In this sense, woody encroachment in fire-suppressed savanna areas is likely to represent a threat for the conservation of the savanna ant fauna not only because the forests established in former savanna areas are inadequate habitats for the savanna specialists (Andersen et al. 2006; Abreu et al. 2017), but also because these forests, over the long run, may not be able to sustain the populations of the species that are not strictly restricted to savanna.

Our study has listed a relatively large number of ant species that are primarily associated with the forest or with the savanna habitats (or, else, are habitat generalists). Compilation of such information in other localities would be instrumental to determine the extent to which savanna and forest ant assemblages represent two alternative compositional states and thus to assess the generality of our findings. Further information about the habitat affinities of different ant species would also be of value for studies that use ants as bioindicators of ecological change (reviewed in Andersen 1997; Ribas et al. 2012). This is evidenced, for instance, by a study which showed that the prevalence of savanna-associated ant species is strongly correlated with the extent of forest fires in the Amazon (Paolucci et al. 2017). Finally, information on habitat affinities may also be of importance for assessing the impacts of climatic change on ants, given that savanna and forest ants can respond differentially to the same climatic drivers (Vasconcelos et al. 2018).

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Author Contribution H. L. V. and G. D. designed the study; K. C. F. N., R. E. O. S. L., and H. L. V. were involved in data collection and preparation; R. M. F. provided taxonomic expertise; H. L. V. led the writing; and all authors contributed to manuscript preparation.

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Declarations

Conflict of Interest HLV is member of the Editorial Board of Neotropical Entomology, and the manuscript was independently handled by another editor.

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