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ECOLOGY, BEHAVIOR AND BIONOMICS

# Patterns of Ant Diversity in the Natural Grasslands of Southern Brazil

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## Abstract

In the south of Brazil, grasslands are naturally widespread over two different biomes, the Pampa in the southernmost region and within the Atlantic Forest in the northern portions. The natural grasslands of the state of Paraná comprise a very particular physiognomy composed of two distinct formations: the Campos Gerais and the grasslands of the southwest. The first is located in the edge of the second plateau of Paraná state, comprising a great diversity of environments. The grasslands of the southwest are more homogeneous, with a continuous herbaceous stratum dominating the landscape. In this context, the aim of this study was to evaluate the patterns of species richness and composition of ants, an ecologically prominent group, along the natural grasslands of Paraná. We also intended to compare the faunal similarity between the two different grassland formations. For that, four different Conservation Unities were sampled along a latitudinal gradient. A remarkable total of 245 ant species was recorded, and the results indicate that species richness decreases as latitude increases along the grasslands of Paraná. There were clear differences in species composition between these two grasslands formations, given the significative number of endemic species in each of these two grassland formations. Ten species were recorded for the first time in the state of Paraná, of which three also for the first time in the Southern Region of Brazil. Overall, our study contributes to a better understanding about the diversity and composition of ant communities in subtropical grasslands.

**Keywords** Diversity · Composition · Inventory · Neotropics · Savanna

## Introduction

Brazil is recognized as a country with a great diversity of biomes, ranging from evergreen forests to grasslands and savannas. Despite the large extent of grassland areas in Brazil, they have historically been neglected in biodiversity research and conservation policies. This is probably due to the erroneous idea that these areas are homogeneous and have a low diversity of species in comparison to forested areas (Overbeck et al. 2015a). Among the grassland areas in Brazil, the term "Campos Sulinos" refers to the grasslands in the three Southern Brazilian states, Paraná (PR), Santa Catarina (SC), and Rio Grande do Sul (RS). Despite their classification as a single environmental unit, the grasslands of Southern Brazil encompass two different and highly heterogeneous biomes. The grasslands in the southwestern of RS belong to the Pampa biome and are characterized as seasonal steppes. On the other hand, the grasslands on the Southern Brazilian Plateau, which includes the northern portion of RS and the states of SC and PR, belong to the Atlantic Forest biome, and are characterized as highland grasslands (Pillar and Lange 2015; Andrade et al. 2019).

Several studies carried out in recent years indicate that grassland physiognomies dominated the entire region of Southern Brazil during the Holocene due to the characteristic dry conditions of this period (Behling 1997; Carlucci et al. 2011). In Paraná, the expansion of grasslands was also influenced by the particularities of the relief in this state. According to Hauck and Passos (2010), during the Last Glacial Maximum (LGM), the PR was exclusively covered by grassland vegetation. During this period, forest and savanna vegetation were fragmented and located in refugia in lower-altitude areas and the bottoms of valleys.

At the end of this period, more humid conditions allowed the Mixed Ombrophilous Forest biome (*Araucaria* forest) to expand in the states of PR and SC, allowing the establishment

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of species therein that were previously restricted to the hottest and most humid regions of the country (Behling et al. 2004). With the expansion of forests, and due to the characteristics of the local relief, the two principal grassland areas in Paraná became separated. The first of these, to the west of the Devonian Escarpment, was defined by Maack (1948) as the "Campos Gerais Paranaenses" (hereinafter Campos Gerais). The second region is formed by the grasslands of the southwest, located in the southwestern part of the state between the coordinates 25°30′S, 51°19′W and 26°34′S, 51°34′W (Fig. 1).

The Campos Gerais is a phytogeographic zone characterized by the prevalence of rocky soils, canyons, caves, and shallow rivers (Melo and Meneguzzo 2001). This region is dominated by open grasslands, permeated by canyons, gallery forests, and patches of Mixed Ombrophilous Forest. With an area of 11,761 km$^2$, this zone extends through approximately 22 municipalities in the center-eastern portion of the state of Paraná. The grasslands of the southwestern part of Paraná are homogeneous, with low incidence of forests and a continuous landscape. There are also patches of Mixed Ombrophilous Forest and Semi-Deciduous Seasonal Forest in this region, which has a colder climate compared to the Campos Gerais (Maack 1981). In addition of being in two different plateaus, the two grassland regions of Paraná are separated by a large extension of Mixed Ombrophilous Forest. Therefore, the phytophysiognomic features of these regions may influence the composition of the local floras and faunas.

The northernmost portion of the Campos Gerais includes patches of Brazilian savanna, belonging to the Cerrado biome. The Brazilian Cerrado corresponds to about 23% of the national territory, with a total area of approximately 2 million km$^2$ (Bridgewater et al. 2004), and consists of a mosaic of plant formations ranging from open grasslands to relatively dense forest (Coutinho 1978). The state of Paraná represents the southern limit of this biome, and the cerrado *sensu stricto* is the most common physiognomy in this region, with woody individuals distributed in a relatively dense form, tree cover of up to 60%, and vegetation height of 3–4 m (Uhlmann et al. 1998; Bridgewater et al. 2004). Although these areas are recognized as part of the Cerrado biome, here we follow the definition of Maack (1981) who considers these savanna patches as belonging to the Campos Gerais zone, since they form a continuous open vegetation along the second geological plateau of the state.

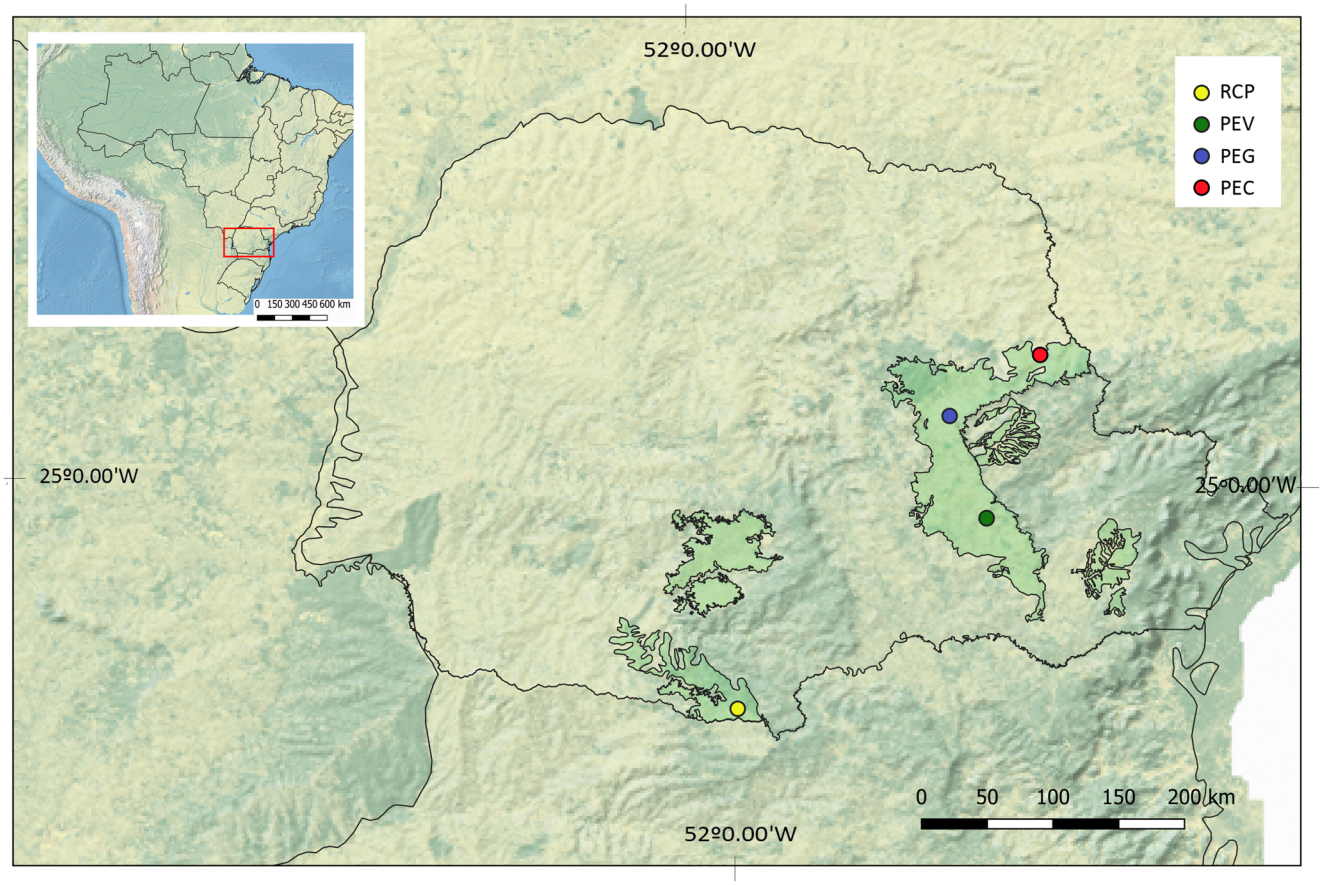


**Fig. 1** Map of the study region within Brazil and location of the four natural grasslands sampled in the state of Paraná: *Campos Gerais* grasslands: PEC, *Parque Estadual do Cerrado*; PEG, *Parque Estadual do Guartelá*; and PEV, *Parque Estadual de Vila Velha*; southwestern grasslands: RCP, *Refúgio de Vida Silvestre dos Campos de Palmas*

Ants constitute a family (Formicidae) of insects with great ecological importance and which participate in diverse interactions with a wide array of other organisms (Wilson and Hölldobler 2005). In Brazil, around 1480 ant species are known, from 112 genera of which nine are endemic (AntWiki.org 2021). Members of this family occupy key ecological positions in most terrestrial habitats, with great importance in trophic networks (Wall and Moore 1999). In addition, ants usually have high rates of spatial turnover (Smith et al. 2005), and the local taxonomic diversity of ants is often correlated with variations in temperature, humidity, resource availability, and the strength of biotic interactions, notably interspecific competition (Andersen 1992; Lewinsohn et al. 2005; Vasconcelos et al. 2018). Therefore, changes in the environment can lead to significant changes in the ant fauna. Considering the historical processes and changes involved in the formation of the grassland areas of Paraná, it is likely that at some point in time, specifically up to the Upper Holocene, these regions shared similar ant faunas (Maack 1981).

In this context, the aim of this study was to describe the richness, diversity, and composition of the ant fauna in the natural grasslands of Paraná, Brazil. We also aimed to (i) compare the ant fauna between the two principal regions of grasslands in the state, the Campos Gerais, including patches of Brazilian savanna (cerrado *sensu stricto*), and the grasslands of the southwestern part of the state and (ii) evaluate the relative contribution of turnover and nestedness in determining eventual differences in species composition between these grasslands. Finally, we also attempted to understand how the adjacent physiognomies of these regions influence the composition of the ant fauna of grasslands in Paraná.

## Materials and methods

### Study areas

Standardized sampling of the ant fauna was conducted in four reserves, encompassing most of the two main areas of natural grasslands in Paraná, Brazil (Fig. 1). For the sake of simplicity, each sampling site is hereafter referred to simply as a "grassland." The sampling areas were the Parque Estadual do Cerrado (PEC), the Parque Estadual do Guartelá (PEG), and the Parque Estadual de Vila Velha (PEV), all located within the Campos Gerais region, and Refúgio de Vida Silvestre dos Campos de Palmas (RCP) reserve, located in the southwestern-grasslands region (Fig. 1). Photographs of the sampling areas are available in the Supplementary Material.

The PEC is located between the municipalities of Jaguariaíva and Sengés (24°10′01″S, 49°39′02″W) and covers an area of 426.6 ha. The local vegetation consists primarily of cerrado *sensu stricto* (typical savanna) species, but with other phytophysiognomies also present (hygrophilous grasslands and riparian forests). In the PEC, there is a predominance of low-lying relief forms, and the climate of the region is of the type Cfb (temperate humid), according to the Köppen classification system, with temperatures between 10 and 22°C.

The PEG, which is located in the municipality of Tibagi (24°39′10″S, 50°15′25″W), has an area of 798.9 ha. The relief is very heterogeneous, and different types of vegetation cover are observed throughout this area, with a predominance of open grasslands, with mosaics of Mixed Ombrophilous Forest and Cerrado areas (Veloso et al. 1991). The climate of the region, according to the Köppen classification system, is of the type Cfb, although it is also directly influenced by a Cfa (humid subtropical) climate type (Itcg 2008).

The PEV is located in the municipality of Ponta Grossa (25°12′34″S, 49°58′04″W) on the second plateau in the state of Paraná. This park covers an area of approximately 3122 ha, with the predominant vegetation cover consisting of grasslands and fragments of Mixed Ombrophilous Forest (Ziller 2000). The relief is extremely undulating, with escarpments, plateaus, and open walls. The rock formations are mostly sandstone outcrops dating from the Paleozoic (Maack 1946). The climate is of the type Cfb, according to the Köppen classification system, with an average temperature between 18 and 22°C (Iapar 1994).

The RCP covers the municipalities of Palmas and General Carneiro (26°31′40″S, 51°36′17″W), comprising an area of 16,582 ha. The region is composed of grasslands historically used for livestock; however, in the area of the Refuge, the natural grasslands have been preserved. The RCP also acts as a protection area for the spring of the Chopim River and for the entire hydrographic network of the region. The climate is of the type Cfb, according to the Köppen classification system, with an average temperature of less than 18°C in the coldest month of the year. Palmas is one of the coldest cities in Paraná, where snow may occasionally fall. The cold weather here is favored by the high local altitude, which ranges from 950 to 1370 m.

### Sampling

In each study area, three 400-m-long transects were established, 1 km apart from each other. In each transect, 20 sampling points were stablished, which were 20 m apart from one another. At each point, four pitfall traps were installed at each corner of a 2 × 2 m grid. Each grid represented a single sample, for a total of 60 samples per area and 240 samples overall (Fig. S1).

Each pitfall trap consisted of a 250 mL plastic cup filled to a third of its volume with a solution of water, salt, and detergent. The traps were each buried so that their opening was level with the soil surface, and were left exposed for 48 h. After this period, all biological material was removed from the traps and stored in 80% ethanol. Pitfall traps like these are considered the most effective method for sampling insects

in grasslands environments (Bestelmeyer et al. 2000). Field sampling was always carried out in the rainy season (a period of high ant activity), between October and February, and only once in each study area.

Samples were processed in the Laboratório de Sistemática e Biologia de Formigas of the Universidade Federal do Paraná (UFPR) and identified to the genus level using the identification keys in Baccaro et al. (2015). Whenever possible, ants were also identified to the species level by checking the taxonomic literature and consulting specialists (see "Acknowledgements").

The sources used for species-level identification for each genus were the following: *Acromyrmex* — Gonçalves (1961); *Anochetus* — Brown Jr 1978), Fernández (2008); *Ectatomma* — Kugler and Brown Jr 1982); *Forelius* — Cuezzo (2000); *Gnamptogenys* — Lattke et al. (2007), Camacho et al. (2020); *Labidus* — Watkins (1976); *Linepithema* — Wild (2007); *Mycetagroicus* — Brandão and Mayhé-Nunes (2001); *Mycetarotes* — Mayhé-Nunes and Brandão (2006); *Mycetomoellerius* — Mayhé-Nunes and Brandão (2005); *Neivamyrmex* — Watkins (1976); *Octostruma* — Brown Jr and Kempf 1960); *Odontomachus* — Brown Jr (1976); *Oxyepoecus* — Albuquerque and Brandão (2009); *Neoponera* and *Pachycondyla* — Mackay and Mackay 2010); *Wasmannia* — Longino and Fernández (2007).

When species determination was not possible, taxa were treated as morphospecies. Voucher specimens were deposited in the Padre Jesus Santiago Moure Entomological Collection at the Universidade Federal do Paraná (DZUP).

All collections were carried out under the authorization of the Environmental Institute of Paraná (IAP; License No. 49.14) and the Chico Mendes Institute for Biodiversity Conservation (ICMBio; License No. 53622-1).

## Analysis

To evaluate our sampling efficiency, we performed a sample coverage analysis using the procedures suggested by Chao et al. (2014). For this, we first built a matrix using information on the presence or absence of each species in each sampling point (i.e., the 2 × 2 m grid with four pitfall traps). Abundances thus represented the number of sampling points in which the species was recorded. To compare the overall species richness and diversity between the four natural grasslands, we fitted interpolation and extrapolation curves of Hill numbers with orders of q = 0 (species richness), q = 1 (Shannon diversity index), and q = 2 (Simpson's diversity index), following the method developed by Chao et al. (2014). The Shannon index is the most widely used diversity index, which takes into account the number of species richness and their abundances, with equal weights given to rare and abundant species (Magurran 2004). The Simpson's index measures the probability that two randomly selected individuals in a sample belong to the same species, but it is sensitive to species dominance (Brower and Zarr 1984). Interpolation (i.e., rarefaction) and extrapolation, sample-based curves were calculated with the R package 'iNEXT' (Hsieh et al. 2016) based on 120 samples and their 95% confidence intervals were estimated based on 1000 permutations.

To compare the number of species recorded per sampling transect in each grassland, we performed a Poisson Generalized Linear Model (GLM), but since overdispersion was detected, we corrected the standard errors using a quasi-Poisson GLMM model. We used the Tukey method for pairwise comparisons using the 'emmeans' package in R 3.6.1 (R Core Team 2019).

To visualize the differences in ant species composition between the four grasslands, we performed an ordination analysis (non-metric multidimensional scaling, nMDS; Legendre and Legendre 1998). The nMDS was run in PC-ORD version 7.08 (MJM Software Design, Gleneden Beach, OR, USA), using the Relative Sørensen index for abundance data (Peck 2010). To evaluate if differences in species composition between grasslands resulted mainly from species turnover or nestedness, we calculated the turnover and nestedness-resultant dissimilarity between grasslands using the 'betapart' package in R (Baselga and Orme 2012).

To further illustrate the faunal dissimilarities between the four grasslands, we performed a two-way cluster analysis in PC-ORD 7.08, using the Bray–Curtis index of similarity and the group average linkage method (Peck 2010). This analysis was based on the relative richness of each genus in each grassland. Relative richness was calculated dividing the number of species from a given genus by the total number of species from all genera found in a given grassland.

# Results

## Ant fauna and patterns

We recorded a total of 245 species of ants, belonging to 46 genera and eight subfamilies (Table S1, Table S3 I). We were able to nominally identify 133 species (54% of the total), while all other species are represented by morphospecies. Considering the richness of genera, the most well-represented subfamily in the samples (transects) was Myrmicinae, with 26 genera, followed by Ponerinae, with seven genera, and Formicinae, with four genera (Table S1 – Supplementary Material). The genus for which the greatest species richness was found was *Pheidole* (Myrmicinae), with 75 species, followed by *Camponotus* (Formicinae), with 26 species, and *Solenopsis* (Myrmicinae), with 19 species.

The species with the highest number of records in the samples was *Pachycondyla striata* Smith, 1858 (Ponerinae), with 145 records, followed by *Wasmannia auropunctata* (Roger, 1863) (Myrmicinae), with 98 records, and *Gnamptogenys*

*striatula* Mayr, 1884 (Ectatomminae), with 94 records. Ten new species were recorded for the first time in the state of Paraná, of which three also represented the first records of these species for the South Region of Brazil (Table S1).

The sample coverage values showed that a high sampling efficiency was achieved in this study, as we collected from 85 to 95% of the species expected to be found in each site (Fig S2 – Supplementary Material). We found a latitudinal decline in species richness, diversity, and evenness (Hill number of orders q = 0, 1 and 2, respectively), from the northernmost (PEC) to the southernmost (RCP) site (Fig. S3). In total, we recorded 129 ant species at PEC, 112 at PEV, 115 at PEG, and 55 at RCP species (Fig. 2, Table S1). The mean number of species was significantly different between grasslands ($\chi^2$ = 20.06, df = 3, P < 0.001), as PEC, PEG, and PEV presented more species than the RCP grassland (Fig. 3).

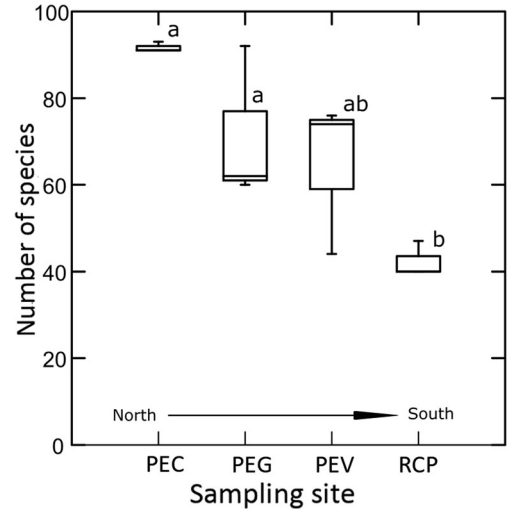


**Fig. 3** Number of ant species per transect. Different letters above the boxplots represent significant differences in mean species richness between sampling sites. Sampling sites are ordered in relation to their geographic position from the northernmost to the southernmost (higher latitude) site

## Species composition

Our analysis indicated a fair degree of dissimilarity in ant species composition between the grasslands we studied (Sorensen dissimilarity index > 0.47 in any pairwise comparison; Fig. 4). It also indicates that ant fauna from the three Campos Gerais grasslands (PEG, PEC, and PEV) were more similar to each other than to the fauna of grassland of the Southwest (RCP) (Fig. 4). Differences in species composition resulted mainly from species turnover, with nestedness contributing little to the overall dissimilarities between the grasslands (Fig. 4b). RCP, although being the less diverse grassland, presented a high proportion of exclusive species as 40.0% of all species collected at this site were only found there. This number was only smaller than the one found at PEC (PEC = 40%, PEG = 30.4%, and PEV = 25.2% of exclusive species). Only nine of the 245 species (3.8%) we collected were found in all four grasslands.

The two-way cluster analysis based on the relative number of species per genus again indicates a greater similarity between the Campos Gerais grasslands as compared to the grassland of the southwest region (Fig. 5). The ant genera included in Group 3 of the two-way cluster analysis (Fig. 5) were either found only in the Campos Gerais region (i.e., in the grasslands PEG and PEV and the savanna reserve PEC) or were comparatively more diverse (relative to the total number of species found) in this region than in the southwest (i.e., in the RCP grassland). In contrast, most of the genera that formed Group 4 had, proportionally to the total number of species found, more species in the RCP grassland than in the Campos Gerais. The remaining four groups of genera included those that were exclusively found or were relatively more diverse in one of the four grasslands (Fig. 5). Most of the genera that were recorded in only one grassland were rare and represented

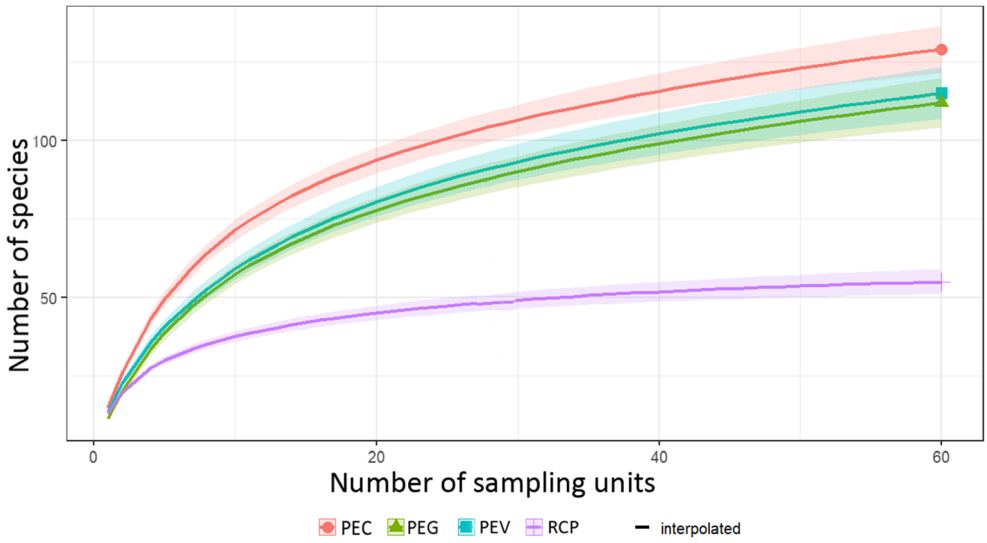


**Fig. 2** Interpolation (continuous line) curves and their 95% confidence intervals (shaded areas) in relation to the number of samples taken in each of the four natural grasslands sampled. *Campos Gerais* grasslands: PEC, *Parque Estadual do Cerrado*; PEG, *Parque Estadual do Guartelá*; PEV, *Parque Estadual de Vila Velha*. Southwestern grasslands: RCP, *Refúgio de Vida Silvestre dos Campos de Palmas*

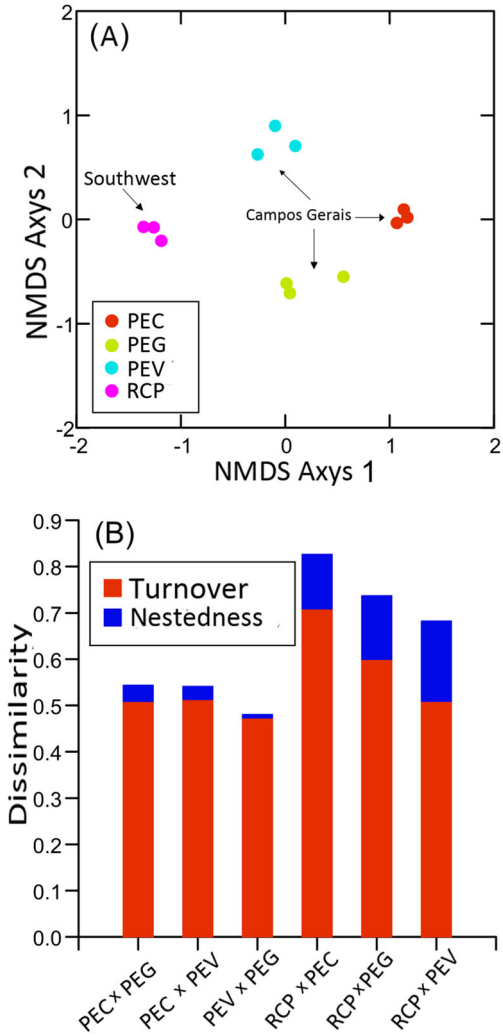


**Fig. 4** (A) Ordination (non-metric multidimensional scaling, NMDS) plot of the sampling sites in relation to the composition of ant species. (B) Overall dissimilarity in species composition (Sørensen index) between the sampling sites and the dissimilarity due to species turnover or nestedness

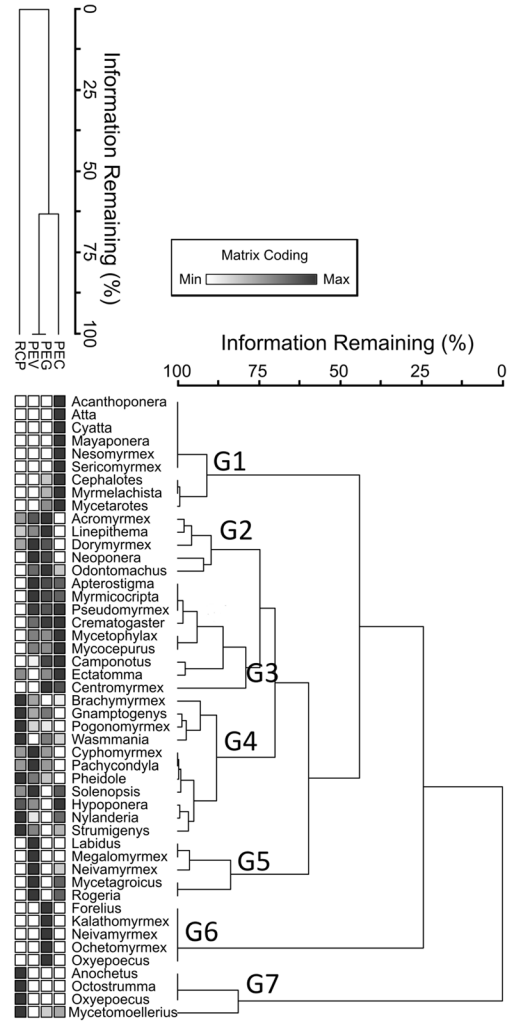


**Fig. 5** Two-way cluster dendrogram showing the similarity of the four natural grasslands, based on the relative richness of each genus in each grassland. The darker the square symbol, the greater the relative species richness of that genus in that particular grassland (white symbols indicate that no species from that genus was recorded)

by a single species (Table S1). Genera that contained species strictly arboreal, such as *Cephalotes*, *Myrmelachista*, were not found in the two southernmost grasslands (PEV and RCP), whereas genera that contain a large proportion of arboreal species, such as *Camponotus*, *Crematogaster*, and *Pseudomyrmex*, were less diverse in the grasslands (notably in PEV and RCP) than in the savanna reserve (PEC) (Fig. 5; Table S1).

## Discussion

### Richness and diversity

The total number of species (245) found in the natural grasslands of Paraná as well as the number found in each sampling area (55 to 129 species) can be considered high when considering the results of previous studies carried in similar environments (Rosado et al. 2012; Dröse et al. 2017; Klunk et al. 2018). In Rio Grande do Sul, Rosado et al. (2012) recorded a total of 72 species in vineyards and grasslands. In the same state, Dröse et al. (2017) sampled six grassland areas, representing two different biomes of the Campos Sulinos (Pampas and Atlantic Forest). The protocol used was similar to that used in the present study and 106 ant species were found, of which 91 species were recorded in the Pampas biome and 61 in the Atlantic Forest grassland areas. In Santa Catarina, Klunk et al. (2018) found a richness of 34 ant species in grasslands areas, also using epigaeic pitfall traps.

Among the subfamilies found, Myrmicinae, Formicinae, and Ponerinae were clearly dominant. This was an expected result since these are the major subfamilies of Formicidae, also known by their high species diversity in the Neotropics (Schmidt and Shattuck 2014; Ward et al. 2014, 2016). The

subfamily Myrmicinae can be considered the most successful ant subfamily in terms of species diversity (Ward et al. 2014) as they have a wide range of feeding, nesting, and reproductive strategies, occupying a wide variety of niches. In fact, myrmicines play an important role in terrestrial ecosystems as predators (generalists or specialists), detritivores, granivores, herbivores, and omnivores (Brown Jr 2000). In addition, Myrmicinae comprises approximately 50% of the species of Formicidae, another fact that contributes to its high abundance in surveys (Bolton 2020).

Among all the genera recorded in this study, the most diverse were *Pheidole*, *Camponotus*, and *Solenopsis*, as expected. The first two genera are the richest in terms of the number of species among all ants. They have a wide distribution and high dominance in tropical regions, especially in the soil (Wilson 1976; Bolton 2020). The genus *Solenopsis* comprises a large number of epigaeic predatory species. It also has a wide distribution and high colonization success rate, being extremely efficient in the dispersion of new colonies (Pacheco and Mackay 2013). Although high numbers of species of these three dominant genera were sampled, *Pheidole* stood out from the others, representing 28% of the species collected.

The dominance of the subfamilies Myrmicinae, Formicinae, and Ponerinae was also evident when considering the frequency of occurrence of the sampled species. The most frequently sampled species was *Pachycondyla striata* Smith, F., 1858, a species of Ponerinae with a large body size that is considered a generalist predator of other arthropods (Mackay and Mackay 2010). This ant species is widely distributed, ranging from northern Argentina to Paraguay, Uruguay, and Brazil (Silva-Melo and Giannotti 2012). The second most common species in our samples, *W. auropunctata*, is known as the "little fire-ant." It is a species of great ecological importance, which is known to easily invade disturbed habitats, such as forest edges or agricultural fields (Ness and Bronstein 2004). Although it is known as an invasive ant, its original distribution range extends from Argentina to Mexico (Kempf 1972; Wetter and Porter 2003).

The ectatommine *Gnamptogenys striatula* Mayr, 1884 does not belong to any of the three dominant subfamilies (Myrmicinae, Ponerinae, and Formicinae). However, it was the third most frequent ant species in the present study. *Gnamptogenys striatula* is widely distributed in Brazil and is commonly collected in the soil of practically all environments in the country. It is a predator of other arthropods, and nests on tree trunks, litter, and in the uppermost layers of the soil (Lattke 1990; Camacho 2013).

Our results showed that there is a negative correlation between ant species richness and latitude in Paraná. These results are in agreement with expectations that ant richness typically declines with increasing latitude based on previous studies done at regional scales (Gotelli and Ellison 2002; Pfeiffer et al. 2003). However, this pattern is the inverse of that found in the Brazilian Cerrado by Vasconcelos et al. (2018) and in the Atlantic Forest biome by Silva and Brandão (2014), where the greatest richness was found at higher latitudes. This result may be because in the state of Paraná the heterogeneity of the vegetal formations increases as the latitude decreases. In addition, the colder climate found in this region can certainly influence this pattern of richness (Overbeck et al. 2007).

The RCP grassland reserve presented the lowest species richness herein (55 species). The number of species found in this grassland area (55) is similar to that found in nearby areas with a similar climate and physiognomy, and where, on average, approximately 60 species were recorded (Marinho et al. 2002; Albuquerque and Diehl 2009; Rosado et al. 2012; Boscardin et al. 2013; Lutinski et al. 2013). The number of species found at the RCP grassland was much lower than that found in the grasslands from Campos Gerais region (PEV: 115; PEG: 112 species). Contrasting with the Southern grasslands, where RCP is located, in the Campos Gerais, the herbaceous stratum is not continuous, but rather interrupted by patches of shrubs and small trees. Consequently, vegetation complexity in the Campos Gerais grasslands is greater than in the southern grasslands, a factor that must certainly had a strong influence on the ant species richness patterns observed here.

Despite being located in the Campos Gerais grasslands zone, the dominant vegetation at PEC is Cerrado savanna. The Cerrado is the second largest biome in the country (Bridgewater et al. 2004). However, it has very little representation in the state of Paraná, the southern limit of this biome (Uhlmann et al. 1998; Bridgewater et al. 2004). The number of species found at the PEC (129 species) is similar to that found in the savannas located at the core area of the Cerrado biome, where the total number of species recorded ranged from 59 to 144 (Vasconcelos et al. 2018).

The number of species collected in the grasslands of Paraná during the present study can be considered high because this is a subtropical region, where ant diversity is expected to be much lower than in tropical regions (Kusnezov 1957). However, as Kaspari (2000) has pointed out, grassland formations in regions with colder climates tend to have a relatively high ant species richness, possibly because ants are thermophilic animals and, consequently, benefit from living in more open areas due to the higher incidence of sun at the soil surface. In addition, the natural grasslands of Southern Brazil, which includes the Campos Gerais and highland grasslands studied here, are old and stable. Stable areas such as those tend to present high levels of species richness and endemism (Andrade et al. 2019).

Despite the relative high ant richness found here, only the epigaeic fauna was sampled, and thus a significant increase in the number of species could be expected if other nesting and foraging strata, such the arboreal or the underground, were

sampled. Even so, the present study added ten new species to the fauna of Paraná, expanding our knowledge of the distributions of many ant groups. It is important to note also that many of the collected species could not be namely identified and thus may constitute additional records to the state or even new species, to be formally described in the future.

## Composition

Our results show that the composition of the ant fauna is distinct between the two different grassland formations in the state of Paraná. The ant faunas of the PEV, PEG, and PEC grasslands (Campos Gerais) were more similar to each other than to the RCP grassland, with differences between any two grasslands being attributed largely to species turnover rather than to nestedness. This result may be again because of the latitudinal gradient in the heterogeneity of the vegetation, which increases as the latitude decreases.

The natural grasslands of Paraná are located in the southern part of the Atlantic Forest biome, and throughout the extent of this physiognomy, they are composed of mosaics in combination with other types of vegetation formations (Overbeck et al. 2015b). In the region of the second plateau, the Mixed Ombrophilous Forest exerts a strong influence on the local environment (Carmo et al. 2007), and in the northernmost areas of the state, the occurrence of grasslands intermixes with the distribution of the Cerrado biome (Ritter 2008). Therefore, it is possible to observe that the studied region is a heterogeneous environment, with the complexity of the vegetal formations present increasing along a gradient that starts with the open grasslands in the southwest and extends to the savannas (cerrado) in the north. This heterogeneity of physiognomies can influence the composition of species in the grasslands there, since it provides a greater availability of different niches and resources (Alonso 2000).

In the RCP reserve, the physiognomy of open fields predominates, a plant formation in which a continuous herbaceous stratum dominates the landscape and there is a low density of small shrubs. A habitat with lower vegetation complexity presents a lower availability of nesting sites, which significantly reduces ant species diversity (Lassau and Hochuli 2004). The open grassland areas in the studied region continue up to the Devonian Escarpment region on the second plateau. The area of the PEV, however, presents a mixed physiognomy, with large patches of forest and "dirty" grassland areas. This formation is characterized by an herbaceous stratum interrupted by larger trees and shrubs at varying densities. The influence of the forest fragments on this area is reflected in the composition of the ant fauna there, since we found species there that are commonly collected in forests, as well as in cryptic and specialized habits.

The open grassland formation continues northward within the Devonian Escarpment, and the PEG is characterized by the dominance of this physiognomy. However, there is still an influence of dirty grasslands in this region, although to a lesser extent than that in PEV, and some portions of the area are covered by Cerrado vegetation. Therefore, the PEG represents a transition between grassland physiognomies within the Atlantic Forest domain and the Cerrado biome. This is reflected in the composition of the species in this area. The PEG shares species with the two adjacent areas (PEV and PEC). In PEG, we sampled species commonly found in open grassland areas, but also other species that are found in Cerrado areas. An example is *Centromyrmex brachycola* (Roger, 1861), an obligatory termite predator species, which was sampled only in PEG and PEC.

Some of the species sampled exclusively in PEG and PEC can also be found in other Cerrado areas in Brazil. In this study, the species *Cyatta abscondita* Sosa-Calvo et al. 2013 was recorded for the first time in the state of Paraná (Oliveira et al. 2016). *Cyatta* Sosa-Calvo et al. 2013 is a monotypic genus of fungus-farming ants that live in areas with sandy soil and low vegetation cover, mainly in the Cerrado and Caatinga biomes (Sosa-Calvo et al. 2013). Another species sampled that has a similar life habit was *Mycetagroicus cerradensis* Brandão and Mayhé-Nunes 2001. *Mycetagroicus* species are also fungus-farming ants found in the Cerrado, and which usually nest in sandy areas (Brandão and Mayhé-Nunes 2008). Species with arboreal habits, such as those of the genera *Crematogaster* and *Cephalotes*, were also sampled in PEG and PEC, indicating an influence of the forest vegetation on the composition of the ant fauna in these areas.

The areas of the Campos Gerais present a similar species composition, which is different from that of the grasslands of the southwest. We found a significative number of endemic components of the ant fauna in the different grassland formations. In the open grasslands of the southwest, we found a higher number of ant species typical of open areas. In the Campos Gerais, the ant composition changes, with a higher number of forest-adapted species, probably due to an increase in the complexity of the vegetation (Table S2).

According to Ab'Sáber (2003), Brazil is composed of sets of landscapes that did not evolve separately. Therefore, the physiognomic domains are not clearly delimited in Brazil, and the limits to these domains are typically represented by transition zones rather than clear boundaries. Inside these zones, elements of the different domains intermix and alternate, so the combination of these elements could form a third intermediate type of landscape. In this sense, the natural grasslands of Paraná could act not only as transitional areas between the Atlantic Tropical Forest domain and the Cerrado biome, but also represent a singular and isolated ecosystem. Many of the morphospecies recorded here (46% of the total) may represent undescribed and endemic species, along species from the adjacent biomes, which may have been ecologically rearranged according to the available conditions in particular parts of the transitional zone.

In short, our study shows that the ant fauna of the grassland formations in the state of Paraná has not only elements from the Atlantic Forest and Cerrado, but also a significative number of endemic species. We hope that our findings stimulate further studies about the ant fauna of these ecologically important and endangered ecosystems.

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