UNIVERSIDADE DE BRASÍLIA
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Ecologia funcional e trófica das formigas em diferentes tipos de uso do solo: implicações para a conservação da biodiversidade

Daniel Antunes Daldegan

Orientador: Prof. Dr. Pedro Henrique Brum Togni

Brasília - DF
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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia do Instituto de Ciências Biológicas da Universidade de Brasília, como parte dos requisitos para a obtenção do título de Mestre em Ecologia

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SUMMARY

Ecologia funcional e trófica de formigas em diferentes tipos de uso do solo: implicações para a conservação da biodiversidade

RESUMO

Existem amplas evidências de que os novos ecossistemas, impulsionados pelas alterações do uso do solo, afetam negativamente a biodiversidade de fornecedores de serviços ecossistêmicos relevantes, como as formigas. Traços funcionais específicos são filtrados em tipos de habitat distintos, afetando o papel das espécies na funcionalidade do ecossistema. Consequentemente, espera-se que os efeitos de filtragem alterem a posição trófica das espécies e o comprimento da cadeia trófica. O objetivo desta dissertação foi investigar como diferentes tipos de uso do solo filtram os traços das espécies de grupos funcionais de formigas e as suas consequências para a posição trófica e o comprimento da cadeia alimentar. Nós amostramos formigas em plantações de soja em larga escala, pastagens, fazendas orgânicas e três formações de vegetação natural (Cerrado *sensu stricto*, vegetação campestre e vegetação de mata) no bioma Cerrado. As espécies foram classificadas em grupos funcionais e traços específicos relacionados ao uso do habitat e comportamento de forrageamento foram medidos, associados à análise de isótopos estáveis de carbono e nitrogênio ($\delta^{13}C$ e $\delta^{15}N$) para entender o uso de recursos e a posição trófica de grupos funcionais em tipos distintos de habitats. Os impactos negativos da agricultura sobre a diversidade taxonômica, funcional e composicional das formigas homogeneizaram as assembleias locais, fazendo com que espécies generalistas e oportunistas prevaleçam, principalmente em áreas intensamente manejadas como as lavouras de soja. O tipo de uso da terra afetou o nicho isotópico e o uso de recursos dentro dos grupos funcionais porque características relacionadas ao tamanho do corpo, comportamento de forrageamento e capacidade sensorial são filtradas de forma diferente nesses habitats. Estas características estão diretamente ligadas à posição trófica dos grupos funcionais e ao seu papel no funcionamento do ecossistema. Apesar destes efeitos adversos, a agricultura orgânica reduziu os impactos negativos na biodiversidade ao atenuar os efeitos de filtragem sobre as assembleias de formigas. Os nossos resultados revelaram que a disponibilidade de recursos e a intensidade da perturbação no habitat são os principais mediadores dos efeitos negativos da mudança de uso do solo sobre a biodiversidade de formigas. Os efeitos combinados destas características afetam o comprimento da cadeia alimentar e a posição trófica dos grupos funcionais de formigas, devido a filtragem de traços funcionais.

Palavras-Chave: Biodiversidade de formigas, intensificação agrícola, Cerrado, serviços ecossistêmicos, grupos funcionais, novos ecossistemas, isótopos estáveis, ecologia trófica.

ABSTRACT

There is broad evidence that novel ecosystems driven by land use change negatively affect the biodiversity of relevant ecosystem service providers like ants. Specific functional traits are filtered in distinct habitat types, affecting species' role in ecosystem functionality. Consequently, filtering effects are expected to change the trophic position of species and the food chain length. The aim of this dissertation was to investigate how different land use types filter the species traits of functional groups of ants and its consequences for the trophic position and food chain length. We sampled ants in large-scale soybean crops, pastures, organic farms, and three natural vegetation formations (Cerrado *sensu stricto*, grassland vegetation and forest vegetation) in the Cerrado biome. Species were classified into functional groups, and specific traits related to habitat use and foraging behavior were measured, associated with carbon and nitrogen stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) to understand resource use and trophic position of functional groups in distinct habitat types. The negative impacts of agriculture on the taxonomical, functional, and compositional diversity of ants homogenize local assemblages, making generalist and opportunistic species prevail, especially in homogeneous and intensively managed areas like soybean crops. Land-use type affects the isotopic niche and resource use within the functional groups because traits related to body size, foraging behavior, and sensory capacity are filtered differently in these habitats. These traits are directly linked to the trophic position of functional groups and their role in ecosystem function. Despite these adverse effects, organic farming reduced the negative impacts on biodiversity by alleviating filtering effects over ant assemblages. Our results revealed that resource availability and disturbance intensity within the habitat may be the main drivers of the negative effects of land use changes on the biodiversity of ants. The combined effects of these features affect the food chain length and the trophic position of ant functional groups due to the filtering of functional traits.

Keywords: Ant biodiversity, agricultural intensification, Cerrado, ecosystem services, functional groups, novel ecosystems, stable isotopes, trophic ecology.

FIGURE LIST

Figure 1. Map of the Brazilian Federal District within the Cerrado biome with the 22 sampling sites of ants in pastures, large-scale soybean crops, small organic farming areas, and native vegetation areas comprising grasslands, typical savannah (Cerrado sensu stricto), and forest vegetation types

Figure 2. Rarefaction curve based on sample size (solid lines) and sampling curve by extrapolation (dashed lines) of the taxonomic assemblages of ants by type of land use. Shades of the same color represent the upper and lower 95% confidence intervals. Nº of bootstraps = 100

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TABLE LIST

Table 1. List of species collected in the six different land uses (Soybean, Pasture, Organic farming, Typical Savannah, Forest and Grassland), their functional groups, number of sites where they were collected, abundances and which were used in the Stable Isotope Analysis (SIA)

Table 2. Diversity indices of ant assemblages (taxonomic and functional groups) between the different land uses

Table 3. PCA loadings between the measured morphological values of the ants

1 | INTRODUCTION

The novel ecosystems emerging from land use changes caused by agriculture expansion threaten biodiversity and ecosystem services loss globally (Cardinale et al., 2012), especially in the tropics (Newbold et al., 2015; Ramos et al., 2020). The structural and compositional changes caused by these novel ecosystems homogenize local taxonomical and functional diversity due to the filters imposed by reduced resource availability and environmental conditions (Cardoso et al., 2020). Consequently, niche breadth and trophic position of species assembling in distinct habitats may vary among land use types (Kraft et al., 2015), creating a mosaic of habitats where species play different roles in ecosystem functioning, depending on habitat features, history, and management intensity (Le Provost et al., 2020).

Ants (Hymenoptera: Formicidae) are relevant ecosystem service providers with abundant scientific evidence on the negative impacts of land use change in this group diversity (Woodcock et al., 2013; Pacheco et al., 2017; Wilker et al., 2024). They are a diverse group in natural and anthropized habitats in the tropics (Baccaro et al., 2015), playing essential role in nutrient cycling, herbivory (Swanson et al., 2019), soil aeration (Leite et al., 2018), biological control (Frizzo et al., 2020), and secondary seed dispersal (Béllo et al., 2023). Ant species have variable feeding habits ranging from nectar feeding or strictly carnivorous to omnivory, positioning them on distinct functional groups (Rabello et al., 2021) and trophic levels (Ribeiro et al., 2019). Anthropogenic disturbances can cause changes in both basal (e.g., herbivory) and higher trophic levels (e.g., predation) in ant assemblages (Woodcock et al., 2013; Helms et al., 2021).

Recent meta-analyses point to a downward trend in ant species richness due to land use changes in forest (Amazon and Atlantic Rainforest) and savanna (Cerrado) biomes in tropical regions (Wilker et al., 2024). These adverse effects also impact the abundance (Wilker et al., 2024) and composition of ant assemblages, generating losses in the ecosystem services provided (Pacheco et al., 2017). Typically, agricultural systems disproportionately benefit generalist and opportunistic species at the expense of specialists, large predators, and arboreal species due to simplification or change of habitat, which consequently affects trophic relationships (Rocha & Fellowes, 2020; Kreider et al., 2021), but the precise ecological mechanisms driving these patterns are not yet fully understood. There is some evidence that soil management (plowing), pesticide application, presence of exotic grasses, and reduced availability of nesting sites may be the primary filters of species traits (Pacheco et al., 2013).

Using ants as bioindicators may help understand how land use changes filter specific traits and their effects on species' trophic position in different habitat types. Over the last decades, the use of carbon and nitrogen stable isotope ratios has become commonplace and related to some aspects of ecological niches, such as resource use and trophic behavior (Shipley & Matich, 2020). Carbon isotope values, expressed as $\delta^{13}C$, of body tissues reflect the isotopic composition of food sources assimilated by the organism during the formation of those tissues (Fry 2006). C3 and C4 plants fractionate carbon from the atmosphere through distinct photosynthetic pathways, resulting in average $\delta^{13}C$ values of –26.5‰ and –12.5‰, respectively (Farquhar et al. 1989). While nitrogen isotope ratios, expressed as $\delta^{15}N$, often reflect animal trophic position within a food web (Hyodo et al. 2015), with enrichment of ^{15}N primarily driven by the excretion of nitrogenous, ^{14}N-enriched waste, combined with the consumption of more ^{15}N-enriched prey (Fry 2006). In general, every 3‰ increase of $\delta^{15}N$ along the trophic chain indicates a change in the trophic level (Cabana & Rasmussen, 1994). Consumers also vary in their diet and the way in which they integrate $\delta^{15}N$ variation over space and time into their own tissues (Post, 2002). The combined use of $\delta^{13}C$ and $\delta^{15}N$ can help understand the complex interactions between ants and their food resources in distinct habitat types to reveal the ecological mechanisms underlying the adverse effects of land use change on biodiversity.

Ants are closely linked to the local environmental conditions, partitioning their habitats in time and space in natural areas (Costa et al., 2018). Therefore, resource availability and composition directly affect ant assemblage taxonomic and functional composition (Fichaux et al., 2019). Possibly, the conversion of native areas to agriculture and livestock will decrease species diversity and alter assemblage composition because filtering effects favor the occurrence of generalist and opportunistic species. The main functional traits filtered should be those related to the foraging behavior and body size of ants due to resource homogeneity and tolerance to harsh conditions. Filtering effects may be more prominent in homogeneous and highly disturbed habitats, like large-scale monocultures. Ultimately, the trophic position and the food chain length of different functional groups of ants are expected to be dictated by land use type.

To test these hypotheses, we evaluated how different land use types filter the species traits of functional groups of ants and its consequences for their isotopic niche and trophic position. Specifically, we seek to answer: 1. How do different land use types affect ants' taxonomic, functional, and compositional diversity? 2. Do these differences affect the use of resources and the trophic position of functional groups in different habitat types? 3. Which traits are filtered on anthropized habitats varying in frequency of disturbance and resource availability? 4. How do the filtering effects of specific traits affect the trophic level of different functional groups?

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted from February 2013 to May 2014 in 22 sites encompassing different land use types in the Brazilian Federal District (15°47'S, 47°55'W), covering an area of approximately 5800 km² (Figure 1). The study areas were in the Cerrado biome, the Brazilian tropical savannah. This is the second largest biome in the country (~ 2 million km²) (IBGE, 2004) and a priority hotspot for biodiversity conservation severely threatened by agricultural expansion (Myers et al., 2000), especially for soybean plantation and livestock (~70 Mha) (Sano et al., 2019; Song et al., 2021). To a lesser extent, small-scale organic farming (up to 70 ha), with predominantly vegetable crops, is also present in diversified farming systems (MapBiomas, 2024).

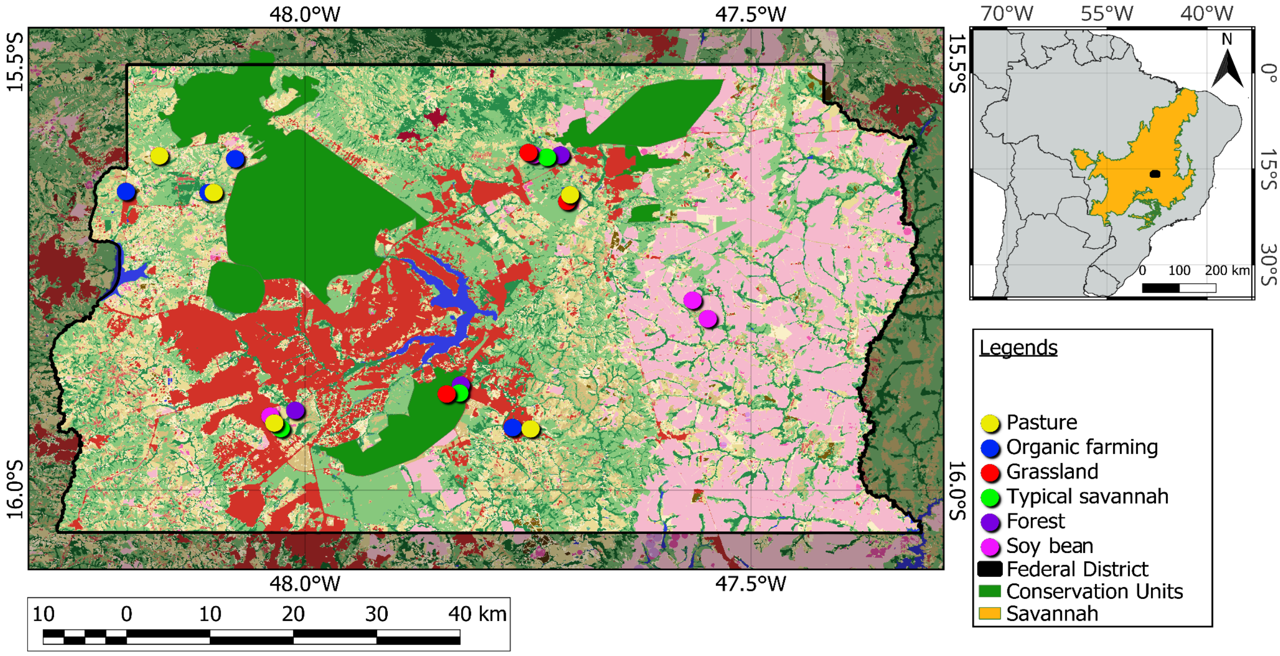


FIGURE 1 Map of the Brazilian Federal District within the Cerrado biome with the 22 sampling sites of ants in pastures, large-scale soybean crops, small organic farming areas, and native vegetation areas comprising grasslands, typical savannah (Cerrado sensu stricto), and forest vegetation types

The Cerrado is composed of a mosaic of plant formations varying from grasslands and savannas to forests (Ribeiro & Walter, 2008). In forest formations, tree species dominate and are usually close to river courses. Savannah formations have 20–70% tree and shrub cover, interspersed with a broad graminoid stratum. Grassland areas are formed by a graminoid stratum and low tree and shrub cover (<5%) (Ribeiro & Walter, 2008). The region's climate is Aw (rainy tropical), according to the Köppen classification, with a marked rainy summer (October~March) and a dry winter (April~September). Average annual temperatures range between 22°C and 27°C, and average annual rainfall is 1400 mm (Cardoso et al., 2014).

In the Brazilian Federal District, soybean crops and pastures occupy ~27% of the territory (EMATER, 2023; MapBiomas, 2024). There are also several small organic farmers with areas ranging from 4 ha to 70 ha that occupy ~0.35% of the agricultural area in the region (CODEPLAN, 2015). Three large permanent conservation units with the region's most important remnants of Cerrado are present in the Federal District. According to Brazilian legislation, at least 20% of the agricultural areas are compulsorily committed to native vegetation conservation (Brasil, 2012). Therefore, most of the remnants of native vegetation are located inside private properties (Soares-Filho et al., 2014).

2.2 | Experimental design and sampling

To understand how land use affects the richness, abundance, and composition of ant assemblages, 100 m-long transects were established in 22 sites representing the different types of land use in the region (Figure 1). Large-scale soybean crop areas (n = 4) were chosen due to their significant presence among the cultivated areas in the Federal District and the annual increase in their disturbance levels due to annual harvests and pesticide applications. Pastures (n = 5) also represent a large portion of the anthropized areas but with lower disturbance intensities due to simplified management and a predominance of grasses. Organic farms (n = 4) are more heterogeneous habitats occupying smaller areas and do not use chemical pesticides, possibly reducing the impacts on biodiversity. The native areas, inside and outside protected areas, represent the different types of Cerrado plant formations (n = 9, being three savannah areas, three grasslands, and three forests), which can present different compositions of ant assemblages (Baccaro et al., 2015). In each transect, one per location, 10 pitfall traps were installed 10 m apart. The traps comprised 200 ml plastic cups containing 100 ml of 70% alcohol solution and 0.5% detergent. The use of detergent proved necessary to increase the efficiency of the trap by breaking the surface tension of the water, causing the immediate submersion of the insects and reducing the evaporation of the alcohol solution. The traps remained active in the field for 24 hours. Samples were then taken to the laboratory and washed in running water to minimize possible detergent contamination; insect specimens were sorted, identified, and stored at -20ºC. The individuals collected were identified to the lowest possible taxonomic level using Bolton et al. (2007) and Fernández (2003) and with the assistance of a taxonomist.

2.3 | Functional classification

To understand how land use change affects the functional composition of ant assemblages, the specimens collected were functionally classified according to the classification proposed for the Neotropics (Silvestre, Brandão & Silva, 2003; Silva & Brandão, 2010). These classifications are discrete measures based on the species' functional traits related to ant morphology and niche measures that potentially affect their interactions within the habitats (McGill et al., 2006). Specifically, the classifications combine the use of traits related to the trophic position (e.g., predator, fungivore and omnivore), diet breadth specificity (specialist and generalist), foraging traits related to habitat use and stratification (arboreal, epigaeic and hypogaeic), habitat specificity (specialist, generalist and opportunist) and foraging behavior (cryptic, scavenger, patroller and scavenging). As a result, we identified 15 different functional groups (Table 1).

TABLE 1 List of species collected in the six different land uses (Soybean, Pasture, Organic farming, Typical Savannah, Forest and Grassland), their functional groups, number of sites where they were collected, abundances and which were used in the Stable Isotope Analysis (SIA)

Subfamily	Species	Functional group	Nº of sites	Abundance	Used in SIA
Myrmicinae	*Acromyrmex* cf. *balzanii*	Fungivorous leaf cutters	1	1	No
Myrmicinae	*Acromyrmex* sp01	Fungivorous leaf cutters	3	8	Yes
Formicinae	*Acropyga* sp01	Minimal soil specialists	3	5	No
Myrmicinae	*Apterostigma* sp01	Fungivorous cryptic attines	2	4	Yes
Myrmicinae	*Atta* sp01	Fungivorous leaf cutters	5	15	Yes
Dolichoderinae	*Azteca* sp02	Small arboreal with massive recruitment	1	1	No
Formicinae	*Brachymyrmex* sp01	Ground and arboreal opportunists	11	110	Yes

Formicinae	*Brachymyrmex* sp02	Ground and arboreal opportunists	8	18	No
Formicinae	*Brachymyrmex* sp03	Ground and arboreal opportunists	11	382	Yes
Myrmicinae	*Cardiocondyla emeryi*	Soil omnivorous	1	9	No
Myrmicinae	*Cardiocondyla* sp01	Soil omnivorous	1	4	No
Myrmicinae	*Carebara urichi*	Hypogaeic specialist	3	16	No
Myrmicinae	*Cephalotes atratus*	Omnivorous arboreal	1	1	Yes
Myrmicinae	*Cephalotes pusillus*	Omnivorous arboreal	2	4	Yes
Myrmicinae	*Crematogaster limata*	Omnivorous arboreal	1	9	No
Myrmicinae	*Crematogaster* sp03	Omnivorous arboreal	1	1	No
Myrmicinae	*Crematogaster* sp06	Omnivorous arboreal	6	45	Yes
Myrmicinae	*Crematogaster* sp11	Omnivorous arboreal	3	95	Yes
Myrmicinae	*Crematogaster* sp12	Omnivorous arboreal	1	4	No
Myrmicinae	*Crematogaster* sp13	Omnivorous arboreal	1	2	No
Myrmicinae	*Cyphomyrmex lectus*	Fungivorous cryptic attines	1	1	No
Myrmicinae	*Cyphomyrmex rimosus*	Fungivorous cryptic attines	4	6	No
Myrmicinae	*Cyphomyrmex* sp04 gr. *rimosus*	Fungivorous cryptic attines	2	7	No
Dolichoderinae	*Dorymyrmex* cf. *brunneus*	Soil omnivorous	11	357	Yes
Dolichoderinae	*Dorymyrmex* cf. *jheringi*	Soil omnivorous	5	19	Yes
Dolichoderinae	*Dorymyrmex* sp01	Soil omnivorous	5	11	No
Ectatomminae	*Ectatomma brunneum*	Generalist epigaeic predators	5	13	Yes
Ectatomminae	*Ectatomma edentatum*	Generalist epigaeic predators	3	24	Yes
Ectatomminae	*Ectatomma opaciventris*	Generalist epigaeic predators	3	11	No
Ectatomminae	*Gnamptogenys* sp01	Generalist epigaeic predators	1	29	Yes
Ectatomminae	*Gnamptogenys* sulcata	Generalist epigaeic predators	3	6	Yes
Formicinae	*Camponotus atriceps*	Omnivorous arboreal	2	3	No

Formicinae	*Camponotus cingulatus*	Generalist patrol Camponotini	3	15	No
Formicinae	*Camponotus* gr. *blandus*	Generalist patrol Camponotini	5	16	No
Formicinae	*Camponotus* gr. *senex*	Generalist patrol Camponotini	4	8	No
Formicinae	*Camponotus lespesii*	Generalist patrol Camponotini	1	1	No
Formicinae	*Camponotus leydigi*	Generalist patrol Camponotini	2	3	No
Formicinae	*Camponotus novagrandensis*	Generalist patrol Camponotini	2	6	No
Formicinae	*Camponotus personatus*	Generalist patrol Camponotini	5	28	No
Formicinae	*Camponotus renggeri*	Generalist patrol Camponotini	1	2	No
Formicinae	*Camponotus rufipes*	Generalist patrol Camponotini	8	57	No
Formicinae	*Camponotus sericeiventris*	Generalist patrol Camponotini	1	1	No
Formicinae	*Camponotus* sp12	Generalist patrol Camponotini	5	30	No
Formicinae	*Camponotus* sp16	Generalist patrol Camponotini	5	41	No
Formicinae	*Camponotus* sp17	Generalist patrol Camponotini	1	1	No
Formicinae	*Camponotus* sp18	Generalist patrol Camponotini	4	5	No
Formicinae	*Camponotus* sp28	Generalist patrol Camponotini	1	1	No
Formicinae	*Camponotus substitutus*	Generalist patrol Camponotini	2	2	No
Myrmicinae	*Hylomyrma* sp02	Soil omnivorous	1	9	Yes
Ponerinae	*Hypoponera* cf. *foreli*	Specialist cryptic predators	2	4	Yes
Ponerinae	*Hypoponera* sp01	Specialist cryptic predators	7	31	Yes

Ponerinae	*Hypoponera* sp03	Specialist cryptic predators	1	18	Yes
Dorylinae	*Labidus coecus*	Legionary	5	195	Yes
Dorylinae	*Labidus praedator*	Legionary	2	551	Yes
Ponerinae	*Leptogenys* sp01	Legionary	1	1	No
Dolichoderinae	*Linepithema* cf. *cerradense*	Omnivorous arboreal	10	144	Yes
Dolichoderinae	*Linepithema* cf. *gallardoi*	Omnivorous arboreal	1	14	Yes
Dolichoderinae	*Linepithema* cf. *neotropicum*	Omnivorous arboreal	1	20	Yes
Dolichoderinae	*Linepithema micans*	Omnivorous arboreal	8	70	Yes
Dolichoderinae	*Linepithema* sp05	Omnivorous arboreal	1	12	No
Myrmicinae	*Megalomyrmex silvestrii*	Soil omnivorous	1	1	No
Myrmicinae	*Mycocepurus goeldii*	Fungivorous cryptic attines	7	27	Yes
Myrmicinae	*Mycocepurus obsoletus*	Fungivorous cryptic attines	1	1	No
Myrmicinae	*Mycocepurus* sp03	Fungivorous cryptic attines	1	1	No
Myrmicinae	*Myrmicocrypta* sp01	Fungivorous cryptic attines	2	5	No
Dorylinae	*Neivamyrmex* sp02	Legionary	1	1	No
Ponerinae	*Neoponera rostrata*	Generalist epigaeic predators	1	1	No
Ponerinae	*Neoponera verenae*	Generalist epigaeic predators	11	64	Yes
Myrmicinae	*Nesomyrmex* sp3	Arboreal predator	1	1	No
Formicinae	*Nylanderia* sp01	Soil omnivorous	8	34	No
Formicinae	*Nylanderia* sp03	Soil omnivorous	3	119	Yes
Formicinae	*Nylanderia* sp04	Soil omnivorous	1	3	No
Ponerinae	*Odontomachus bauri*	Generalist epigaeic predators	2	2	Yes
Ponerinae	*Odontomachus chelifer*	Generalist epigaeic predators	5	12	Yes
Ponerinae	*Odontomachus laticeps*	Generalist epigaeic predators	4	5	Yes

Myrmicinae	*Oxyepoecus* cf. *vezenyii*	Hypogaeic omnivores and scavengers	4	72	Yes
Ponerinae	*Pachycondyla harpax*	Generalist epigaeic predators	8	19	Yes
Ponerinae	*Pachycondyla striata*	Generalist epigaeic predators	2	13	Yes
Myrmicinae	*Pheidole gertrudae*	Soil omnivorous	14	1011	Yes
Myrmicinae	*Pheidole* sp01	Soil omnivorous	18	1043	Yes
Myrmicinae	*Pheidole* sp02	Soil omnivorous	3	195	Yes
Myrmicinae	*Pheidole* sp03	Soil omnivorous	14	231	Yes
Myrmicinae	*Pheidole* sp04	Soil omnivorous	6	83	Yes
Myrmicinae	*Pheidole* sp05	Soil omnivorous	2	21	Yes
Myrmicinae	*Pheidole* sp08	Soil omnivorous	2	8	No
Myrmicinae	*Pheidole* sp09	Soil omnivorous	5	72	Yes
Myrmicinae	*Pheidole* sp10	Soil omnivorous	6	81	Yes
Myrmicinae	*Pheidole* sp11	Soil omnivorous	7	63	Yes
Myrmicinae	*Pheidole* sp13	Soil omnivorous	14	353	Yes
Myrmicinae	*Pheidole* sp16	Soil omnivorous	2	5	No
Myrmicinae	*Pheidole* sp18	Soil omnivorous	1	4	No
Myrmicinae	*Pheidole* sp19	Soil omnivorous	4	33	Yes
Myrmicinae	*Pheidole* sp20	Soil omnivorous	8	112	Yes
Myrmicinae	*Pheidole* sp22	Soil omnivorous	7	41	Yes
Myrmicinae	*Pheidole* sp23	Soil omnivorous	4	19	Yes
Myrmicinae	*Pheidole* sp24	Soil omnivorous	8	303	Yes
Myrmicinae	*Pheidole* sp26	Soil omnivorous	3	97	No
Myrmicinae	*Pheidole* sp27	Soil omnivorous	1	18	No
Myrmicinae	*Pheidole* sp28	Soil omnivorous	1	2	No
Myrmicinae	*Pheidole* sp29	Soil omnivorous	2	7	No
Myrmicinae	*Pheidole* sp31	Soil omnivorous	3	7	No
Myrmicinae	*Pheidole* sp32	Soil omnivorous	2	10	Yes
Myrmicinae	*Pheidole* sp33	Soil omnivorous	1	5	No
Myrmicinae	*Pheidole* sp34	Soil omnivorous	2	2	No
Myrmicinae	*Pheidole* sp35	Soil omnivorous	2	5	No
Myrmicinae	*Pheidole* sp36	Soil omnivorous	1	9	Yes

Myrmicinae	*Pheidole* sp42	Soil omnivorous	2	11	No
Myrmicinae	*Pogonomyrmex naegile*	Ground specialist	5	23	No
Amblyoponinae	*Prionopelta punctulata*	Specialist cryptic predators	1	2	No
Pseudomyrmecinae	*Pseudomyrmex gracilis*	Arboreal predator	2	2	No
Pseudomyrmecinae	*Pseudomyrmex pallidus*	Ground and arboreal opportunists	1	1	No
Pseudomyrmecinae	*Pseudomyrmex termitarius*	Ground specialist	2	4	Yes
Ponerinae	*Rasopone* sp01	Soil omnivorous	2	2	No
Myrmicinae	*Sericomyrmex* sp01	Fungivorous cryptic attines	1	1	No
Myrmicinae	*Solenopsis* cf. *loretana*	Soil omnivorous	2	20	No
Myrmicinae	*Solenopsis saevissima*	Soil omnivorous	7	318	Yes
Myrmicinae	*Solenopsis* sp01	Soil omnivorous	17	241	Yes
Myrmicinae	*Solenopsis* sp02	Soil omnivorous	2	3	No
Myrmicinae	*Solenopsis* sp03	Soil omnivorous	3	25	Yes
Myrmicinae	*Solenopsis* sp04 pr. *loretana*	Soil omnivorous	6	116	Yes
Myrmicinae	*Solenopsis* sp08	Soil omnivorous	2	22	Yes
Myrmicinae	*Solenopsis tridens*	Soil omnivorous	2	18	Yes
Myrmicinae	*Strumygenys* sp01	Specialist cryptic predators	3	3	No
Dolichoderinae	*Tapinoma* sp02	Omnivorous arboreal	1	5	No
Myrmicinae	*Tetramorium* cf. *similum*	Soil omnivorous	1	1	No
Ponerinae	*Thaumatomyrmex* cf. *mutilatus*	Specialist cryptic predators	1	1	No
Myrmicinae	*Trachymyrmex* sp03	Fungivorous cryptic attines	2	2	No
Myrmicinae	*Trachymyrmex* sp05	Fungivorous cryptic attines	2	4	No
Myrmicinae	*Trachymyrmex* sp06	Fungivorous cryptic attines	1	2	No
Myrmicinae	*Trachymyrmex* sp07	Fungivorous cryptic attines	1	1	No
Myrmicinae	*Trachymyrmex* sp08	Fungivorous cryptic attines	1	1	No

Myrmicinae	*Tranopelta gilva*	Minimal soil specialists	2	3	No
Myrmicinae	*Wasmannia auropunctata*	Hypogaeic omnivores and scavengers	4	25	Yes
Myrmicinae	*Wasmannia* sp02	Hypogaeic omnivores and scavengers	1	4	No
Myrmicinae	*Wasmannia* sp03	Hypogaeic omnivores and scavengers	1	1	No

2.4 | Measures of functional traits

To understand which morphological traits of ants are filtered by different habitat types, we measured the morphological characters of six individuals from 19 species in different functional groups. Species that did not meet this minimal sample size were excluded from this analysis. We selected morphological traits related to the interaction with the habitat and the type of foraging behavior that can affect the trophic position of a particular species or functional group. The functional traits we measured were based on Fowler et al. (1991), Kaspari & Wiser (1999), Yates et al. (2014), and Gibb & Parr (2013). Specifically, we measured the following morphological traits: 1. Weber's length – the distance from the front edge of the pronotum to the lower rear edge of the mesosoma, which is a proxy for body size; 2. hind femur length – the distance between the trochanter articulation point and the distal tip of the metafemur, indicating foraging speed and ability to exploit complex habitats; 3. mandible length – the distance extending from the mandible's insertion point to the tip of its most apical tooth, related to species diet type; 4. eye length – the distance along the eye longest axis, indicating visual ability for foraging and foraging time through the day; 5. scapular length – the distance between the antennal insertion and the distal margin of the scape, which indicates the chemosensory ability and 6. inter-ocular distance – measured by the distance between the nearest edges of the two eyes, related to hunting strategy and performance. Using a standard magnification for all specimens, the measurements were taken using a stereoscopic microscope (Leica EZ4HD) in the Leica Application Suite EZ version 3.4.0.

2.5 | Stable isotope analysis

We sought to understand whether the trophic niches of ant assemblages are affected by habitat type and whether morphological traits affect the niche and trophic position of the ants using stable isotope analysis. The ants' abdomens were removed to avoid bias in the isotopic values, eliminating undigested food tissues from the analysis (Feldhaar et al., 2010). The individuals were cleaned with chloroform and methanol (2:1 ratio), dried in lyophilization chamber for 48 hours, and milled to a fine powder. The samples that reached the required weight, 0.4-0.5 mg, were packed in tin capsules and sent to the Center for Nuclear Energy in Agriculture-CENA (University of São Paulo, Piracicaba, Brazil) for measurement of the isotopic ratio of C ($\delta^{13}C$) and N ($\delta^{15}N$). If the individual masses of the ants were smaller than the equipment's reading capacity, aggregations were made of individuals of the same species within the same locality. We obtained 239 measurements from 77 species belonging to 10 functional groups. Twenty-two soil samples (1.5 mg conditioned in silver capsule) from each sampling site were also sent to stable isotope analysis to correct the isotopic values of the insects, thus eliminating possible values associated with the fertilization of some areas, such as in soybean crops and organic farming areas. The analysis was conducted on a Thermo Finnigan DELTA Plus mass spectrometer coupled to an elemental analyzer (Carlo Erba, CHN-1100).

The isotope ratios were calculated using the equation

$$\delta^{13}C \text{ or } \delta^{15}N\ (‰) = (R_{sample} - R_{standard})/R_{standard} \times 1000,$$

where R_{sample} and $R_{standard}$ represent the molar ratio between the heavy/light isotope of the analyzed sample and the standard defined by the methodology, respectively. The results are given in delta notation (δ) in parts of a thousand (‰), according to the international reference standards of atmospheric air for Nitrogen (15N:14N) and Vienna Pee Dee Belemnite (13C:12C) for Carbon. Internal standards (sugarcane leaves) are routinely interspersed with target samples to correct for mass effects and instrumental drift during and between runs. Duplicate isotopic measurements were performed on about 10% of all unknown samples and yielded an absolute difference of less than 0.3‰ for both $\delta^{13}C$ and $\delta^{15}N$. Long-term analytical error for the internal standards are of 0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$. The values obtained were used to calculate both the isotopic niche and the trophic level of the ants collected.

2.6 | Statistical analyses

All analyses were performed in the Software R version 4.3.1 (R Development Core Team, 2023). In all the analyses, abundance was obtained from the frequency of occurrence of the ant species in the pitfalls within the transects in each area. To compare the species richness of the ant assemblages in the different land use types and the species richness of functional groups, we fitted individual-based rarefaction curves using the Chao-1 estimator (Gotelli & Colwell, 2010). To complement the interpretation of the structural patterns of the taxonomic and functional diversity of ant assemblages, we also calculated Shannon's diversity index, Berger-Parker's dominance index, and Pielou's evenness (Gotelli et al., 2024). The abundance of ants and the abundance by functional group were compared between the different land use types using the Kruskal-Wallis test, followed by Dunn's post hoc test, due to the lack of normality of the data. The abundance or richness of functional groups per area was considered for the functional group analyses.

To test whether the taxonomic and functional composition of the ant assemblages differed between land use types, a Non-Metric Multidimensional Scaling (nMDS) analysis was carried out for each variable separately (Laakel et al., 2024). To check for differences in species taxonomic and functional composition, we used a Permutational Multivariate Analysis of Variance (PERMANOVA) and a Permutational Multivariate Analysis of Dispersion (PERMDISP) to check for homogeneity of variances between the groups (Anderson et al., 2008).

To model the isotopic niches of the ants in the different land uses, we calculated the standard areas of the ellipses corrected for small (<20) samples (SEAc) with a 40% confidence interval, considering the $\delta^{13}C$ and $\delta^{15}N$ values of the samples. We also calculated the width of the isotopic niche using the MCMC method, with Bayesian credibility intervals of 50, 75, and 95% using the package “SIBER” (Jackson et al., 2011). To avoid possible biases in the $\delta^{15}N$ values related to management factors, we corrected all the $\delta^{15}N$ values obtained for the ants with the $\delta^{15}N$ values obtained from the soils where the sample was collected, subtracting the two values (Cronin et al., 2015). The samples were first grouped by land use type, irrespective of species taxonomic and functional identity, to identify differences in the isotopic niche of ants in different habitat types. After that, we also modelled the isotopic niche for the functional groups soil omnivores, generalist epigaeic predators and generalist patrolling Camponotini to understand how each functional group responds to habitat type. We only used these functional groups because they were the only groups with enough mass for the stable isotope analysis and more than five samples to estimate the SEAc.

We calculated the isotopic niche overlap between land use types as proposed by Cucherousset and Villéger (2015). In short, we transformed the values of $\delta^{13}C$ and $\delta^{15}N$ into 0 and 1 based on the maximum and minimum values for each isotope in all samples, irrespective of habitat type, to ensure an equal contribution of the two isotopes in the calculations. Thus, we calculated the isotopic similarity (ISim), the ratio between the volume of the intersection and the union of the two convex hulls in the multivariate space of stable isotopes calculated by the SEAc. ISim ranges from 0 (no overlap for convex hulls) to 1 (complete overlap between convex hulls).

We estimated the trophic position of ants and calculated the number of trophic levels from the isotopic data considering the range of δ^{15}N for ants or for specific functional groups (see above) in the land use types we sampled. We considered the trophic magnification between trophic levels as ~3‰ of enrichment in δ^{15}N values. We then used the formula trophic position = $\lambda + \delta^{15}$N secondary consumer/Δn, where λ is a known trophic position (here we use 0 for soil), δ^{15}N secondary consumer is the measured value of δ^{15}N for an ant taxonomic group and Δn is the value between levels (~3‰) (Post, 2002).

After measuring the morphological traits of ants' functional groups, we fitted a Principal Component Analysis (PCA) to understand how the morphological traits influence the separation of the isotopic values of selected functional groups (Machado et al., 2024). The first principal component (PC1) scores were then extracted from the PCA. To understand how the morphological traits separating the functional groups affect the trophic position of ants, we fitted a Generalized Linear Mixed Effect Model (GLMM) using the functional groups as a random factor (Pompermaier et al., 2020). In this model, the PC1 scores were used as a predictor variable, and δ^{15}N values of the ants used in the PCA analysis were used as the response variable without any a priori classification. The error distribution used in the model was the t distribution, with an identity link function. The fit of the model was checked using residual analysis, using the DHARMa package (Hartig et al., 2024), to assess the goodness of fit of the model.

3 | RESULTS

3.1 | Diversity of ant assemblages in different types of land use

We collected 7590 individuals classified in 8 subfamilies of Formicidae, distributed in 44 genera and 135 species. The most abundant species were respectively *Pheidole* sp1 (Myrmicinae, n = 1043 individuals), *Pheidole gertrudae* (Myrmicinae, n = 1011), *Labidus praedator* (Dorylinae, n = 551), *Brachymyrmex* sp03 (Formicinae, n = 382), *Dorymyrmex* cf. *brunneus* (Dolichoderinae, n = 357) and *Pheidole* sp13 (Myrmicinae, n = 353). These species comprise ~48% of the total abundance (Table 1).

We found the highest observed (S_{obs}) and estimated (S_{est}) species richness in the grassland (S_{obs} = 76 species, S_{est} = 81.08 species), followed respectively by Cerrado sensu stricto (S_{obs} = 61, S_{est} = 78.1), organic farming (S_{obs} = 56, S_{est} = 72.5), forest (S_{obs} = 52, S_{est} = 63), pasture (S_{obs} = 51, S_{est} = 55) and soybean (S_{obs} = 12, S_{est} = 14). The grasslands also presented the highest taxonomic diversity (Shannon's diversity index - H'= 3.327), highest equitability, and lower dominance, while soybean areas had the lowest taxonomic diversity (H'= 1.67), lower equitability, and higher dominance. Other land use types presented intermediate values for these metrics and did not differ from each other (Figure 2, Table 2). Soybeans had the lowest number of functional groups per site (3), while other land use types had an average of 12.2 ± 0.37 (mean ± SD) groups per site (Figure 3, Table 2).

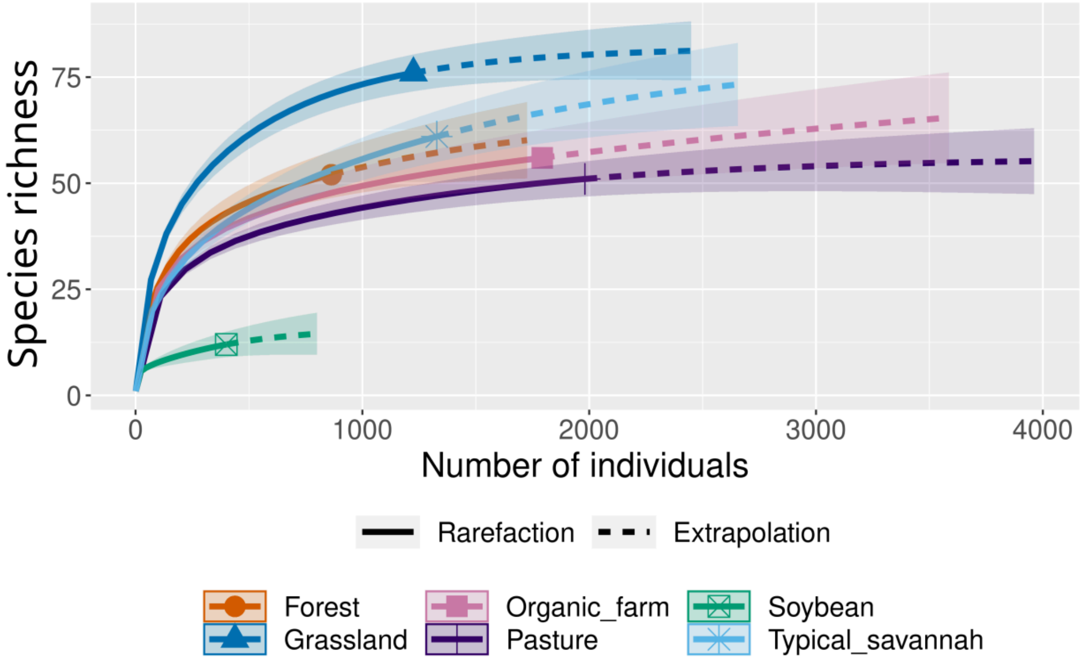


FIGURE 2 Rarefaction (solid lines) and extrapolation (dashed lines) curves based on sample size of the taxonomic assemblages of ants by type of land use. Shades of the same color represent the upper and lower 95% confidence intervals. Nº of bootstraps = 100

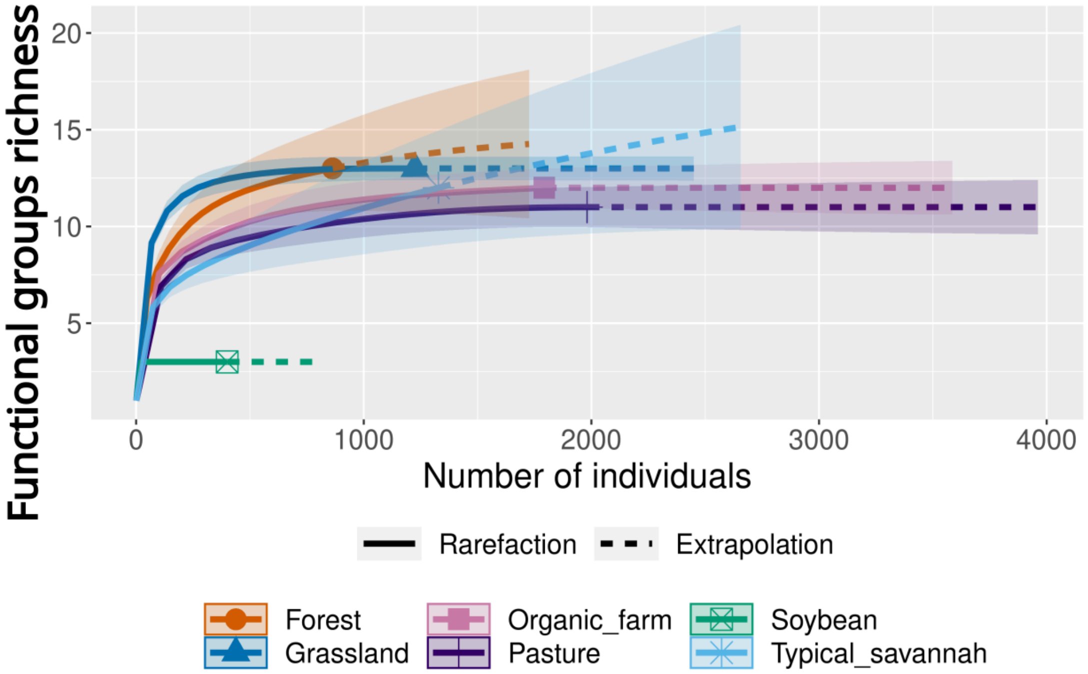


FIGURE 3 Rarefaction (solid lines) and extrapolation (dashed lines) curves based on sample size of ant functional group assemblages by land use type. Shades of the same color represent the upper and lower 95% confidence intervals. Nº of bootstraps = 100

TABLE 2 Diversity indices of ant assemblages (taxonomic and functional groups) between the different land uses

Taxonomic	Soy	Pasture	Org. farm	T. Savannah	Grassland	Forest
Richness	12	51	56	61	76	52
Abundance	400	1981	1793	1328	1225	863
Shannon_H	1.669	2.854	2.877	2.73	3.327	2.6577
Equitability_J	0.6718	0.7259	0.7148	0.664	0.7682	0.6725
Berger-Parker	0.36	0.1519	0.2627	0.247	0.1951	0.3801
Chao-1	14	55	72.5	78.1	81.08	63

Functional	Soy	Pasture	Org. farm	T. Savannah	Grassland	Forest
Richness	3	11	12	12	13	13
Abundance	400	1981	1793	1328	1225	863
Shannon_H	1.03	0.6036	1.229	0.9181	1.575	1.174
Equitability_J	0.9376	0.2517	0.4945	0.3695	0.614	0.4577
Berger-Parker	0.46	0.8788	0.5622	0.7485	0.5518	0.6721
Chao-1	3	11	12	15	13	13.5

3.2 | Abundance and taxonomic and functional composition of ant assemblages

Overall, the abundance of the ants differed between the land use types, with the highest abundance found in pastures (396.2 ± 76.47 individuals per area) and the lowest in soybeans (n = 100 ± 36.64 individuals per area) ($H = 28.53$; df = 5; $p < 0.001$) (Figure 4). However, the abundance of ants in pastures and organic farming areas, savannas, forests, and grasslands were similar but higher than in the soybean areas (Table 2). When we grouped the species into functional groups, we found no differences in the abundance of functional groups between the habitats ($H = 8.52$; df = 5; $p = 0.13$) (Table 2).

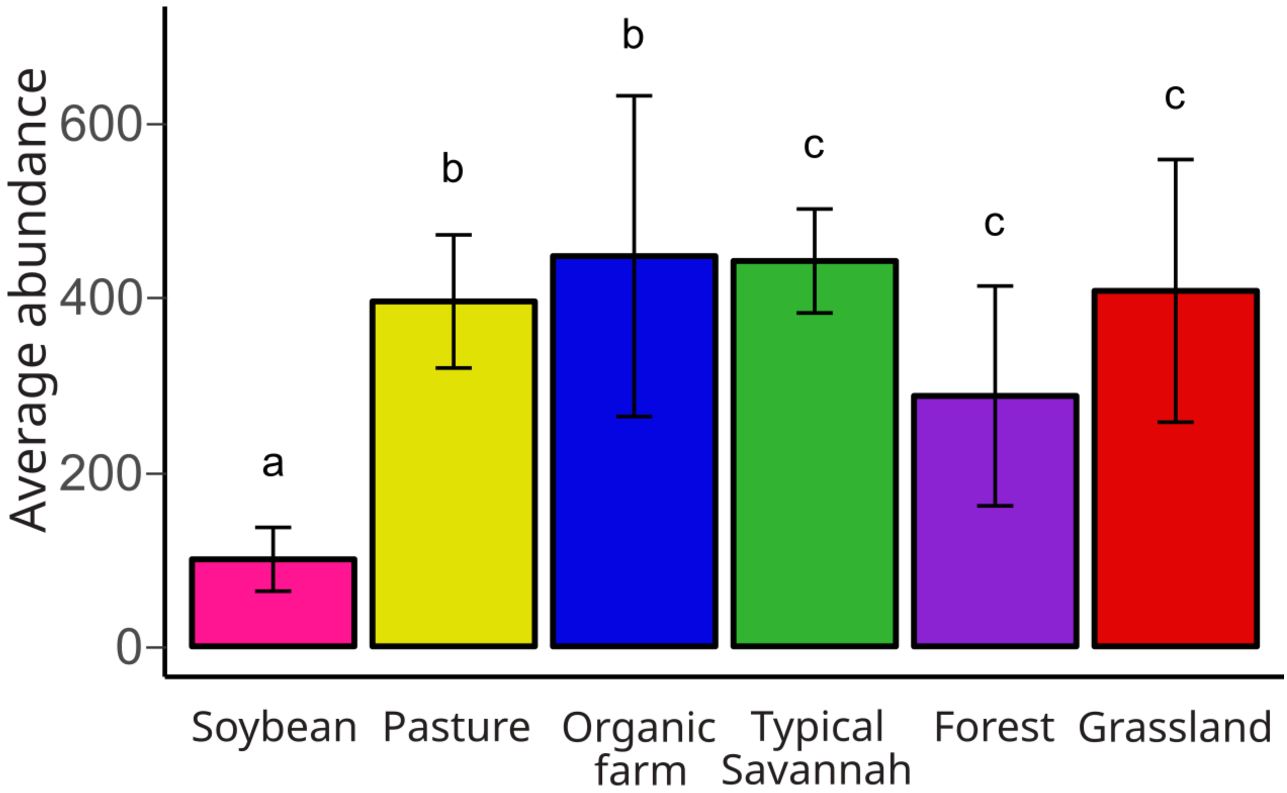


FIGURE 4 Abundance of ants (Mean ± SE) collected in different land use types in the Brazilian Federal District. Means followed by the same letter did not differ according to the Kruskal-Wallis analysis, followed by the Dunn test ($p > 0.05$). Soy = large-scale soybean crops, Pasture = pastures with cattle, Organic farm = small and diversified organic farming areas, Typical Savannah = Cerrado sensu stricto, Forest = forest areas close to watersheds, and Grassland = native grassland areas

We found differences in the taxonomic ($F = 1.79$; df = 5; $p < 0.001$) and functional ($F = 3.20$; df = 5; $p < 0.001$) composition of ant assemblages between habitat types, according to the PERMANOVA. The pastures had a different composition of ant species than the native vegetation areas and the soy plantations, and the ant assemblages on the organic farms had a different composition than the savannah areas (Figure 5a). However, only soybean crops presented a distinct functional composition from the other land use types (Figure 5b). These differences were not due to the heterogeneity within groups (PERMDISP taxonomic: $F = 1.11$; df = 5.16; $p = 0.390$; PERMDISP functional: $F = 1.45$; df = 5.16; $p = 0.250$).

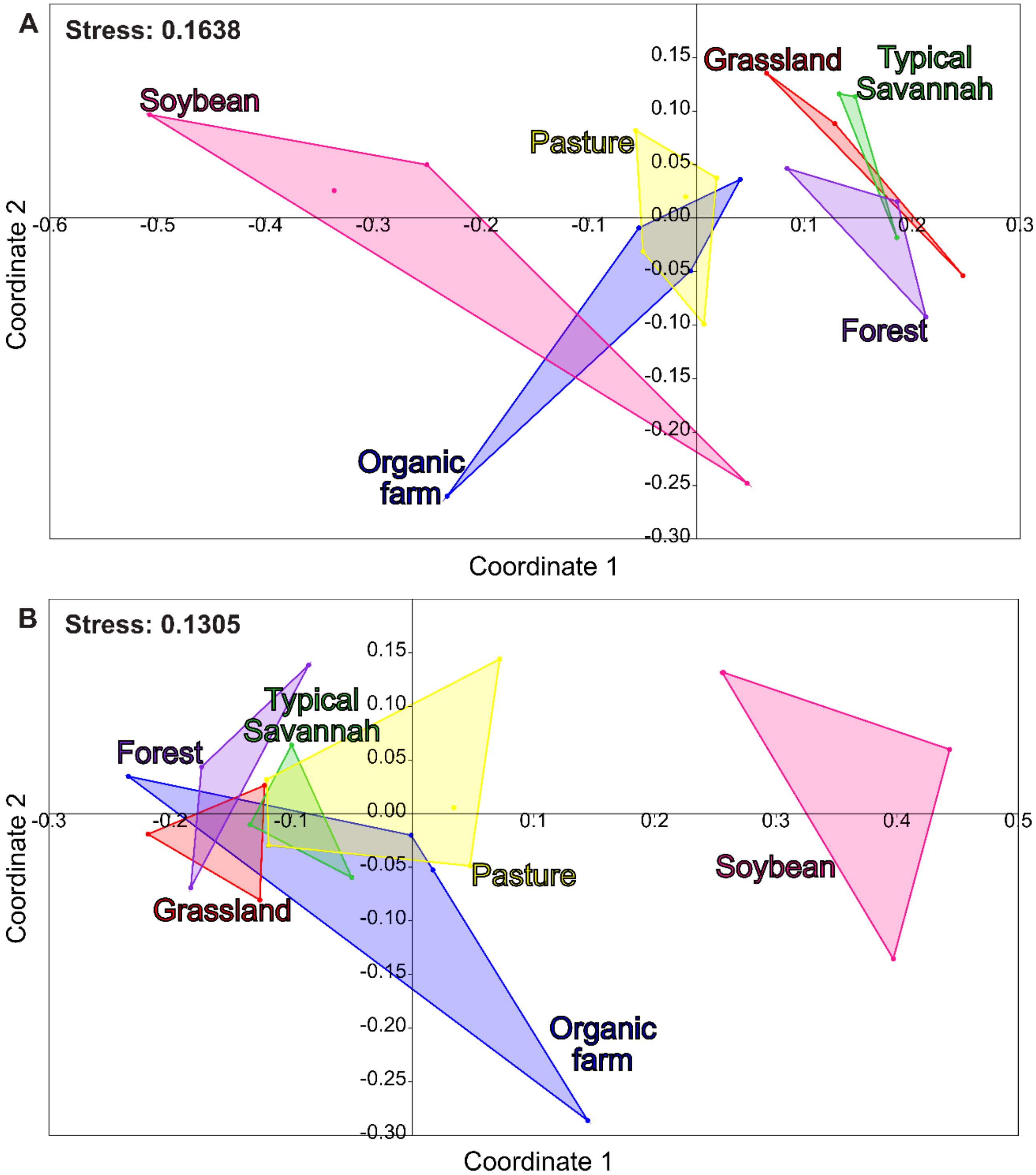
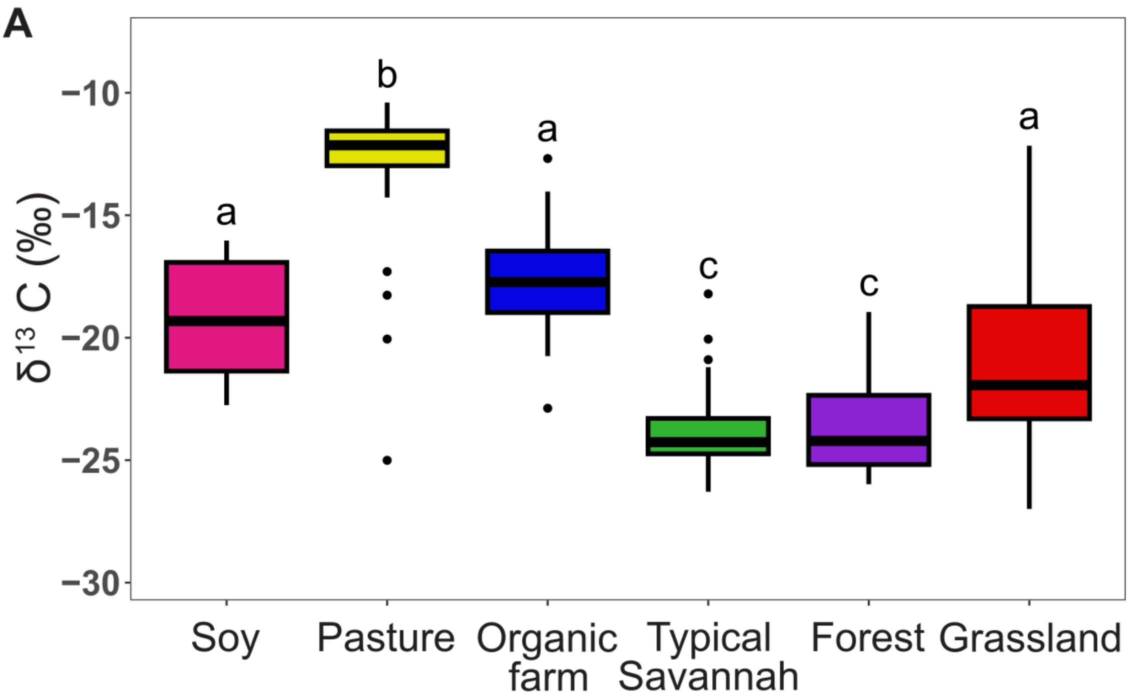


FIGURE 5 Non-metric multidimensional scaling (nMDS) ordination of ant assemblages at taxonomic level (A) and functional group level (B) at different land use types in the Brazilian Federal District, using the Jaccard index of similarity.

3.3 | Isotopic niche and trophic position of ants

We found significant differences in the isotopic values of $\delta^{13}C$ ($H = 152.58$; df = 5; $p < 0.001$) (Figure 6a) and $\delta^{15}N$ ($H = 44.451$; df = 5; $p < 0.001$) (Figure 6b) of ants in different land use types. We found the higher trophic ranges in the pastures (5.56 trophic levels; $\delta^{15}N$ = -4.4‰ – 12.3‰) and the lowest trophic range in the soybean areas (1.39 trophic levels; $\delta^{15}N$ = -0.4‰ – 3.8‰), with the other areas all showing less than 2.90 trophic levels. As for $\delta^{13}C$, the Cerrado and forest only showed values for C3 plants (Cerrado $\delta^{13}C$ = -26.3‰ – -18.2‰; forest $\delta^{13}C$ = -26.0‰ – -19.0‰). In the pastures, the predominant basal resource was more related to C4 plants, with average $\delta^{13}C$ values of -12.82 ± 6.42‰ (Figure 7a). In addition, the pasture exhibited the highest values of isotopic niche width (Figure 7b), followed by the forest, grassland and organic farm, and typical savannah. Soybean areas showed a low Standard Ellipse Area (SEA), but with a wide variation in the 95% credible intervals, suggesting no significant differences in SEA compared to these land use types, with the exception of the pasture. The isotopic niches of the ants showed high overlap (ISim > 0.88) between the areas of savannah and forest, grassland and savannah and grassland and forest, and low overlap between the areas of organic farming and forest (ISim = 0.06). However, a few individuals were responsible for a large part of these isotopic spaces (INest > 0.81) in most pairwise comparisons, except for organic farming and pastures (INest = 0.33) (Figure 8). We found significant differences between the values of both $\delta^{13}C$ and $\delta^{15}N$ among the functional groups in different land use types ($\delta^{13}C$: $H = 34.69$; df = 9; $p < 0.001$ and $\delta^{15}N$: $H = 97.31$; df = 9; $p < 0.001$) (Figure 9).



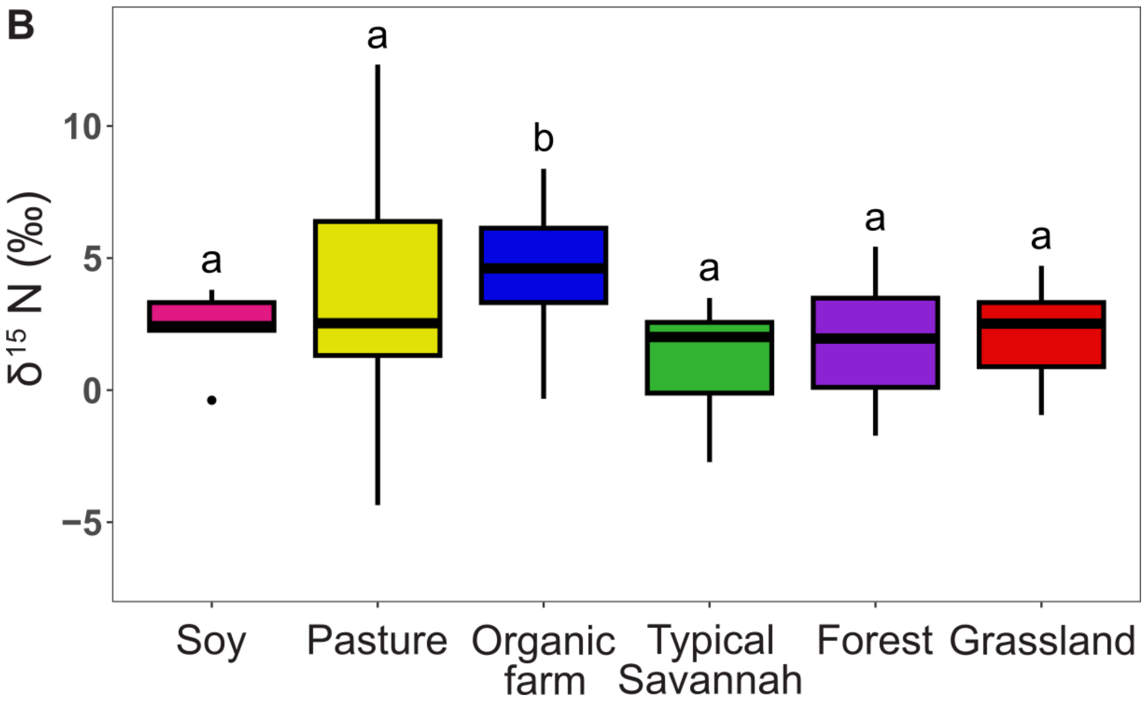


FIGURE 6 Mean values (± SE) of $\delta^{13}C$ of the ants collected in different land use types (A). Mean values (± SE) of $\delta^{15}N$ of the ants collected in different land use types (B). Means followed by the same letter did not differ according to the Kruskal-Wallis analysis, followed by the Dunn's test ($p > 0.05$)

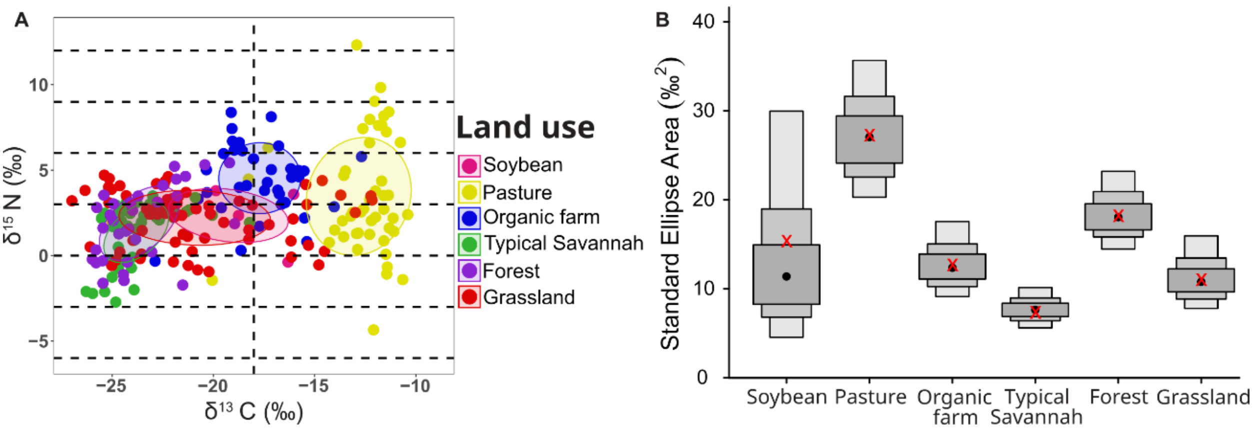


FIGURE 7 Isotopic ratios ($\delta^{13}C$ and $\delta^{15}N$) of ant assemblages collected in different land use types with their respective corrected standard ellipses (SEAc) confidence intervals for each land use type in the Brazilian Federal District (A). Horizontal axis at $\delta^{13}C$ = -18‰ represents the bending point between C3 and C4 plants. Dashed lines in the vertical axe represent changes in every 3‰ for $\delta^{15}N$, indicating a transition of trophic level. Isotopic ratios are associated with the estimate of isotopic niche space width of ant assemblages in each land use type, with 50%, 75%, and 95% (dark to light grey) confidence intervals (B). Black dots represent the median values and 'x' the centroid of the SEAc values

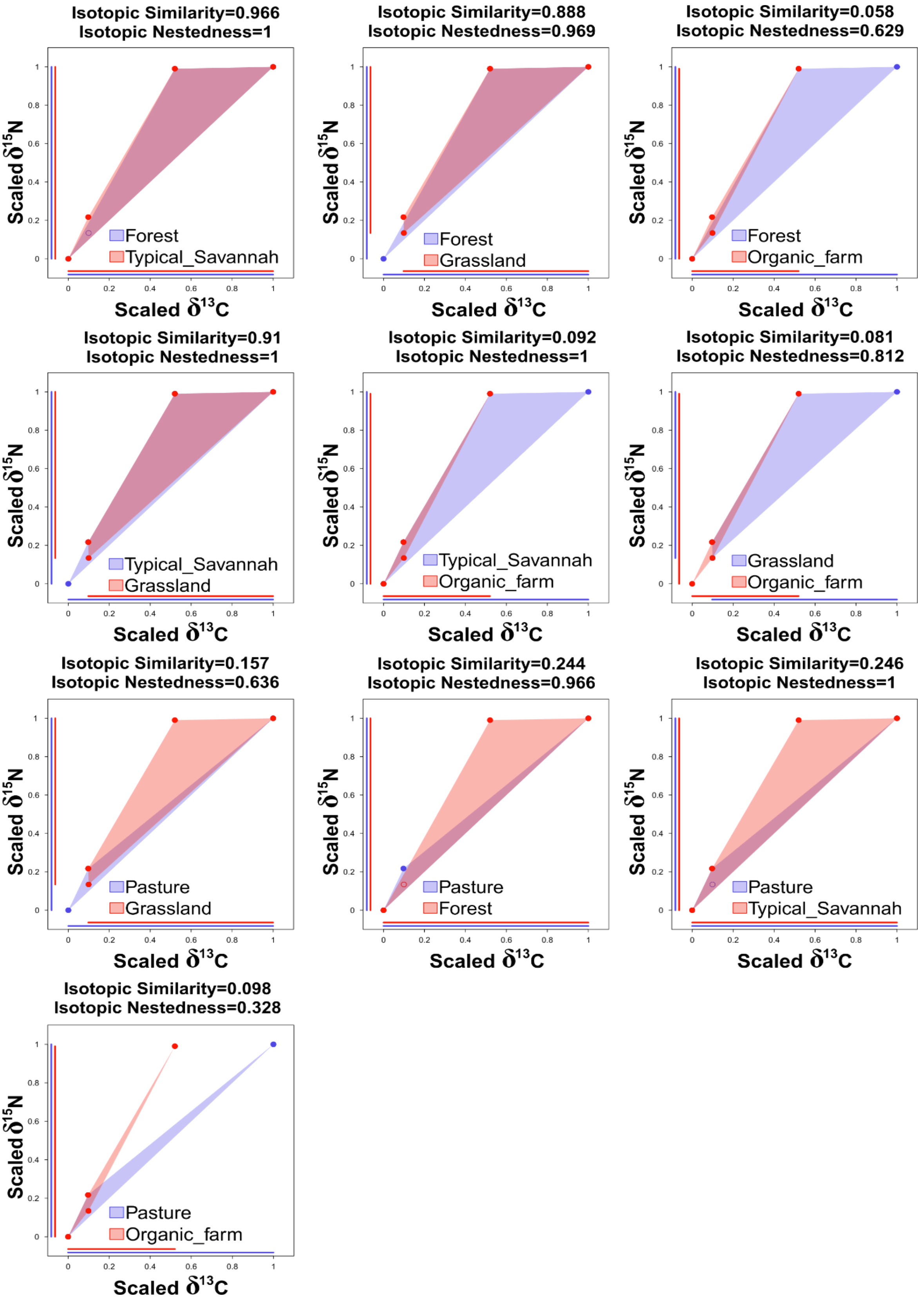


FIGURE 8 Overlapping isotopic niches of ant assemblages in different land uses. The overlaps were calculated with complementary metrics: Isotopic Similarity (ISim) and Isotopic Nestedness (INes), using the areas of the assemblages (convex hull) and the value of the shared isotopic space

(shaded intersection area). The colored bars on each axis represent the amplitudes of the stable isotopes

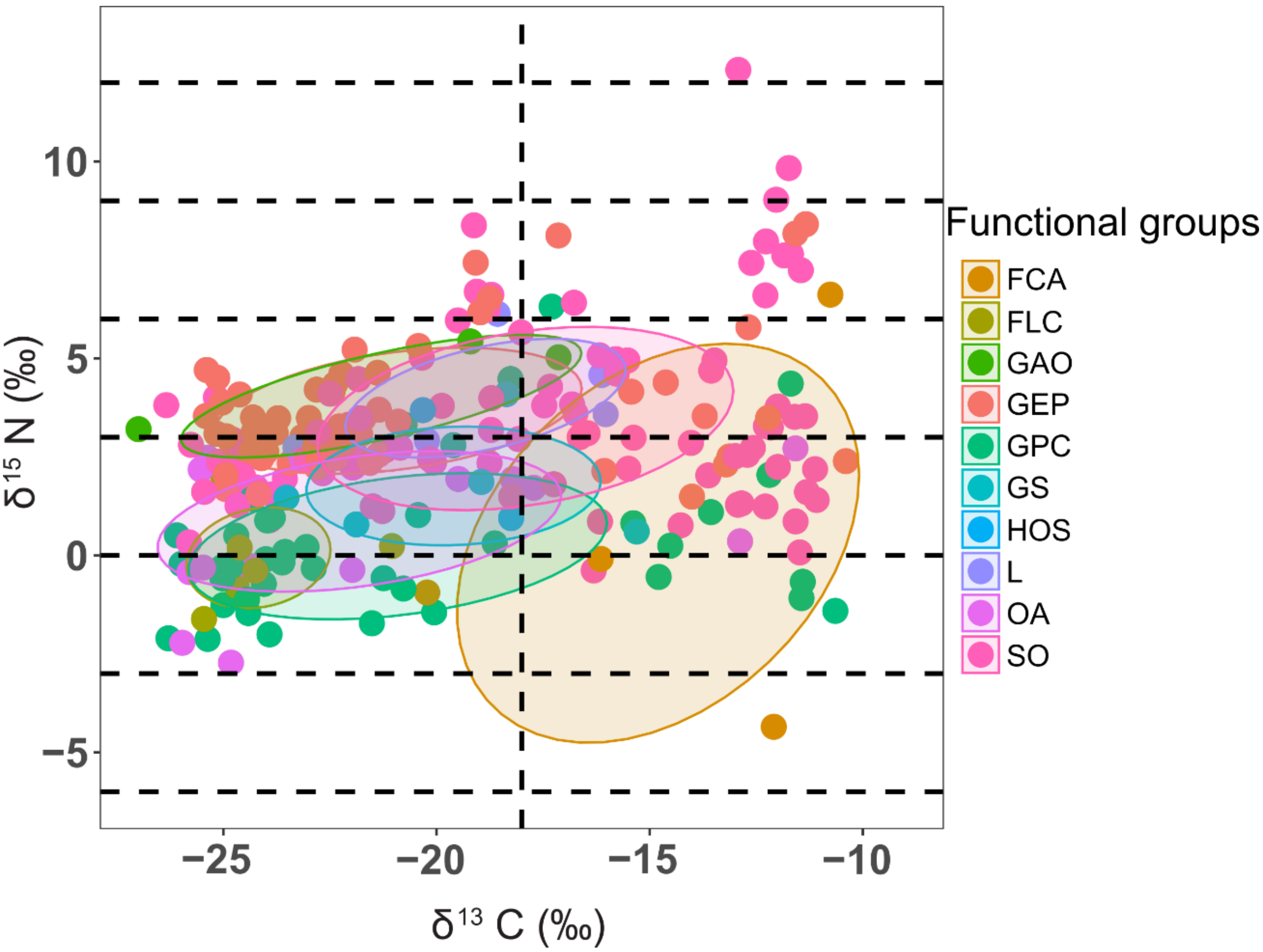


FIGURE 9 Trophic niches of the ant functional groups assemblages, irrespective of land use type (analyzed for δ^{13}C and δ^{15}N) showing the small sample size corrected standard ellipses (SEAc). Vertical line at x = -18‰, bending point between C3 and C4 plants, and horizontal lines every 3‰, average transition value between trophic levels. GEP = Generalist epigaeic predator, FCA = Fungivorous cryptic attines, FLC = Fungivorous leaf cutters, GAO = Ground and arboreal opportunist, GPC = Generalist patrolling Camponotini, GS = Ground specialist, HOS = Hypogaeic omnivores and scavengers, L = Legionary, OA = Omnivorous arboreal, SO = Soil omnivorous

Irrespective of land use type, legionary ants, omnivores, and epigaeic predators presented higher δ^{15}N values than the other groups, which did not differ from each other ($H = 95.31$; df = 7; $p < 0.001$) (Figure 10a). However, when considering land use types, soil omnivores (SO) ($F = 5.43$; df = 5.88; $p < 0.001$), generalist epigaeic predators (GEP) (F = 10.3; df = 4; p < 0.001), and generalist patrolling Camponotini (GPC) ($F = 3.35$; df = 4; $p < 0.05$) showed significantly different isotopic levels of δ^{15}N between habitat types (Figure 10b). All of them had their highest trophic level in the pasture, but the lowest levels were in soybean crops (SO), pasture (GEP), and typical savannah (GPC). However, each land use type affected functional groups differently. Soil omnivores showed the greatest trophic amplitude (4.24 trophic levels, δ^{15}N = -0.4‰ – 12.3‰), patrolling generalist Camponotini presented intermediate values (2.81 trophic levels, δ^{15}N = -2.1‰ – 6.3‰), and generalist epigaeic predators had the lower range of trophic levels (2.30 trophic levels, δ^{15}N = 1.5‰ – 8.4‰) (Figure 11).

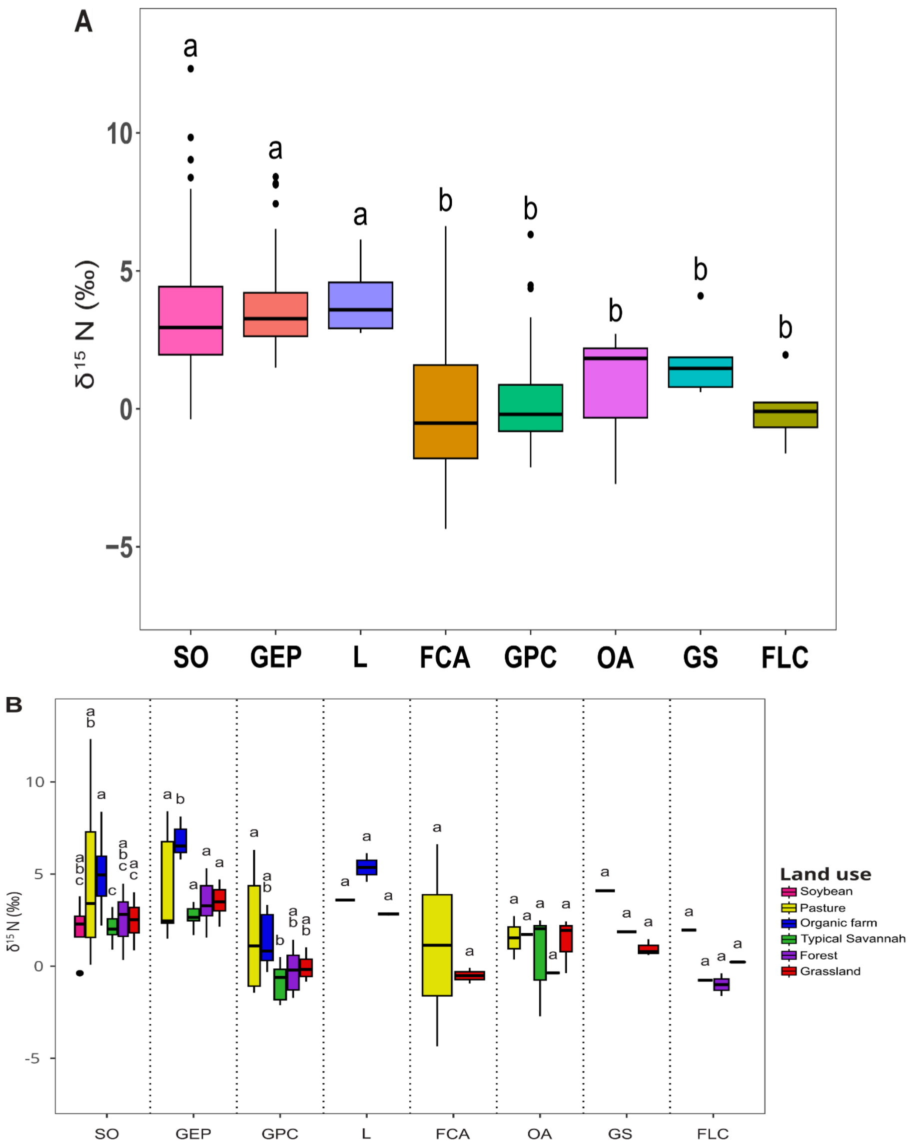


FIGURE 10 Mean values (± SE) of δ^{15}N of the ants' functional groups assemblages, regardless of land use type (A). Mean (± SE) δ^{15}N values of the ants in different land use types grouped by their functional groups assemblages (B). HOS and GAO omitted due to low number of samples per location. Means followed by the same letter did not differ according to the Kruskal-Wallis analysis,

followed by the Dunn's test ($p > 0.05$). GEP = Generalist epigaeic predator, FCA = Fungivorous cryptic attines, FLC = Fungivorous leaf cutters, GPC = Generalist patrolling Camponotini, GS = Ground specialist, L = Legionary, OA = Omnivorous arboreal, SO = Soil omnivorous

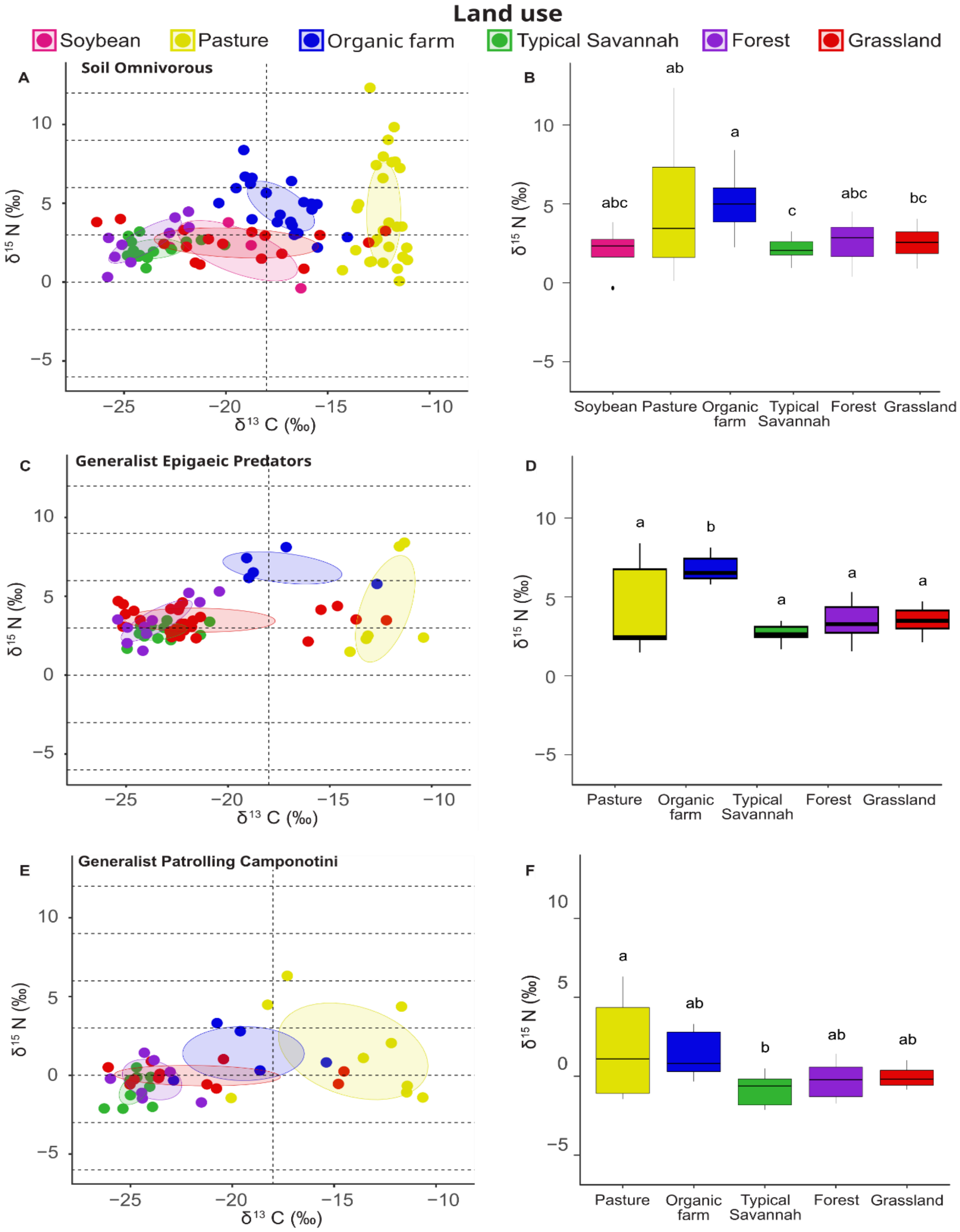


FIGURE 11 Isotopic ratios ($\delta^{13}C$ and $\delta^{15}N$) representing the isotopic niche space and width of soil omnivorous ants (A), generalist epigaeic predators (C), and generalist patrolling Camponotini (E) collected in different land use types in the Brazilian Federal District. Horizontal axe at $\delta^{13}C$ = -18‰, represents the bending point between C3 and C4 plants. Dashed lines in the vertical axe represent changes in every 3‰ for $\delta^{15}N$, indicating a transition of trophic level. Isotopic ratios are accompanied by mean values (± SE) of δ15N of omnivorous ants (B), generalist epigaeic predators

(D), and generalist patrolling Camponotini (F) comparing their trophic position in different land use types with a Kruskal-Wallis analysis. Mean followed by the same lowercase letter did not differ by post hoc Dunn test ($p > 0.05$)

3.4 | Morphological traits affecting the trophic position of functional groups

The PCA summarizing the ants´ morphological traits showed that most of the data variation is explained by component 1 (96.82% of the variation) (Figure 12). Component 1 was associated (factor loading > 0.45) with the Weber length, hind tibia length, and scape size (Table 3). The adjusted GLMM shows a strong influence of the PCA scores on the $\delta^{15}N$ values ($\beta = -0.65$; $F = 27.06$; df = 3; $p < 0.001$), indicating that the changes in the Weber length, hind tibia length, and scape size in the ants affect the $\delta^{15}N$ values, and consequently the trophic position of ants (Figure 13).

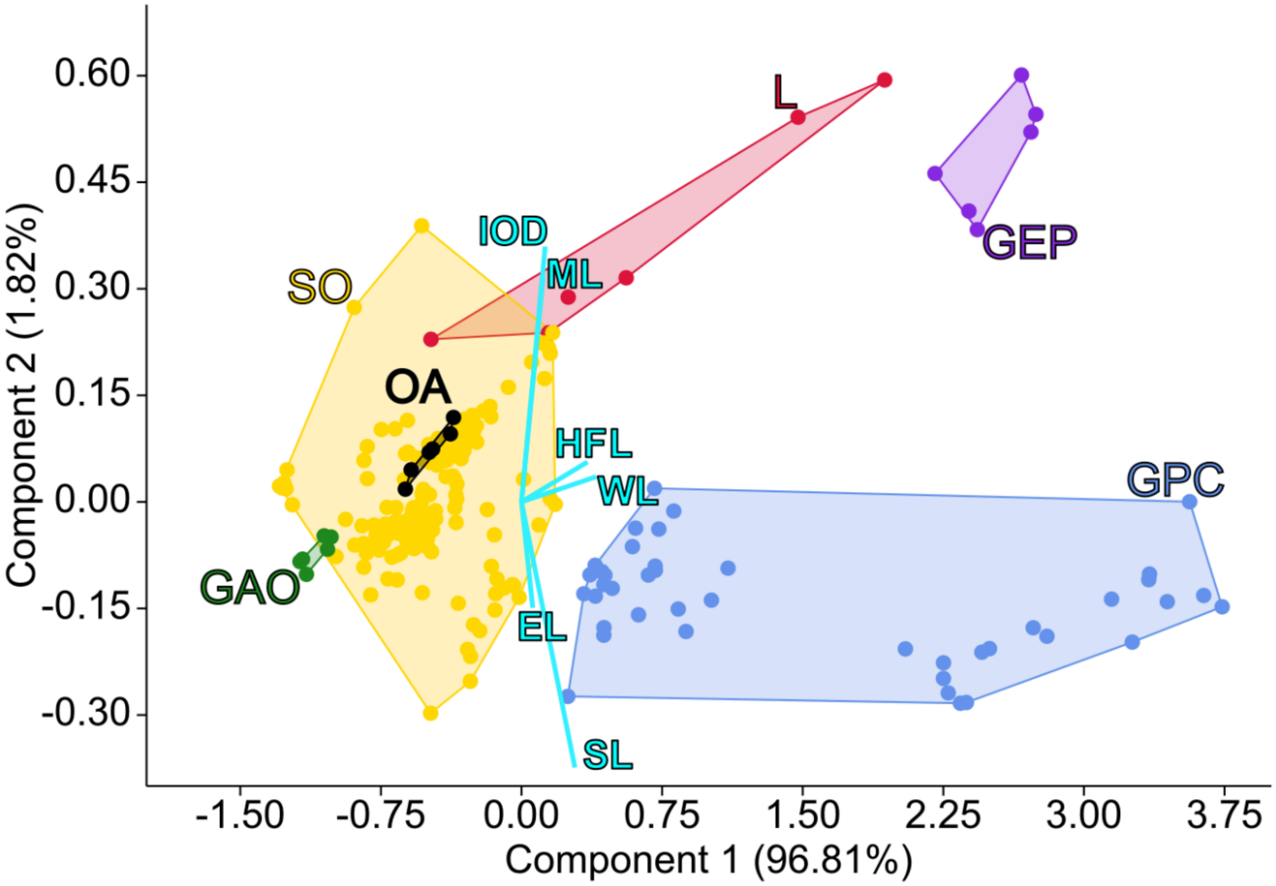


FIGURE 12 Principal Component Analysis (PCA) of the ants' morphological traits (inter-ocular distance - IOD, mandible length - ML, hind femur length - HFL, Weber's length - WL, Eye length - EL, Scape length - SL) separating the ant functional groups in the Brazilian Federal District. Variance of PC1 (96.81%) and PC2 (1.82%). Dots represent ant individuals that had their functional

traits measured and then classified into the following functional groups: L = legionary, OA = Omnivorous arboreal, SO = Soil omnivorous, GAO = Ground and arboreal opportunist, GEP = Generalist epigaeic predator, GPC = Generalist patrolling Camponotini. The arrows indicate the contribution of the variables to the separation of the groups in component 1 and component 2

TABLE 3 PCA loadings between the measured morphological values of the ants

	PC 1	**PC 2**	**PC 3**	**PC 4**	**PC 5**	**PC 6**
Weber's length	0.632	0.056227	-0.728	0.092435	-0.15865	-0.18361
Eye length	0.095421	-0.23727	-0.18605	0.13913	0.16085	0.92453
Hind femur length	0.5593	0.089385	0.43623	-0.59232	-0.31506	0.19695
Inter-ocular distance	0.20076	0.57172	0.32211	0.67805	-0.22966	0.12875
Scape length	0.45284	-0.59462	0.37592	0.35129	0.34714	-0.23695
Mandible length	0.18242	0.50211	-0.0056538	-0.19521	0.82246	-0.0048221

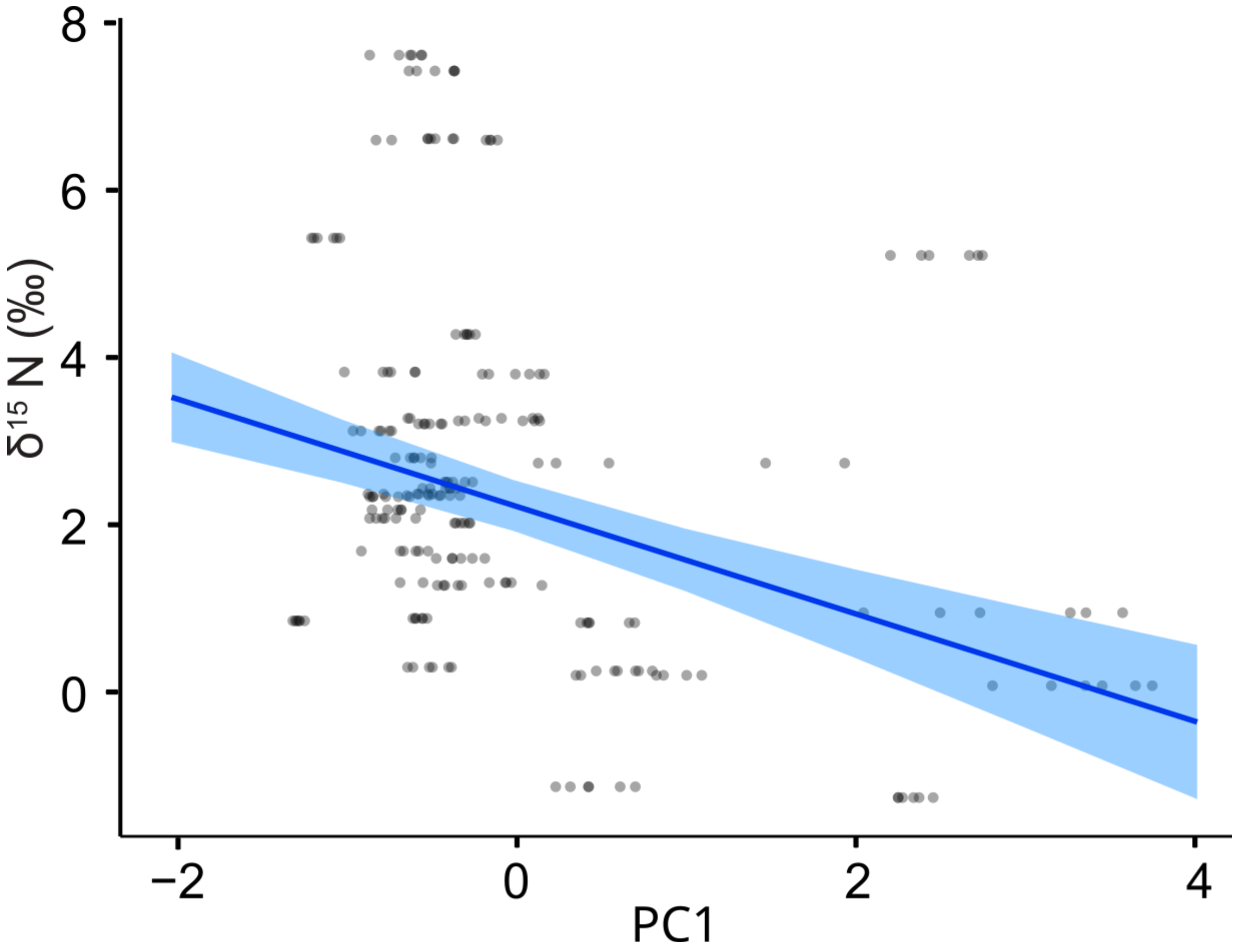


FIGURE 13 Relationship between the scores obtained for PC1 indicating how changes in the morphological traits affect the separation of ant functional groups and the $\delta^{15}N$ values of these ants. The dots represent the observed $\delta^{15}N$ values, while the line represents the trend fitted by the Generalized Linear Mixed Model (GLMM) with t distribution ($y = -0.6337x + 2.5831$). The light blue shaded band represents the model's confidence interval

4 | DISCUSSION

We demonstrated that land use change drives adverse effects on ant biodiversity with consequent changes in the isotopic niche and trophic position of different functional groups. We confirmed that changes in land use affect the taxonomical and functional diversity of ants and that these effects may depend on how natural areas are converted to different agricultural uses (Santos et al., 2021). Isotopic analyses revealed that habitat type alters the range and the trophic position of functional groups, which in turn is influenced by the different filtering effects of functional traits imposed by anthropization. Functional traits related to foraging and sensory capacity (Weber length, hind tibia, and scapus length) directly influenced the trophic position ($\delta^{15}N$) of the ants. Overall, more homogeneous habitats, with fewer resources and greater disturbance by insecticides, especially large-scale soybean crops, present the most severe filters to species and affect their role and functionality in ecosystems.

Areas of native vegetation, especially grasslands, were the main reservoirs of the taxonomic and functional diversity of ants in our study system. These areas vary in structural complexity, with different degrees of plant stratification (Ribeiro & Walter, 2008), providing distinct resources and nesting sites for several functional groups of ants (Baccaro et al., 2015). Conversely, anthropized habitats like large-scale soybean crops reduce and homogenize the resources and increase habitat disturbance with insecticide applications and plowing, making it a harsh environment for ant species occurrence and functionality (Nunes et al., 2020). However, such effects may be alleviated, especially by organic farming management that makes habitats less homogeneous or less disturbed. Pastures are also habitats with low disturbance after their establishment and produce landscapes similar to grasslands, allowing the occurrence of an intermediate number of ant species. These results show the relevance of habitat loss, resource heterogeneity, and disturbance intensity as the main drivers of ant species loss in agricultural systems (Wilker et al., 2024).

We found that ant assemblages' taxonomic and functional composition varied considerably between the different land uses. Generalist species like *Pheidole* spp. and *Brachymyrmex* spp. and other soil omnivores or vegetation opportunists stood out in anthropized areas. These ants have a great dispersal ability, are less sensitive to disturbances, and are highly adaptable to different environments (Tsang et al., 2020). Conversely, in the native vegetation areas, there are more exclusive specialist species and functional groups, such as hypogaeic specialists. Although these results may vary between study systems and land use types in other regions' groups (Newbold et al., 2015; Rabello et al., 2021), it is clear that differences in the taxonomic and functional composition of ant assemblages reflect the diversity of resources exploited by different ant species, and that native vegetation types complement each other in terms of biodiversity maintenance (Zhang et al., 2022.)

This is reinforced by isotopic niche width and isotopic niche overlap of ants in distinct native vegetation types associated with a higher trophic length. The native vegetation areas are functionally connected regarding resource use at the landscape (Weber et al., 2023). The low isotopic niche overlap in some anthropized areas suggests the formation of discrete and less connected assemblages due to differences in resource use (Salas-López et al., 2022) and increased competition for scarce resources (Neumann & Pinter-Wollman, 2022). This isolation of populations increases the risk of local extinction and loss of functionality (Cajaiba et al., 2022). These effects are even more worrying in large-scale soybean areas with few functional groups and species exploring similar and homogeneous resources.

The trophic position of ants, inferred from the $\delta^{15}N$ values, was also shown to be influenced by land use change. Overall, there is a tendency for ants to occupy higher trophic levels in anthropized habitats due to the higher availability of prey (e.g., pests) for predatory or generalist species (Wilker et al., 2023). However, these effects depend on the functional group because they can play different roles in each land use type (Tsang et al., 2020). Soil omnivores, for example, may be acting as predators in organic and soybean farms, while they play a role as detritivores more often in pastures (Helms et al., 2021). On the other hand, generalist epigaeic predators showed less variation in the trophic position but high plasticity in prey use among habitats. However, they rely more on prey availability than the other groups. The generalists patrolling Camponotini, however, are more dependent on floral resources, extrafloral nectaries, and honeydew (Soares & Oliveira, 2021). Such responses represent a change in the ecological role of the same functional group when faced with an excess or lack of specific resources since different groups respond differently to changes in resources and environmental conditions (Santos et al., 2021).

These patterns suggest that land use changes may filter the species or the functional traits of species able to survive in anthropogenic habitats. The filtering of functional traits, such as foraging capacity, body size, tolerance to disturbances, and resource dependence, are some mechanisms that explain the differences in isotopic niches of ants (Drager et al., 2023). Notably, this filtering process can lead to a loss of functional diversity within ant assemblages. That can have cascading effects on ecosystem processes, such as nutrient cycling, predation, and seed dispersal (Frizzo et al., 2020; Cajaiba et al., 2022).

We found a strong influence of morphological traits on the trophic niche of ants. Our results align with other studies, where predatory ants are larger than omnivorous ants (Gibb et al., 2015). However, it is crucial to consider the environmental filtering process that influences the trophic position of ants. The availability of food resources and interactions with other species can shape the food preferences and, consequently, the trophic position of ants, regardless of their morphological traits (Helms et al., 2021). In addition, competition for resources and predation pressure can lead to food specialization and the occupation of specific trophic niches (Salas-López et al., 2022). The reason for high trophic values for legionary or Camponotini ants may be related to their non-specialized dietary choice, as they can feed on animals from higher trophic levels that are already decomposing or even their feces. These results show the opposite of what has already been found for neotropical ants, where omnivorous genera tend to have proportionally larger bodies (Weiser & Kaspari, 2006). These patterns can be explained by the size-grain hypothesis. Large ants perceive the environment in a more homogeneous way than smaller ants. Smaller bodies, therefore, allow them to access a greater variety of environments in search of resources (Farji-Brener et al., 2004). Such connection among morphology, resource use, and trophic position demonstrates how functional traits influence the trophic niche of ants and reflect ecological adaptations to the environmental pressures imposed by different land uses.

In summary, the ecological mechanisms driving the adverse effects of land use change on ant biodiversity include habitat homogenization, reduced diversity of food resources, and the intense disturbance regime imposed by agricultural management. Isotopic analysis revealed how these mechanisms directly affect the trophic structure of ant groups, with soybeans showing the simplest trophic structure and length, indicative of a reduced range of ecological roles. We found that functional characteristics related to foraging and sensory capacity (Weber's length, hind tibia, and scapus length) directly influence the trophic position of ants, in terms of $\delta^{15}N$, highlighting the importance of the process of filtering characteristics in the response of ants to changes in land use. This filtering, by favoring generalist species with specific traits, leads to a less diverse and potentially less resilient ant assemblage. Less intensive practices, such as organic farming, have the potential to partially mitigate these impacts by providing refuge for some species, and maintaining a greater diversity of functional roles. Furthermore, other types of land use, such as pastures, limit producers primarily to grasses. However, they may also enhance the trophic chain by increasing the availability of detritivorous prey, such as beetles that feed on cattle feces. These beetles can serve as an important food source for ants in pastures, unlike in areas of native vegetation, highlighting how different land-use types support distinct trophic pathways. Although the conservation of areas of native vegetation is essential for the functionality and ecosystem services of ants. This goes beyond the most legally protected forest areas and includes grassland and savannah areas, as they can complement each other in providing ecosystem services (Estrada-Carmona et al., 2022; Novaes et al., 2024; Marins et al., 2024). Our results with ants reinforce this need to maintain a mosaic of plant formations in order to maintain the taxonomic and functional diversity of ants and their services, facilitating the exchange of species between localities.. Therefore, conservation units associated with the protection of different types of vegetation in tropical regions are crucial and should be treated as economic assets due to their importance for biodiversity conservation and ecosystem functioning, because these diverse habitats support the complex interactions and functional roles that underpin a healthy ecosystem.

REFERENCES

Anderson, M. J., Gorley, R. N., & Clarke, K. R. (2008). *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods*. PRIMER-E.

Baccaro, F. B., Feitosa, R. M., Fernández, F., Fernandes, I. O., Izzo, T. J., Souza, J. L. P., & Solar, R. R. C. (2015). *Guia para os gêneros de formigas do Brasil*. Editora INPA. https://doi.org/10.5281/zenodo.32912

Béllo Carvalho, R., Malhi, Y., & Oliveras Menor, I. (2023). Frugivory and seed dispersal in the Cerrado: Network structure and defaunation effects. *Biotropica*, 55, 849–865. https://doi.org/10.1111/btp.13234

Bolton, B., Alpert, G., Ward, P. S., & Naskrecki, P. (2007). *Bolton's catalogue of ants of the world: 1758-2005*. Harvard University Press

Brasil (2012). Lei Federal nº 12.651, de 25 de maio de 2012. Brazilian Forest Code. *Diário Oficial da União*, *102*(Seção 1), 1-8.

Cabana, G., & Rasmussen, J. B. (1994). Modelling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. *Nature, 372*, 255-257. https://doi.org/10.1038/372255a0

Cajaiba, R. L., da Silva, W. B., Gonzalez, D. C., Crespi, A. M. L., Santos, M., & Périco, E. (2023). Linking disturbances in neotropical landscapes with ecosystem functional traits: A preliminary assessment using epigaeic and leaf-litter ant communities. *Ecological Entomology, 48*, 186-198. https://doi.org/10.1111/een.13213

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, 486, 59–67. https://doi.org/10.1038/nature11148

Cardoso, M. R. D., Marcuzzo, F. F. N., & Barros, J. R. (2014). Classificação climática de Köppen-Geiger para o estado de Goiás e o Distrito Federal. *Acta Geográfica, 8*(16), 40-55. https://doi.org/10.5654/actageo2014.0004.0016

Cardoso, P., Barton, P. S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., Fukushima, C. S., Gaigher, R., Habel, J. C., Hallmann, C. A., Hill, M. J., Hochkirch, A., Kwak, M. L., Mammola, S., Noriega, J. A., Orfinger, A. B., Pedraza, F., Pryke, J. S., Roque, F. O., Settele, J., et al. (2020). Scientists' warning to humanity on insect extinctions. *Biological Conservation, 242*, 108426. https://doi.org/10.1016/j.biocon.2020.108426

CODEPLAN - Companhia de Planejamento do Distrito Federal (2015). *O mercado de produtos orgânicos: mecanismos de controle*. https://codeplan.df.gov.br/wp-content/uploads/2018/02/Mercado-Produtos-Orgânicos-Mecanismo-de-Controle.pdf. Accessed on January 10, 2025.

Costa, F. V., Blüthgen, N., Viana-Junior, A. B., Guerra, T. J., Di Spirito, L., & Neves, F. S. (2018). Resilience to fire and climate seasonality drive the temporal dynamics of ant-plant interactions in a fire-prone ecosystem. *Ecological Indicators, 93*, 247-255. https://doi.org/10.1016/j.ecolind.2018.05.001

Cronin, A. L., Donnerhack, O., Seidel, F., & Yamanaka, T. (2015). Fine-scale variation in natural nitrogen isotope ratios of ants. *Entomologia Experimentalis et Applicata, 157*, 354-359. https://doi.org/10.1111/eea.12370

Cucherousset, J., & Villéger, S. (2015). Quantifying the multiple facets of isotopic diversity: New metrics for stable isotope ecology. *Ecological Indicators, 56*, 152-160. https://doi.org/10.1016/j.ecolind.2015.03.032

Drager, K. I., Rivera, M. D., Gibson, J. C., Ruzi, S. A., Hanisch, P. E., Achury, R., & Suarez, A. V. (2023). Testing the predictive value of functional traits in diverse ant communities. *Ecology and Evolution, 13*, e10000. https://doi.org/10.1002/ece3.10000

EMATER - Empresa de Assistência Técnica e Extensão Rural do Distrito Federal (2023). *Informações agropecuárias do Distrito Federal - 2023*. https://emater.df.gov.br/wp-content/uploads/2018/06/Relatorio_de_Informacoes_Agropecuaria_RIA_2023__DF.pdf. Accessed on January 06, 2025

Estrada-Carmona, N., Sánchez, A. C., Remans, R., & Jones, S. K. (2022). Complex agricultural landscapes host more biodiversity than simple ones: A global meta-analysis. *Proceedings of the National Academy of Sciences, 119*, e2203385119. https://doi.org/10.1073/pnas.2203385119

Farji-Brener, A. G., Barrantes, G., & Ruggiero, A. (2004). Environmental rugosity, body size and access to food: a test of the size-grain hypothesis in tropical litter ants. *Oikos, 104*, 165-171. https://doi.org/10.1111/j.0030-1299.2004.12740.x

Farquhar, G. D., Ehleringer, J. R., & Hubick, K. T. (1989). Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology, 40*, 503-537.

Feldhaar, H., Gebauer, G., & Blüthgen, N. (2010). Stable isotopes: past and future in exposing secrets of ant nutrition (Hymenoptera: Formicidae). *Myrmecological News, 13*, 3-13. https://doi.org/10.25849/myrmecol.news_013:003

Fernández, F. (Ed.). (2003). *Introducción a las Hormigas de la Región Neotropical*. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.

Fichaux, M., Béchade, B., Donald, J., Weyna, A., Delabie, J. H. C., Murienne, J., Baraloto, C., & Orivel, J. (2019). Habitats shape taxonomic and functional composition of Neotropical ant assemblages. *Oecologia, 189*, 501-513. https://doi.org/10.1007/s00442-019-04341-z

Fowler, H. G., Forti, L. C., Brandão, C. R. F., Delabie, J. H. C., & Vasconcelos, H. L. (1991). Ecologia nutricional de formigas. In A. R. Panizzi & J. R. P. Parra (Eds.), *Ecologia Nutricional De Insetos e suas implicações para o manejo de pragas* (pp. 131-223). Manole.

Fry, B. (2006). *Stable isotope ecology* (1st ed.). Springer New York. https://doi.org/10.1007/0-387-33745-8

Frizzo, T. L. M., Souza, L. M., Sujii, E. R., & Togni, P. H. B. (2020). Ants provide biological control on tropical organic farms influenced by local and landscape factors. *Biological Control, 151*, 104378. https://doi.org/10.1016/j.biocontrol.2020.104378

Gibb, H., & Parr, C. L. (2013). Does Structural Complexity Determine the Morphology of Assemblages? An Experimental Test on Three Continents. *PLoS ONE, 8*(5), e64005. https://doi.org/10.1371/journal.pone.0064005

Gibb, H., Stoklosa, J., Warton, D. I., Brown, A. M., Andrew, N. R., & Cunningham, S. A. (2015). Does morphology predict trophic position and habitat use of ant species and assemblages? *Oecologia, 177*, 519-531. https://doi.org/10.1007/s00442-014-3101-9

Gotelli, N. J., Chao, A., & Colwell, R. K. (2024). Measuring and Estimating Species Richness, Taxonomic and Phylogenetic Diversity, and Related Biotic (Dis)similarity Indices from Sampling Data. In S. M. Scheiner (Ed.), *Encyclopedia of Biodiversity (Third Edition)* (pp. 314-339). Academic Press. https://doi.org/10.1016/B978-0-12-822562-2.00104-3

Gotelli, N. J., & Colwell, R. K. (2010). Estimating species richness. In A. E. Magurran & B. J. McGill (Eds.), *Biological Diversity: Frontiers in Measurement and Assessment* (pp. 39-54). Oxford University Press.

Hartig, F. (2024). *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models*. R package version 0.4.7, https://CRAN.R-project.org/package=DHARMa

Helms, J. A., IV, Roeder, K. A., Ijelu, S. E., Ratcliff, I., & Haddad, N. M. (2021). Bioenergy landscapes drive trophic shifts in generalist ants. *Journal of Animal Ecology, 90*, 738-750. https://doi.org/10.1111/1365-2656.13407

Hyodo, F. (2015). Use of stable carbon and nitrogen isotopes in insect trophic ecology. *Entomological Science, 18*, 295-312. https://doi.org/10.1111/ens.12128

IBGE - Instituto Brasileiro de Geografia e Estatística (2004). Cartas e Mapas: Biomas. https://www.ibge.gov.br/geociencias/cartas-e-mapas/informacoes-ambientais/15842-biomas.html?edicao=16060&t=downloads

Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology, 80*, 595-602. https://doi.org/10.1111/j.1365-2656.2011.01806.x

Kaspari, M., & Weiser, M. D. (1999). The size-grain hypothesis and interspecific scaling in ants. *Functional Ecology, 13*, 530-538. https://doi.org/10.1046/j.1365-2435.1999.00343.x

Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology, 29*, 592-599. https://doi.org/10.1111/1365-2435.12345

Kreider, J. J., Chen, T. -W., Hartke, T. R., Buchori, D., Hidayat, P., Nazarreta, R., Scheu, S., & Drescher, J. (2021). Rainforest conversion to monocultures favors generalist ants with large colonies. *Ecosphere, 12*(8), e03717. https://doi.org/10.1002/ecs2.3717

Laakel, N., Aissat, L., Bounab, L., & Yahiaoui, C. (2024). Diversity and Species Composition of Ants in Urban and Suburban Environments in Bejaia City (Algeria). *Sociobiology, 71*(2), e9698. https://doi.org/10.13102/sociobiology.v71i2.9698

Le Provost, G., Badenhausser, I., Le Bagousse-Pinguet, Y., Clough, Y., Henckel, L., Violle, C., Bretagnolle, V., Roncoroni, M., Manning, P., & Gross, N. (2020). Land-use history impacts functional diversity across multiple trophic groups. *Proceedings of the National Academy of*

Sciences of the United States of America, 117, 1573-1579. https://doi.org/10.1073/pnas.1910023117

Leite, P. A. M., Carvalho, M. C., & Wilcox, B. P. (2018). Good ant, bad ant? Soil engineering by ants in the Brazilian Caatinga differs by species. *Geoderma, 323*, 65-73. https://doi.org/10.1016/j.geoderma.2018.02.040

Machado, A. F. P., Camargo, N. F., de Souza, N. B., Nakasu, E. Y. T., Inoue-Nagata, A. K., & Togni, P. H. B. (2024). Spread your wings: insect-plant-landscape interactions mediate the wing shape of a multivoltine polyphagous insect. *Oikos, 2024*, e10318. https://doi.org/10.1111/oik.10318

Marins, G., Santos de Aquino, M. F., da Silva, A. C., de Queiroz, H. A. C., Laumann, R. A., & Togni, P. H. B. (2024). Through the green mosaic: Different tropical vegetation types have complementary effects on parasitoid diversity and biological control in organic agroecosystems. *Agriculture, Ecosystems & Environment, 374*, 109162. https://doi.org/10.1016/j.agee.2024.109162

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution, 21*, 178-185. https://doi.org/10.1016/j.tree.2006.02.002

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature, 403*, 853-858. https://doi.org/10.1038/35002501

Neumann, K., & Pinter-Wollman, N. (2022). The effect of resource availability on interspecific competition between a native and an invasive ant. *Philosophical Transactions of the Royal Society B: Biological Sciences, 377*, 20210146. https://doi.org/10.1098/rstb.2021.0146

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennett, D. J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhusseini, T., Ingram, D. J., et al. (2015). Global effects of land use on local terrestrial biodiversity. *Nature, 520*, 45-50. https://doi.org/10.1038/nature14324

Novaes, D. R., Sujii, P. S., Rodrigues, C. A., Silva, K. M. N. B., Machado, A. F. P., Inoue-Nagata, A. K., Nakasu, E. Y. T., & Togni, P. H. B. (2024). Natural Habitat Connectivity and Organic Management Modulate Pest Dispersal, Gene Flow, and Natural Enemy Communities. *Ecological Applications, 34*(2), e2938. https://doi.org/10.1002/eap.2938

Nunes, L. A. P. L., Pessoa, M. M. C., Araujo, A. S. F., Sousa, R. S., Silva, J. D. C., Leite, L. F. C., & Barbosa, L. R. (2020). Characterization of edaphic fauna in different monocultures in Savanna of Piauí. *Brazilian Journal of Biology, 81*, 657-664. https://doi.org/10.1590/1519-6984.228799

Pacheco, R., Vasconcelos, H. L., Groc, S., et al. (2013). The importance of remnants of natural vegetation for maintaining ant diversity in Brazilian agricultural landscapes. *Biodiversity and Conservation, 22*, 983-997. https://doi.org/10.1007/s10531-013-0463-y

Pacheco, R., Camacho, G. P., Frizzo, T. L. M., & Vasconcelos, H. L. (2017). Effects of land-use changes on ecosystem services: decrease in ant predation in human-dominated landscapes in central Brazil. *Entomologia Experimentalis et Applicata, 162*, 302-308. https://doi.org/10.1111/eea.12542

Pompermaier, V. T., Kisaka, T. B., Ribeiro, J. F., & Nardoto, G. B. (2020). Impact of exotic pastures on epigaeic arthropod diversity and contribution of native and exotic plant sources to their diet in the central Brazilian savanna. *Pedobiologia, 78*, 150607. https://doi.org/10.1016/j.pedobi.2019.150607

Post, D. M. (2002). Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology, 83*, 703-718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Projeto MapBiomas – Coleção 9 (1985-2023) da Série Anual de Mapas de Cobertura e Uso da Terra do Brasil. https://plataforma.brasil.mapbiomas.org/. Accessed on November 14, 2024.

R Development Core Team (2023). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rabello, A. M., Parr, C. L., Queiroz, A. C. M., Braga, D. L., Santiago, G. S., & Ribas, C. R. (2021). Taxonomic and functional approaches reveal different responses of ant assemblages to land-use changes. *Basic and Applied Ecology, 54*, 39-49. https://doi.org/10.1016/j.baae.2021.04.001

Ramos, D. D. L., Cunha, W. L. D., Evangelista, J., Lira, L. A., Rocha, M. V. C., Gomes, P. A., Frizzas, M. R., Togni, P. H. B. Ecosystem Services Provided by Insects in Brazil: What Do We Really Know? *Neotropical Entomology* 49, 783–794 (2020). https://doi.org/10.1007/s13744-020-00781-y

Ribeiro, J. F., & Walter, B. M. T. (2008). As principais fitofisionomias do bioma Cerrado. In S. M. Sano, S. P. Almeida, & J. F. Ribeiro (Eds.), *Cerrado: Ecologia e Flora* (Vol. 1, pp. 151-212). Embrapa Cerrados.

Ribeiro, L. F., Solar, R. R. C., Sobrinho, T. G., et al. (2019). Different trophic groups of arboreal ants show differential responses to resource supplementation in a neotropical savanna. *Oecologia, 190*, 433-443. https://doi.org/10.1007/s00442-019-04414-z

Rocha, E. A., & Fellowes, M. D. E. (2020). Urbanization alters ecological interactions: Ant mutualists increase and specialist insect predators decrease on an urban gradient. *Scientific Reports, 10*, 6406. https://doi.org/10.1038/s41598-020-62422-z

Salas-López, A., Violle, C., Munoz, F., Menzel, F., & Orivel, J. (2022). Effects of Habitat and Competition on Niche Partitioning and Community Structure in Neotropical Ants. *Frontiers in Ecology and Evolution, 10*, 863080. https://doi.org/10.3389/fevo.2022.863080

Sano, E. E., Rodrigues, A. A., Martins, E. S., Bettiol, G. M., Bustamante, M. M. C., Bezerra, A. S., Couto, A. F., Vasconcelos, V., Schüler, J., & Bolfe, E. L. (2019). Cerrado ecoregions: A spatial framework to assess and prioritize Brazilian savanna environmental diversity for conservation. *Journal of Environmental Management, 232*, 818-828. https://doi.org/10.1016/j.jenvman.2018.11.108

Santos, R. J., Dodonov, P., & Delabie, J. H. C. (2021). Effects of Habitat Conversion on Ant Functional Groups: A Global Review. *Sociobiology, 68*(2), e6071. https://doi.org/10.13102/sociobiology.v68i2.6071

Shipley, O. N., & Matich, P. (2020). Studying animal niches using bulk stable isotope ratios: an updated synthesis. *Oecologia, 193*, 27-51. https://doi.org/10.1007/s00442-020-04654-4

Silva, R. R., & Brandão, C. R. F. (2010). Morphological patterns and community organization in leaf-litter ant assemblages. *Ecological Monographs, 80*, 107-124. https://doi.org/10.1890/08-1298.1

Silvestre, R., Brandão, C. R. F., & Da Silva, R. R. (2003). Grupos funcionales de hormigas: el caso de los gremios del Cerrado. In F. Fernández (Ed.), *Introducción a las Hormigas de la Región Neotropical* (pp. 113-148). Instituto de Investigación de Recursos Biológicos Alexander von Humboldt

Soares, H., Jr., & Oliveira, P. S. (2021). Foraging and Spatial Ecology of a Polydomous Carpenter Ant, *Camponotus leydigi* (Hymenoptera: Formicidae), in Tropical Cerrado Savanna: A Natural History Account. *Environmental Entomology, 50*, 19-27. https://doi.org/10.1093/ee/nvaa164

Soares-Filho, B., Rajão, R., Macedo, M., Carneiro, A., Costa, W., Coe, M., Rodrigues, H., & Alencar, A. (2014). Cracking Brazil's Forest Code. *Science, 344*, 363-364. https://doi.org/10.1126/science.1246663

Song, X. -P., Hansen, M. C., Potapov, P., Adusei, B., Pickering, J., Adami, M., Lima, A., Zalles, V., Stehman, S. V., Di Bella, C. M., Conde, M. C., Copati, E. J., Fernandes, L. B., Hernandez-Serna, A., Jantz, S. M., Pickens, A. H., Turubanova, S., & Tyukavina, A. (2021). Massive soybean expansion in South America since 2000 and implications for conservation. *Nature Sustainability, 4*, 784-792. https://doi.org/10.1038/s41893-021-00729-z

Swanson, A. C., Schwendenmann, L., Allen, M. F., Aronson, E. L., Artavia-León, A., Dierick, D., Fernandez-Bou, A. S., Harmon, T. C., Murillo-Cruz, C., Oberbauer, S. F., Pinto-Tomás, A. A., Rundel, P. W., & Zelikova, T. J. (2019). Welcome to the Atta world: A framework for understanding the effects of leaf-cutter ants on ecosystem functions. *Functional Ecology, 33*, 1386-1399. https://doi.org/10.1111/1365-2435.13319

Tsang, T. P. N., Guénard, B., & Bonebrake, T. C. (2020). Omnivorous ants are less carnivorous and more protein-limited in exotic plantations. *Journal of Animal Ecology, 89*, 1941-1951. https://doi.org/10.1111/1365-2656.13249

Weber, S., Cullen, J. A., & Fuentes, M. M. P. B. (2023). Isotopic niche overlap among foraging marine turtle species in the Gulf of Mexico. *Ecology and Evolution, 13*(11), e10741. https://doi.org/10.1002/ece3.10741

Weiser, M. D., & Kaspari, M. (2006). Ecological morphospace of New World ants. *Ecological Entomology, 31*, 131-142. https://doi.org/10.1111/j.0307-6946.2006.00759.x

Wilker, I., Lasmar, C. J., Schmidt, F. A., da Costa, M. M. S., Almeida, D. F., Dutra, D. B. d. S., et al. (2023). Land-use change in the Amazon decreases ant diversity but increases ant-mediated predation. *Insect Conservation and Diversity, 16*, 379-392. https://doi.org/10.1111/icad.12632

Wilker, I., Queiroz, A. C. M., Ribas, C. R., Morini, M. S. C., Lasmar, C. J., Schmidt, F. A., Feitosa, R. M., Nogueira, A., Baccaro, F. B., Ulysséa, M. A., Izzo, T., Paolucci, L. N., Quinet, Y. P., Vargas, A. B., Harada, A. Y., Sobrinho, T. G., Marques, T. G., Souza, J. L. P., Del-Claro, K., Lange, D., et al. (2024). A systematic review of the land use change effects on ant diversity in

Neotropics. *Biological Conservation, 299*, 110778. https://doi.org/10.1016/j.biocon.2024.110778

Woodcock, P., Edwards, D. P., Newton, R. J., Vun Khen, C., Bottrell, S. H., Hamer, K. C. (2013). Impacts of intensive logging on the trophic of ant communities in a biodiversity hotspot. *PLOS ONE, 8*(4), e60756. https://doi.org/10.1371/journal.pone.0060756

Yates, M. L., Andrew, N. R., Binns, M., & Gibb, H. (2014). Morphological traits: predictable responses to macrohabitats across a 300 km scale. *PeerJ, 2*, e271. https://doi.org/10.7717/peerj.271

Zhang, X., Lu, Z. -x., Zhang, N. -n., & Chen, Y. -q. (2022). Data of ant community compositions and functional traits responding to land-use change at the local scale. *Biodiversity Data Journal, 10*, e85119. https://doi.org/10.3897/BDJ.10.e85119