UNIVERSIDADE FEDERAL DE UBERLÂNDIA
INSTITUTO DE BIOLOGIA

Programa de Pós-Graduação em Ecologia e Conservação de Recursos Naturais

MUDANÇAS NO USO E NA COBERTURA DA TERRA E SEU EFEITO SOBRE A ESTRUTURA TRÓFICA E MORFOLÓGICA DE COMUNIDADES DE FORMIGAS (HYMENOPTERA: FORMICIDAE) NO BRASIL CENTRAL

JÉSICA VIEIRA

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Tese apresentada à Universidade Federal de Uberlândia, como parte das exigências para obtenção do título de Doutora em Ecologia e Conservação de Recursos Naturais.

Orientador

Prof. Dr. Heraldo Luís de Vasconcelos

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Reuniu-se no Anfiteatro do Bloco 4K, Campus Umuarama, da Universidade Federal de Uberlândia, a Banca Examinadora, designada pelo Colegiado do Programa de Pós-graduação em Ecologia e Conservação de Recursos Naturais, assim composta: Doutores: Ricardo Ildefonso de Campos - UFV; Flávio de Carvalho Camarota - UFV; Jamir Afonso do Prado Júnior - INBIO/UFU; Alessandra Bartimachi Neves - INBIO/UFU; Heraldo Luis de Vasconcelos - INBIO/UFU, orientador(a) do(a) candidato(a).

Iniciando os trabalhos o(a) presidente da mesa, Dr(a). Heraldo Luis de Vasconcelos, apresentou a Comissão Examinadora e o candidato(a), agradeceu a presença do público, e concedeu ao Discente a palavra para a exposição do seu trabalho. A duração da apresentação do Discente e o tempo de arguição e resposta foram conforme as normas do Programa.

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Dedico essa tese à duas grandes mulheres:

minha mãe e minha avó materna.

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O correr da vida embrulha tudo,
a vida é assim: esquenta e esfria,
aperta e daí afrouxa,
sossega e depois desinquieta.
O que ela quer da gente é coragem.
O que Deus quer é ver a gente
aprendendo a ser capaz
de ficar alegre a mais,
no meio da alegria,
e inda mais alegre
ainda no meio da tristeza!
A vida inventa!
A gente principia as coisas,
no não saber por que,
e desde aí perde o poder de continuação
porque a vida é mutirão de todos,
por todos remexida e temperada.
O mais importante e bonito, do mundo, é isto:
que as pessoas não estão sempre iguais,
ainda não foram terminadas,
mas que elas vão sempre mudando.
Afinam ou desafinam. Verdade maior.
Viver é muito perigoso; e não é não.
Nem sei explicar estas coisas.
Um sentir é o do sentente, mas outro é do sentidor.

("Grande Sertão Veredas", Guimarães Rosa)

Sumário

Resumo geral

As características estruturais e as condições abióticas dos ambientes são importantes fatores que moldam as comunidades de espécies, no entanto, pouco se sabe como as mudanças no uso e na cobertura da terra afetam a estrutura trófica e a estrutura morfológica das comunidades de formigas. Primeiramente, eu avaliei como as diferenças na estrutura trófica de comunidades de formigas de solo e de vegetação variam entre floresta e savana. Para isso, utilizei análises de isótopos estáveis de carbono ($\delta^{13}C$) e de nitrogênio ($\delta^{15}N$) em 70 espécies de formigas coletadas em áreas de floresta semidecidual e de cerrado sentido restrito. As diferenças na estrutura trófica das formigas de solo e formigas arborícolas foram as mesmas no cerrado e na floresta, para tanto para $\delta^{15}N$ quanto para $\delta^{13}C$. Nos dois hábitats, a comunidade de formigas arborícolas apresentou um $\delta^{15}N$ significativamente menor do que a comunidade do solo. Esses resultados indicam uma similaridade bem maior na estrutura trófica das comunidades de floresta e de cerrado do que entre a comunidade arbórea e de solo. Isto é explicado ao menos em parte pelas diferenças na composição da fauna que foram muito mais marcadas entre estratos do que entre hábitats. Após isso, eu avaliei se a morfologia das espécies de formigas pode ser usada como um preditor de sua posição trófica. Primeiro, eu avaliei as relações entre os caracteres morfológicos com a posição trófica relativa das mesmas 70 espécies coletas na floresta e cerrado do capitulo anterior. Posteriormente, utilizei modelos de regressão múltipla com o objetivo de criar um modelo que melhor explique a variação da posição trófica entre as espécies. Para isso eu fiz medidas de 11 traços morfológicos considerados relevantes para esse estudo e utilizei os dados da assinatura isotópica de nitrogênio ($\delta^{15}N$) para calcular a posição trófica relativa (RTP) das formigas. Individualmente, os caracteres morfológicos mostraram associações fracas com a RTP das espécies, enquanto que combinados nos modelos de regressão múltipla, explicaram grande parte da variação da RTP. No entanto, o poder preditivo aumentou significativamente quando levei em consideração o hábitat de forrageamento/nidificação e/ou algumas afinidades taxonômicas das espécies em separado. Esses resultados sugerem que os caracteres morfológicos, quando combinados, tem um grande potencial para ser usado na predição da posição trófica das espécies de formigas. Por último, eu avaliei se a estrutura morfológica e/ou trófica das comunidades de formigas difere entre diferentes usos da terra e se essas diferenças estão associadas com a cobertura arbórea desses hábitats. Eu amostrei formigas em cinco tipos de hábitats representando um gradiente de aumento na cobertura vegetal: plantação de soja, pastagem, cerrado típico, plantação de eucalipto e floresta. As formigas de solo foram coletadas ao longo de oito transectos em cada tipo de hábitat (totalizando 40 áreas), utilizando armadilhas do tipo *pitfall*. A estrutura trófica e morfológica das comunidades de formigas foram afetadas pelo tipo de uso da terra e alguns caracteres morfológicos foram fortemente correlacionados com complexidade estrutural do hábitat. Hábitats com maior cobertura árborea apresentaram uma maior abundância de formigas com tamanho do corpo maior, olhos pequenos e posicionados dorsalmente. Além disso, as comunidades de formigas das plantações de soja e das pastagens tiveram posição trófica mais alta que aquelas da floresta, cerrado ou plantação de eucalipto. De maneira geral, esta tese fornece evidências de que o ambiente e suas características estruturais influenciam a prevalência de certos traços funcionais na comunidade de formigas.

Palavras-chave: Agroecossistemas, Cerrado, morfologia, posição trófica, traços funcionais, complexidade ambiental, isótopos, cobertura arbórea, dieta

General abstract

The structural features and abiotic conditions of the environments play a critical role in shaping the communities of the species; however, little is known about how changes in land use and land cover affect the trophic structure and the morphological structure of ant communities. First, I evaluated in what extent the differences in the trophic structure between ground-dwelling and arboreal ant communities vary between forests and savannas. For this, I used stable isotope analyzes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) on 70 species of ants collected in areas of semideciduous forest and woodland savanna. Differences in the trophic structure of the arboreal and ground-dwelling ant communities were the same in savanna as they were for forest for both $\delta^{15}N$ and $\delta^{13}C$. In both habitats, most arboreal species presented low $\delta^{15}N$ values (similar to herbivorous) whereas ground-dwelling ants presented high $\delta^{15}N$ values (similar to predator). Although $\delta^{13}C$ values were higher in savanna than in forest, reflecting the prominence of C_4 grasses in savanna, few savanna ant species obtained most of their carbon from C_4 grasses. This indicates that savanna has the vertical segregation in $\delta^{15}N$ values as found in the forest, despite the structural differences between these habitats. This can be explained by the much greater differences in taxonomic composition, both at the species and at the genus level, between the different strata than between habitats. After that, I assessed whether the ant species' morphology can be used as a predictor of their trophic position. First, I evaluated the relationships between morphological traits with the relative trophic position of the same species collected in the forest and savanna of the previous chapter. Subsequently, I used multiple regression models in order to create a model that better explains the variation in the trophic position among species. For this I took measurements of 11 morphological traits considered relevant for this study and used the data of the isotopic nitrogen signature ($\delta^{15}N$) to calculate the relative trophic position (RTP) of the ants. Individually, the morphological characters showed weak associations with the species' RTP, while combined in multiple regression models, they explained most of the variation in RTP. Moreover, the predictive power increased significantly when I took into account the foraging/nesting habitat and/or some taxonomic affinities of the species separately. These results suggest that the morphological traits, when combined, have a great potential to be used in the prediction of the trophic position of ant species. Finally, I assessed whether the morphological and/or trophic structure of ant communities vary in different land uses and whether these differences are associated with the tree cover of these habitats. I sampled ants in five types of habitats representing a gradient of increasing tree cover: soy plantation, pasture, woodland savanna, eucalyptus plantation and semideciduous forest. The trophic and morphological structure of ant communities were affected by the type of land use and certain morphological traits were strongly correlated with the structural complexity of the habitat. Habitats with a greater tree cover showed a greater abundance of ant species with larger body size, small and dorsally positioned eyes. In addition, ant communities of the soy plantations and pastures had higher trophic position than those of the forest, savanna or eucalyptus plantation. In general, this thesis provides evidence that the environment and its structural characteristics influence the prevalence of certain functional traits in the ant community.

Key-words: Agroecosystems, Cerrado, morphology, trophic position, functional traits, environmental complexity, isotopes, tree cover, diet

Introdução geral

Identificar os mecanismos que estruturam as comunidades em diferentes ecossistemas é um desafio central para a comunidade ecológica (McGill et al 2006). Os processos bióticos e abióticos desempenham um papel fundamental para explicar muito da diversidade das comunidades animais. Em uma escala global, a história biogeográfica e os parâmetros climáticos são preditores da variação na densidade e riqueza de espécies de uma comunidade (Gaston 2000, Whittaker 2000). Em uma escala local, as interações bióticas e as variações na diversidade de espécies também são influenciadas pelas condições ambientais locais (ex. temperatura, precipitação e produtividade primária), as quais atuam como um importante filtro de espécies (Huston 1999, Harrison and Cornell 2008, Belote et al 2009). Dessa forma, as espécies que persistem nas comunidades locais devem apresentar funções fisiológicas, morfológicas e/ou história de vida compatíveis com as características do hábitat (Southwood 1988).

Muitos hábitats variam em sua estrutura física, tais como: tipo de solo, formação rochosa, cobertura de dossel, quantidade de gramíneas ou de serapilheira; e essas variações podem promover diferentes microclimas, quantidade e tipos de recursos para diferentes espécies. A "hipótese da heterogeneidade ambiental" (MacArthur and MacArthur 1961, MacArthur e Wilson 1967) propõe que hábitats com uma maior complexidade ambiental fornecem uma quantidade maior de recursos, tanto para alimentação quanto para abrigo, e consequentemente suportam um maior número de espécies. No entanto, distúrbios ambientais (causados ou não por ações antrópicas) têm frequentemente modificado a estrutura dos ecossistemas naturais, e por sua vez, tornando os hábitats menos complexos, levando assim a um efeito cascata na composição das espécies e nas funções ecológicas que elas exercem (Foley et al. 2005, Walther 2010, Pacheco et al. 2013, Solar et al. 2016).

Muitos estudos tem utilizado principalmente a diversidade taxonômica para avaliar como as comunidades de animais e de plantas variam de acordo com o hábitat. No entanto, pouco se sabe como as mudanças na estrutura do hábitat afetam a estrutura trófica e morfológica das comunidades, especialmente em grupos de espécies pouco estudadas como os invertebrados. A estrutura trófica das comunidades biológicas refletem as fontes de carbono (C) e proteína (N) disponíveis no ambiente (Bryant et al. 1985; Davidson 1997; Kaspari and Yanoviak 2001), sendo que a utilização desses recursos pelos organismos é um resultado da interação entre a sua disponibilidade e a capacidade individual em utiliza-lo. Muitos organismos possuem adaptações morfológicas que auxiliam na utilização de determinado recurso (Wainwright 1994). Por exemplo, borboletas com probóscides longas podem acessar o néctar de flores mais profundas, enquanto espécies com probóscides menores não conseguem (Kunte 2007). Da mesma forma, formigas com mandíbulas maiores conseguem capturar presas de diferentes tamanhos e formas (Fowler et al. 1991).

A morfologia reflete a maneira com que os organismos interagem fisicamente com o ambiente (Wainwright 1994) e podem ser associada com muitos aspectos da ecologia de um organismo. Muitos caracteres morfológicos (ex. tamanho do corpo, tamanho da mandíbula) possuem relações com várias funções ecológicas, incluindo uso do hábitat e hábitos alimentares (Barton et al. 2010, Gibb et al. 2015, Nooten et al. 2019). Por exemplo, alguns estudos sugerem que formigas com olhos pequenos são associadas à hábitats com pouca disponibilidade de luz (Weiser e Kaspari 2006, Schofield et al. 2016) e que formigas de tamanho menor e pernas menores são mais abundantes em hábitats com pouca serrapilheira

(Parr et al. 2003). Além disso, formigas maiores e com olhos posicionados lateralmente parecem ter posição trófica mais alta (Gibb et al. 2015). Estudos também tem mostrado que a posição trófica das formigas varia de acordo com a abundância de determinados recursos no ambiente. Nas florestas tropicais, por exemplo, onde as espécies de formigas são verticalmente segregadas, a dieta das formigas arborícolas tende a ser mais baseada em carbono em comparação com as formigas que forrageam no solo, devido a grande disponibilidade de carboidrato líquido no dossel (Yanoviak and Kaspari 2000, Davidson 2005). Considerando a importância da estrutura dos hábitats em fornecer diferentes microclimas e tipos de recursos (alimentar e para nidificação), assim como as respostas das espécies em explorar esses recursos e em interagir com o ambiente, ambos caracteres morfológicos e informações sobre a dieta (ex. posição trófica das espécies na cadeia alimentar) fornecem um grande potencial para serem utilizados como preditores dos impactos das mudanças ambientais causadas pelo homem. Uma vez que, os distúrbios antrópicos têm efeitos significativos na estrutura da vegetação e consequentemente influenciam as comunidades de espécies que ali ocorrem.

As formigas são um grupo de insetos dominante na maioria dos ecossistemas terrestres e são capazes de ocupar quase todos os níveis tróficos em uma cadeia alimentar (Hölldöbler e Wilson 1990). Além disso, as formigas apresentam um elevado grau de associação com habitats específicos e são sensíveis à degradação ambiental (Majer 1983, Andersen e Majer 2004, Hoffmann 2010), sendo bons organismos modelos para o estudo de como as diferenças nos hábitats, em detrimento ou não de distúrbios causados pelo homem, impactam as comunidades. As savanas tropicais são um dos biomas mais afetados por distúrbios causados pelos homens (Parr e Chown 2001, Myers et al. 2000, Lehmann et al.

2009), onde grande parte da vegetação nativa (incluindo florestas e cerrados) vem sendo transformadas em monoculturas (Furley 1999, Klink e Machado 2005). Esse mosaico de vegetação nativa e não nativa com diferentes níveis de complexidade estrutural me permitiu avaliar como diferentes hábitats influenciam a estrutura trófica e a estrutura morfológica das comunidades de formigas. Para isso utilizei abordagens diferentes, porém complementares. Primeiramente, eu avaliei se a estrutura trófica da comunidades de formigas de solo e da vegetação arbórea varia entre dois hábitats contrastantes: floresta e cerrado. Posteriormente, relacionei a posição trófica relativa dessas espécies com alguns de seus caracteres morfológicos. Por último, avaliei se mudanças no uso na terra e na cobertura vegetal afetam a estrutura trófica e morfológica das formigas à nível de comunidade. Mais especificamente busquei respostas para as seguintes questões: a) em qual extensão as diferenças na estrutura trófica entre as comunidades de formigas de solo e arborícolas variam entre floresta e cerrado? b) em que extensão a variação morfológica entre as espécies de formigas podem ser usada para explicar sua posição trófica relativa? c) a estrutura morfológica e/ou trófica das comunidades difere entre diferentes usos da terra? Essas eventuais diferenças estão correlacionadas com as variações na cobertura arbórea dos hábitats?

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CAPÍTULO 1

Trophic structure of arboreal and ground dwelling ants in savannas and forests of central brazil

Abstract

The trophic structure of biological communities reflects the carbon- and nitrogen-derived food resources available in the environment. The analysis of stable-isotopes has been used successfully in ecological studies to assess the trophic structure of biological communities and the trophic position of organisms within food chains. Previous studies indicate that ant assemblages are often composed of species that occupy largely different trophic positions. However, most of the studies conducted so far have focused on assemblages within a single site, and only a few studies have investigated the differences in the trophic structure of ant communities in contrasting habitats. Here, I performed carbon (C) and nitrogen (N) stable isotopes analyses to assess potential differences in the trophic structure between ant assemblages associated with different habitats (forest or savanna), and foraging strata (ground or arboreal). I collected samples of ants, herbivorous insects, spiders, plants, and soil, in adjacent forest and savanna habitats within a savanna-dominated landscape in central Brazil. The arboreal ant communities of forest and savannas had a significantly lower mean $\delta\ ^{15}N$ than the ground-dwelling communities. However, there were no differences in mean $\delta\ ^{15}N$ between the forest and savanna ant communities as a whole (i.e., including the ground and the arboreal fauna), even when the analysis was restricted to species from the same genus or functional group. In both forests and savannas, there was a positive correlation between $\delta^{15}N$ and $\delta^{13}C$, indicating that species with higher $\delta^{13}C$ levels occupy a higher trophic position. Interestingly, most (91.5%) of the savanna ant species, obtained less than half of their carbon from C_4 grasses, even though they are extremely abundant in Neotropical savannas. Overall, the results obtained here indicate that there is a much greater similarity in the trophic structure of ant communities between forest and savanna than between the arboreal and ground-nesting/foraging strata. This fact seems to be explained mainly by the much greater differences in taxonomic composition, both at the species and at the genus level, between the different strata than between habitats. However, there was also evidence in some cases that the same ant species can exhibit plasticity in their diet across the different habitats. Furthermore, the fact that distinct species from the same genus but associated with different strata had different isotopic signatures indicates that the evolution of different nesting habits in ants has promoted the evolution of different dietary preferences.

Key-words: Ants, *Cerrado,* stable isotopes, trophic level, $\delta^{13}C$

Introduction

The analysis of stable isotopes has been a helpful tool for investigating the flow of energy and nutrients in different biological systems (Hobson et al. 2000). The ratio between the heavier and lighter isotopes of nitrogen ($\delta^{15}N$) provide evidence about the trophic position of organisms, whereas both carbon and nitrogen isotope analyses provide evidence of their primary nutrient sources (DeNiro and Epstein 1978; 1981; Blüthgen et al. 2003; Hood-Nowotny and Knols 2007). Traditionally, the trophic position and nutrient sources of animal species has been determined by direct observations of their foraging activity (Blüthgen et al. 2003). However, the difficulties and restrictions to perform such task can lead to inaccuracies in establishing the trophic relationships of organisms (Blüthgen et al. 2003; Bearhop et al. 2004). This is especially true for organisms with cryptic feeding behavior, such as many invertebrates, for which the analysis of stable isotopes is a safe and quick alternative approach (Peterson and Fry 1987; Hood-Nowotny and Knols 2007; Cronin et al. 2015; Gannes et al. 1997; Robinson 2001).

Ants compose a large part of the arthropod biomass in most terrestrial ecosystems and occupy almost all trophic levels (Hölldobler and Wilson 1990). Although most ants present generalist or opportunistic feeding habits, specialization can also occur, such as among species that feed on living prey, nectar, seeds, or fungi (Carroll and Janzen 1973; Hunter 2009). Stable isotopes studies have uncovered a wide variety of topics regarding the trophic ecology of ants. Included are studies that have analyzed the differences among different castes in a colony (Smith and Suarez 2010), among colonies from different developmental stages (Barriga et al. 2013), between invasive and native species (Tillberg et al. 2007), as well as those examining the trophic relationship between ants and plants (Clement et al. 2008) or between ants and bacteria (Feldhaar et al. 2010). Nevertheless, studies that have compared the trophic structure of ant communities in different habitats are still relatively scarce (but see Fiedler et al. 2007; Gibb and Cunningham 2011; Pfeiffer et al. 2014), and in some cases have produced contrasting results. For instance, some studies have found that ant species can show dietary flexibility and occupy different trophic positions in different habitats (Pfeiffer et al. 2014; Duyck et al. 2011), whereas Gibb and Cunningham (2011) found evidence that the trophic position of distinct ant genera remains unaltered when comparing habitats with different vegetation types.

The trophic structure of biological communities is known to reflect the sources of carbon and protein available in the environment (Bryant et al. 1985; Davidson 1997; Kaspari and Yanoviak 2001). The quantity and quality of these nutrients play a fundamental role in ecological and evolutionary processes (Bihn et al. 2008; Kaspari et al. 2012), as the availability of such resources varies in space and time according to the structural features of the habitat and their abiotic conditions (Southwood 1988; Yanoviak and Kaspari 2000; Davidson 2005, Kaspari et al. 2012). The canopy and soil of rainforests, for example, present marked differences in the provision of carbon and nitrogen, with high availability of carbohydrates released by nectaries or hemipterans in the canopy, and an abundance of leaf-litter arthropods in the soil (Yanoviak and Kaspari 2000).

Ants represent an abundant and diverse insect group in Neotropical forests and savannas (Fitkau and Kling 1973, Vasconcelos et al. 2018). Previous studies have revealed that species that inhabit adjacent forest and savanna sites tend to be distinct (Vasconcelos and Vilhena 2006; Camacho and Vasconcelos 2015). In addition, within each habitat, there are marked differences in composition between the ground- and tree-dwelling faunas (Vasconcelos and Vilhena 2006; Campos et al. 2008; Camacho and Vasconcelos 2015). Furthermore, there is evidence that the demand for different nutrients varies between species that forage in different strata (Yanoviak and Kaspari 2000; Kaspari and Yanoviak 2001; Vieira and Vasconcelos 2015), but not necessarily between habitat generalists that occur both in forests and savannas (Vieira and Vasconcelos 2015). Nevertheless, the extent to which differences in the nutrient demand and availability of nutrients for species that inhabit the ground and canopy of forest and savannas, or in dietary flexibility of habitat generalists, results in differences in the trophic structure of these communities is not clear. Thus, this study proposed to answer the following questions: i) Are there differences in the mean values of $\delta^{15}N$ between savanna/forest and arboreal/ground ant communities? ii) If so, are they caused by the differences in taxonomic composition between communities, or is there evidence of the same species (or species within the same taxon) present dietary flexibility and thus occupy distinct trophic positions in different habitats? iii) Are there differences in the mean values of $\delta^{13}C$ between arboreal and ground ant communities in savanna and in forest? iv) Does the carbon obtained by savanna ants originate primarily in food chains based on C_3 or on C_4 plants? C_4 grasses are key vegetation elements in neotropical savannas and present rather distinct $\delta^{13}C$ values from C_3 plants (Klink and Joly 1989; Magnusson et al. 1999), but the relative importance of such a source of carbon for ants in savannas is still not well understood.

Material and Methods

Study site

This study was performed in the Panga Ecological Reserve (PER), a 409-hectare protected area located 35 km south of the city of Uberlândia (MG), in southeastern Brazil (19°10’S, 48°24’W). The region presents a tropical climate characterized by rainy summers and dry winters, with an annual mean temperature between 20ºC and 25ºC, and an annual rainfall of 1,600 mm (Rosa et al. 1991). The study site is situated within the Cerrado savanna biome of central Brazil, which, like other tropical savanna biomes, is characterized as a mosaic of vegetation types, including savannas (the dominant vegetation), grasslands and forests (Cardoso et al. 2009). For this study, we selected areas of cerrado *sensu stricto* (savanna) and seasonal (semideciduous) forests. Most of PER is covered by savannas. Around 71% of the reserve is occupied by extensive patches of typical cerrado savanna with a predominance of grass and shrubs, and trees (0.4-6 m tall) scattered throughout the landscape. Semideciduous forests, on the other hand, have trees taller than 12 m and occupy about 9% of the reserve. Such forest areas occur on the lower part of hillsides and adjacent to the gallery forests, *cerradão* (dry forest), or typical savanna (Cardoso et al. 2009).

Ant sampling

Ants were collected in March and April 2016 along six transects, three of them in the savanna areas, and the three others in the semideciduous forests. The transects were at least 600 meters apart from each other and contained ten sampling points each. The sampling points had a minimum distance of 40 meters from each other and were set with four pitfall traps each (in 2 x 2m grid). These traps consisted of 250 ml plastic cups half-filled with water and detergent and buried into the ground so that their openings were leveled off with the soil surface. We also collected 1 m^2 of litter at each point, sifted this material onto a 0.8 cm mesh, and then put it in Winkler extractors for 48 hours. Four other pitfall traps were taped onto the branches of the closest tree to each point. Traps were set at the height of 2.5 to 3.5 m in the savanna trees and of at the height of 8.5 m high in forest trees. Arboreal traps were filled with a solution of soapy water and human urine (2:1) as an attractant (Powell et al. 2011). All traps remained active for 48 hours before being removed. After this, they were immediately water-washed to eliminate possible urine or detergent contaminations. The samples were then kept in alcohol and identified at the genus, morphospecies and, whenever possible, to species level, through comparison with specimens deposited in the zoological collection of the Federal University of Uberlândia (codes for the morphospecies listed in the present study are the same used in the referred collection; see Table S1).

Stable isotope analyses

Only the most abundant ant species in each habitat were used to determine their carbon and nitrogen isotopic signatures (43 species in forests and 47 in savanna). We sent sent one to five samples per species to isotopic analysis (Table S1). During sampling preparation, ant workers had their gaster removed to eliminate any possible effect from recently ingested food items on the analysis (Blüthgen et al. 2003; Tillberg et al. 2006). As a reference, we also determined the carbon and nitrogen isotopic signatures of herbivore and predatory species. For this, we collected at least three caterpillars and six spiders (three on ground and three in the arboreal vegetation) in each transect. Data on the isotopic signatures of grasses and tree leaves were obtained from a previous study in the same reserve (Silva 2017). Finally, because nitrogen content differed between forest and savanna soils (see below), soil samples (0-10 cm deep, three per transect) were also sent for isotopic analysis, as to obtain comparative (corrected) δ^{15}N values for the organisms collected in different habitats (Cronin et al. 2015).

Caterpillar, spider and ant samples were dried in an oven at 60 ºC for 48 hours and then crushed using an agate mortar and pestle. The soil was sifted and then dried in an oven at 40 ºC for 48 hours. The dried samples were put into small tin capsules in precisely weighed amounts (1.25-1.5 mg for arthropods and 25-26 mg for soil). These capsules were then molded into a spherical shape, put on ELISA dishes and sent to the University of California Stable Isotope Facility, in Davis, California, USA, for analysis.

The obtained results were expressed in delta notation per thousand, with an internationally acknowledged standard as reference. The equation for the isotopic signatures is defined as $\delta^{15}N$ or $\delta^{13}C$ (‰) = $(R_{sample} – R_{standard}) / R_{standard}$ x 1.000, with R representing the molar ratio of the heavy/light isotope of the samples and the used standard. Atmospheric air is the standard used for nitrogen ($R_{standard} = 0.0036765$), whereas Peedee Belemnite is used for carbon (Vienna PDB; $R_{standard} = 0.01118$).

Statistical analyses

Forest soil presented significantly higher $\delta^{15}N$ values than savanna soils (t= 6.08; gl= 11; *P* < 0.001). Consequently, before the statistical analyses, we corrected the $\delta^{15}N$ values of each forest ant species and the “reference arthropods” (caterpillars and spiders) using the formula: δ^{15}Nanimal - δ^{15}Nsoil. We did not correct the $\delta^{13}C$ values since comparative analysis of carbon signatures only involved species collected in different strata within the same habitat.

We compared the number of species per genus between habitats and strata with the Kolmogorov-Smirnov test for independent samples. The Bray-Curtis index was used to reveal dissimilarity in faunal composition between habitats and strata at the species and the genus level (presence/absence data, and the number of species per genus, respectively).

Differences in the mean corrected $\delta^{15}N$ values of ant communities from distinct habitats and strata were determined by a factorial ANOVA, with the corrected $\delta^{15}N$ of the most abundant species from both habitats and strata as the response variables. We additionally removed the effect from differences in taxonomic composition and compared the $\delta^{15}N$ values of the savanna and forest communities in a paired t-test. This test evaluated the differences in $\delta^{15}N$ considering only the species found in the two environments.

We also used a factorial ANOVA to compare the $\delta^{15}N$ between species of the same taxon (the same genus whenever possible, or the next taxon above it) occurring in different habitats, but only for groups with at least three species in each habitat. While a t-test for independent samples was used to compare the mean $\delta^{15}N$ between colonies of the same species from different habitats. Such analysis was done to all species presenting at least three sampled colonies in each habitat.

The relative contribution of C_3 plants to the diet of savanna ants was calculated used the formula: ‘$P_{C3} = (\delta^{13}C_A - \delta^{13}{}_{C4}) / (\delta^{13}{}_{C3} - \delta^{13}{}_{C4})$’, in which $\delta^{13}C_A$ is the $\delta^{13}C$ value of the ant species, $\delta^{13}{}_{C3}$ is the mean $\delta^{13}C$ of C_3 plants, and $\delta^{13}{}_{C4}$ is the mean $\delta^{13}C$ of C_4 plants. Assuming a $\delta^{13}C$ fractionation of 1‰ per trophic level (Fry and Sherr 1984), we corrected the mean $\delta^{13}C$ of the species by subtracting the fractionation value relative to their trophic level: 1‰ for herbivores, 1.5‰ for omnivores and 2‰ for predators (Forsberg et al. 1993; Magnusson et al. 1999).

For the correction, we classified the predator ants according to their nitrogen isotope ratios (those with a higher $\delta^{15}N$ than ground predators). The leaf-cutting ants of the genera *Atta* and *Acromyrmex* were considered herbivores, while the remaining species were considered omnivores.

Differences between the P_{C3} and $\delta^{13}C$ values of arboreal and ground communities were assessed with a t-test for independent samples. To check for correlation between the $\delta^{13}C$ and the $\delta^{15}N$ ratios, we used a Spearman rank correlation.

Results

In total, we obtained data on the isotopic signature for 70 ant species from 27 genera (Table 1; Fig. 1). Of these, 27 species were found only in the savanna transects, 23 only in the forests, and 20 in both habitats. Among these 70 species, 36 were collected in the arboreal vegetation (24 in forests and 22 in savanna) and 34 on the ground (19 in forests and 25 in savanna). The frequency distribution of the number of species per genus did not differ significantly between forest and savannas, as in both habitats, the most speciose genera were *Camponotus*, *Pheidole*, *Cephalotes,* and *Ectatomma* (Kolmogorov-Smirnov Test, Dmax = 0.11, *P* = 0.991) (Table 1). We found, however, a significant difference between strata (Kolmogorov-Smirnov Test, Dmax = 0.37, *P* = 0.042), since a total of 15 *Camponotus* species and six *Cephalotes* species were found in the canopy, but just one *Camponotus* and no *Cephalotes* were found on the ground. On the other hand, species of fungus-growing ants, as well as species of *Pheidole*, *Odontomachus*, and *Pachycondyla* were found only in the ground samples (Table S1; Table 1). Dissimilarity in faunal composition was consequently higher between strata than between habitats, and this was true both at the species (Bray-Curtis Index on species presence/absence data; ground *versus* canopy = 0.028, forest *versus* savanna = 0.444) and at the genus level (Bray-Curtis using data on the number of species per genus; ground *versus* canopy = 0.229, forest *versus* savanna = 0.667).

On average, there was no significant difference between the δ^{15}N corrected-values between the forest and savanna ant assemblages ($F_{1,86}$= 2.297; *P*= 0.133), and no significant interaction between habitat type and foraging stratum ($F_{1,86}$= 0.016; *P*= 0.899). The corrected δ^{15}N values of the ant species collected in forests varied from -3.30‰, in *Camponotus* sp.75, to 3.35‰ in *Pachycondyla harpax*, whereas that of the savanna species varied from -2.48‰

in *Camponotus melanoticus* to 5.32‰ in *Neoponera marginata*. Nevertheless, there were marked differences between the arboreal and ground-dwelling faunas, with the latter presetting on average significantly higher $\delta^{15}N$ values ($F_{1,86}$= 73.9; $P < 0.001$) (Fig. 1). Comparing the isotope values of arboreal ants to those of the different feeding groups revealed that, in general, arboreal ants presented higher $\delta^{15}N$ values than caterpillars but lower than ground spiders. Ground-dwelling ants (except for the fungus-growing ants and some *Camponotus*), in contrast, had higher $\delta^{15}N$ values than spiders found in tree foliage predators and lower than that of the ground spiders (Fig. 1).

There was a significant effect of genus or functional groups ($F_{5, 58}$= 48.03; $P < 0.001$) but not between forest and savanna ($F_{1,58}$= 1.99; $P = 0.163$) on mean $\delta^{15}N$ signature of ant species, and no significant interaction ($F_{5,58}$= 0.42; $P = 0.828$) (Fig. 2). Similarly, there was no difference when analyzing the mean $\delta^{15}N$ signature of the 20 species that occurred in both habitats (t = 1.17; df = 19; $P = 0.25$) (Fig. 3). For four of these 20 species, there was data for different colonies (32 samples) within each habitat. However, for most of these species no evidence of dietary flexibility was detected. The only exception was *Pseudomyrmex gracilis* which presented significantly higher $\delta^{15}N$ values in the savanna than in the forest (Table 2). Within both the forest and savanna habitats we found that species with higher $\delta^{15}N$ values tended also to present higher $\delta^{13}C$ values, as indicated by the positive and significant correlations between $\delta^{15}N$ and $\delta^{13}C$ (Spearman rank correlation, forest: $r_s = 0.535$, $P < 0.001$; savanna: $r_s = 0.382$, $P < 0.01$ excluding *A. landolti*) (Fig. 1).

The $\delta^{13}C$ varied between -32.11‰ and -22.59‰ in forests and between -26.24‰ and -11.64‰ in savanna. Nevertheless, except for the grass-cutting ant *Acromyrmex landolti* ($\delta^{13}C$ = -11.64), all ants from the savanna had a $\delta^{13}C$ ranging from -26.24‰ to -19.04‰. Ground-dwelling ants presented a significantly higher $\delta^{13}C$ signature than did the arboreal ants, and this was true in both forests and savannas (forest: t = 5.60; df= 41; $P < 0.0001$, savanna: t = 3.01; df= 45; $P = 0.003$ with all species, and t = 3.42; df= 44; $P = 0.001$ excluding *A. landolti*).

Almost all savanna species (43 out of 47 species) obtained more than half of their carbon from food chains based on C_3 plants. *Acromyrmex landolti* stands out from all other species for having 100% of its carbon coming from C_4 grasses (Fig. 4). Overall, C_3 plants contributed comparatively more to the diet of arboreal than to that of the ground-dwelling species (t = 2.98; df= 45; $P = 0.005$) (Fig. 4).

Discussion

Trophic position of species from different habitats or foraging stratum

Studies that evaluate the extent to which the trophic structure of ant communities differs between contrasting habitats are relatively rare. This study is the first to compare the trophic structure of the ant communities inhabiting adjacent forest and savanna habitats. Our first aim was to determine whether there were differences in the mean values of $\delta^{15}N$ between the savanna and forest ant communities. Our results showed that, although less than one-third of the species analyzed were found in both habitats, mean $\delta^{15}N$ values did not differ significantly between forest and savanna, and similar results were obtained involving all the species, only those from a particular genera or functional group, or only the habitat generalists found both in forest and in savanna. In addition, there was no interaction between the effects of habitat and nesting/foraging stratum indicating that our results apply both to the arboreal and ground-dwelling communities. The fact that we found no interaction between the effects of habitat and nesting/foraging stratum also indicates that the observed differences in the trophic structure between the arboreal and the ground-dwelling communities were as marked in the forest as they were in the savanna, despite the clear differences in the height of trees between these habitats.

We also asked whether eventual differences in trophic structure were caused by differences in the taxonomic composition between communities, or because the same species occupy distinct trophic positions in different habitats. According to previous studies, the same ant species may present distinct isotopic signatures in different habitats (i.e. presented dietary flexibility), likely as result of differences in the availability of different food resources (Resasco et al. 2012; Pfeiffer et al. 2014). However, dietary flexibility probably contributed little to the observed differences in trophic structure observed in here since different habitats, and different strata within habitats, shared relatively few species. Furthermore, for only one of the four species analyzed in our study, *Pseudomyrmex gracillis,* there was a significant difference in mean $\delta^{15}N$ values between colonies living in different habitats.

Based on the species we sampled for stable isotope analysis, we found that forest and savanna communities share less than one-third of their species. However, although the species found in each habitat in general were different, at the genus level, the taxonomic composition of ant communities in forests and savannas was quite similar. As previous studies (Gibb and Cunningham 2011) and ours indicate, species from the same genus tend to maintain their relative trophic position across habitats. In other words, and as found here and elsewhere (Davidson et al. 2003; Blüthgen et al. 2003; Davidson 2005; Fiedler et al. 2007; Pfeiffer et al. 2013), species of *Camponotus*, for example, present low $\delta^{15}N$ values (pointing to a diet composed mainly of nectar and/or honeydew) whenever the habitat in which they are found, whereas most species of *Pheidole, Ectatomma*, and most poneromorphs feed higher on the food chain and thus tend to present the highest $\delta^{15}N$ values, in either the forest or the savanna communities. Such finding suggests that the lack of differences in mean $\delta^{15}N$

values between the two communities is at least partly related to their similar genera composition. In contrast, the differences between the ground-dwelling and the faunas found within each habitat were strikingly more pronounced both at the species and at the genus level, which also helps explain the marked differences in trophic position between ants that forage and nest on ground versus those that forage in trees. We found a prevalence of species of *Azteca*, *Cephalotes*, *Camponotus*, and *Pseudomyrmex* in the arboreal vegetation, all of which had lower $\delta^{15}N$ values than those on ground, with the exception of the fungus-growing ants. Additionally, differences in trophic position were also observed for some congeneric species with distinct nesting or foraging habits. For example, of the four *Solenopsis* species we sampled two are arboreal and two nest on the ground. However, while the former had a $\delta^{15}N$ ranging between 2.2% and 4%, the latter was above 6.4%. Similarly, whereas *Ectatomma tuberculatum*, a ground-nesting ant that forages in the vegetation, presented a $\delta^{15}N$ between 3.6% and 4.4%, the remaining *Ectatomma* species, all of which are strictly terrestrial, had values ranging from 5.2% to 7.1%. These findings are indicative of differences in food preferences which, as suggested earlier, may be a major evolutionary force for speciation in ants (Pfeiffer et al. 2014). Furthermore, the fact that closely related species presented different $\delta^{15}N$ values reinforces the view that the differential demand and use of a certain nutrient might result not only from phylogenetic proximity but also from ecological convergence (Vieira and Vasconcelos 2015).

Contribution of C_3 and C_4 plants

As the carbon isotopic ratios ($\delta^{13}C$) differ strongly between C_3 and C_4 plants (Smith et al. 1976), they have been frequently used to determine the origin of the carbon consumed by heterotrophic organisms (Ponsard and Arditi 2000; Hood-Nowotny and Knols 2007).

Studies in the Amazonian savannas, for instance, showed that while some invertebrates have a diet based primarily on C_3 plants (including mainly trees and shrubs), lizards and anurans are usually more dependent on C_4-based (manly grasses) food chains (Magnusson et al. 1999). Our results suggest that the majority of the savanna ant species (43 species or 91.5% of the total) obtain most of their carbon (between 56% and 89%) from C_3-based food chains. Among the remaining species, three seem to acquire carbon from C_3 and C_4 plants in similar proportions, while *Acromyrmex landolti*, a fungus-growing grass-cutting ant, had a diet exclusively based on C_4 plants. Moreover, arboreal ants had, on average, proportionally more C_3 carbon than did the ground-dwelling ants. One possibility is that ants that forage on ground have a greater access to C_4-derived food than does those that forage in trees. Although this may well be the case in savannas, where the ground is covered mainly by C_4 grasses, it certainly is not in forests, where ground-dwelling ants forage on the leaf-litter. However, the leaf-litter has a great availability of detritivorous invertebrate prey, and these are known to have higher $\delta^{13}C$ values than herbivore insects and other invertebrate prey in general (Hyodo et al. 2010b). It is also known that predators present higher $\delta^{13}C$ values than their prey (Hyodo et al. 2010a, b), which helps to explain why we detected a positive correlation between the $\delta^{13}C$ and $\delta^{15}N$ values, at both the forest and the savanna communities.

Concluding remarks

The results of this paper indicate that there is a much greater similarity in the trophic structure of ant communities between forest and savanna than between the arboreal and ground nesting/foraging strata. This is explained at least partly by the differences in faunal composition, which were much more marked between strata than between habitats. Nevertheless, there is evidence that a given species may present some extent of plasticity in their diets depending on the habitat they occupy. Additionally, the fact that congeneric species that nest in different strata presented distinct isotopic signatures indicates that nesting habits played a key role in the evolution of feeding habits in ants. Lastly, our results indicate that few savanna ant species obtain carbon from C_4 grasses in spite of the high abundance of these plants in Neotropical savannas.

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Tables

Table 1. Number of species within each of the ant genera found in forests and savannas and in the arboreal and ground nesting/foraging strata in both habitats.

Genus	**Habitat**		**Stratum**		**Total**
	Forest	Savanna	Arboreal	Ground	
Acromyrmex	0	1	0	1	1
Atta	1	1	0	2	2
Azteca	2	1	2	0	2
Camponotus	12	10	15	1	16
Cephalotes	5	3	6	0	6
Crematogaster	0	2	1	1	2
Dolichoderus	1	1	1	0	1
Dorymyrmex	0	1	0	1	1
Ectatomma	3	6	2	4	6
Gnamptogenys	0	1	0	1	1
Labidus	1	1	0	1	1
Mycetagroicus	0	1	0	1	1
Mycoceourus	0	1	0	1	1
Myrmelachista	1	0	1	0	1
Neoponera	1	4	2	2	4
Nomamyrmex	1	0	0	1	1
Nylanderia	1	0	0	1	1
Odontomachus	2	1	0	3	3
Pachycondyla	2	1	0	2	2
Pheidole	4	3	0	5	5
Pogonomyrmex	0	1	0	1	1
Pseudomyrmex	1	2	2	0	2
Sericomyrmex	1	0	0	1	1
Solenopsis	2	2	2	2	4
Tapinoma	1	0	1	0	1
Trachymyrmex	1	2	0	2	2
Wasmmania	0	1	0	1	1

Table 2. Comparison of mean $\delta^{15}N$ values between savanna and forest ant colonies. Shown are means and ± SE of base-line corrected $\delta^{15}N$ isotope values.

Species	**Subfamily**	**Forest $\delta^{15}N$**	**Savanna $\delta^{15}N$**	***df***	***t*-value**	***p***
Camponotus bonariensis	Formicinae	-2.58 (0.37)	-2.313 (0.22)	6	0.67	0.530
Camponotus senex	Formicinae	-1.70 (0.38)	-1.655 (0.12)	6	0.14	0.894
Camponotus sericeiventri	Formicinae	-1.17 (0.42)	-0.654 (0.48)	6	1.24	0.261
Pseudomyrmex gracillis	Pseudomyrmycinae	-0.45 (0.32)	-1.674 (0.13)	6	4.13	*0.006*

Figures

Figure 1. Isotope composition ($\delta^{15}N$ and $\delta^{13}C$) of ants, plants, herbivores (caterpillar), predators (spiders), from **a** forest and **b** savanna. Mean and SD bars are shown for plants, herbivores and predators (for sample size and full species names, see Supplementary information)

Figure 2. Mean corrected $\delta^{15}N$ values of species within same genera, subfamily or tribe collected in both forest and savanna habitats. Sample size (f = number of species analyzed in forest, s = number of species analyzed in savanna) Attini: f = 3, s= 6; Camponotus: f = 12, s = 10; Cephalotes: f = 5, s = 3; Ectatomma: f = 3, s = 6; Pheidole: f = 4, s = 3; Ponerinae: f = 5, s = 6.

Figure 3. Mean ± SE ant corrected $\delta^{15}N$ for 20 species that occurred in both forest and savanna.

Figure 4. Estimated mean proportions of carbon from C_3 plants in the diets of **a** arboreal and **b** ground-dwelling ants from forest and savanna.

Figures

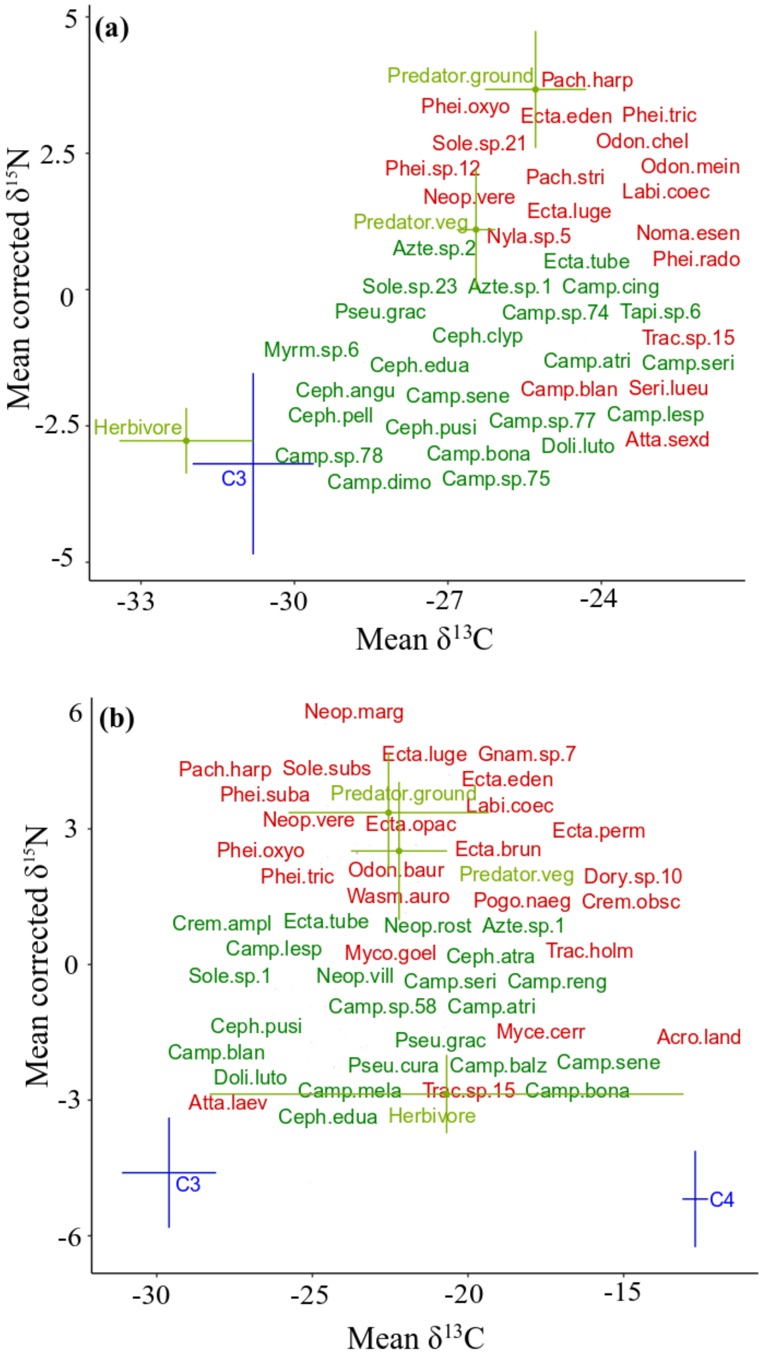

Figure 1.

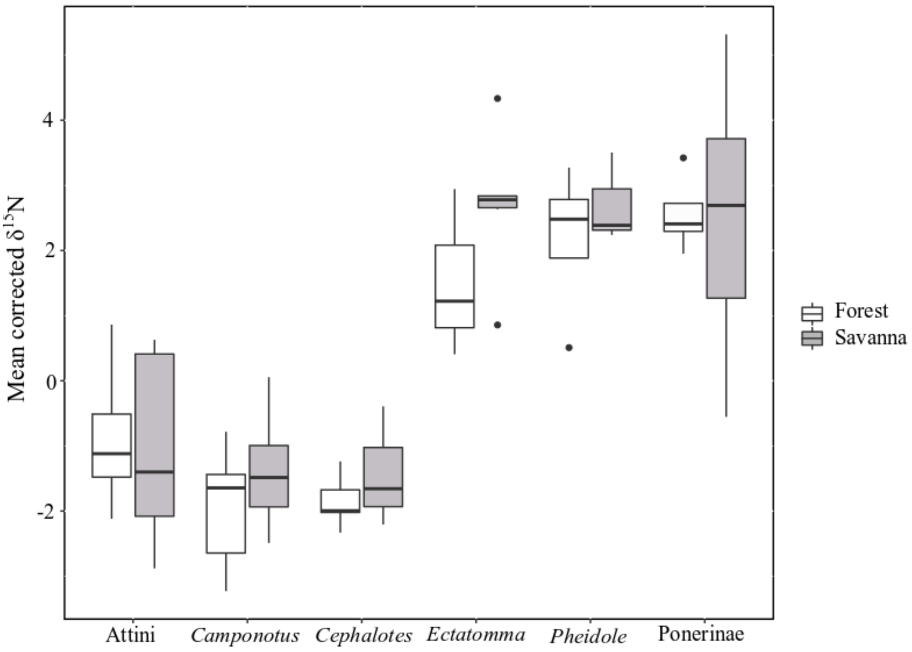

Figure 2.

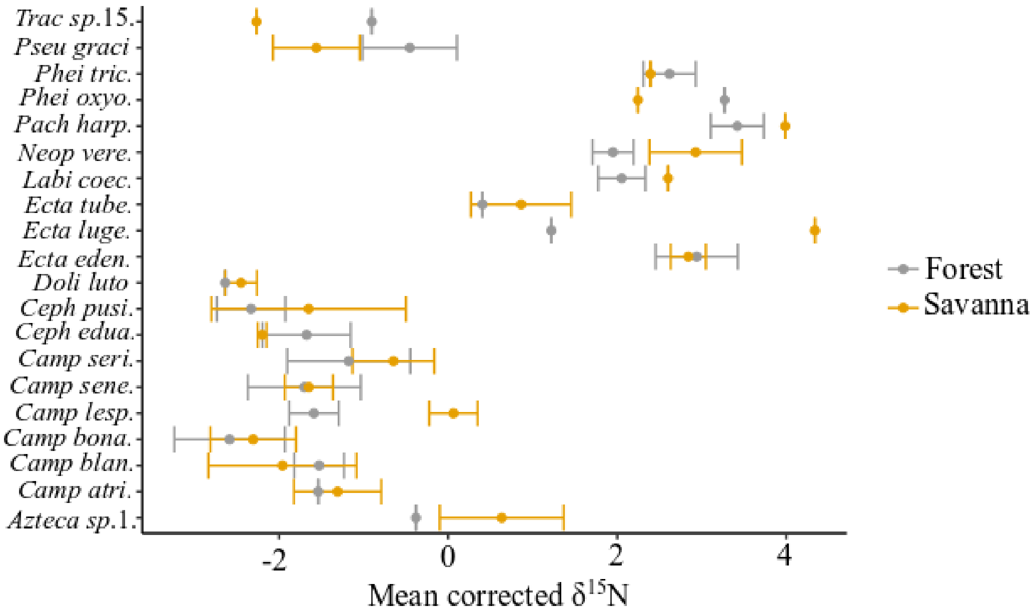

Figure 3.

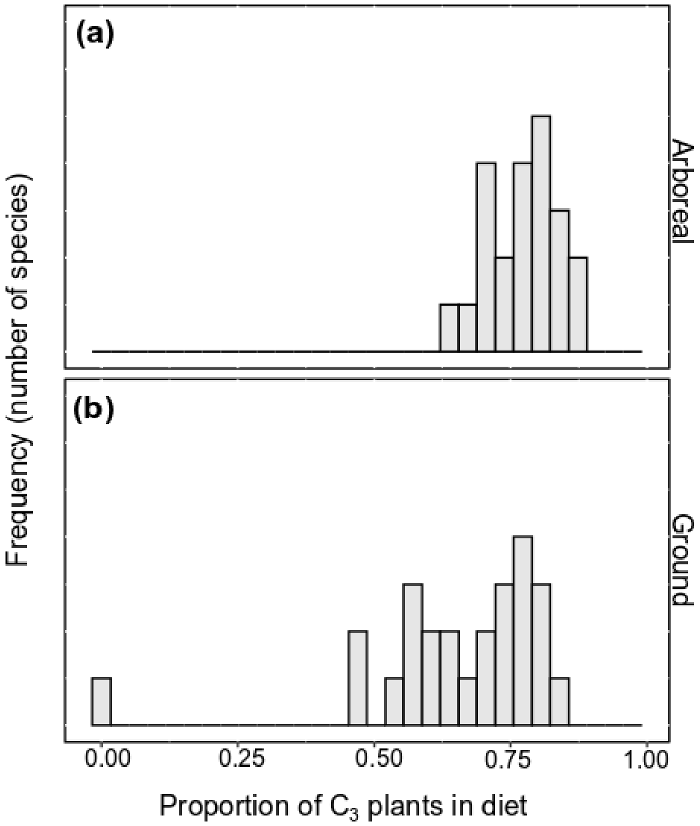
(a)
Arboreal
(b)
Ground
Frequency (number of species)
0.00
0.25
0.50
0.75
1.00
Proportion of C3 plants in diet

Figure 4.

Supplementary information

Table S1. Mean δ^{15}N and δ^{13}C values of ant species/morphospecies collected in forest and/or savanna, and the nesting/foraging stratum which they were found. Sample size is given in parenthesis after the species code

Species	Species code	Taxonomic group	Strata/Habitat	δ^{15}N mean	$\delta\ ^{13}$C mean
Dolichoderinae					
Azteca sp.1	Azte sp.1 (5)	Leptomyrmecini	arboreal/savanna	3.414	-23.021
Azteca sp.1	Azte sp.1 (1)	Leptomyrmecini	arboreal/forest	3.622	-25.498
Azteca sp.2	Azte sp.2 (3)	Leptomyrmecini	arboreal/forest	4.865	-26.337
Dolichoderus lutosus	Doli luto (2)	Dolichoderinae	arboreal/savanna	0.329	-25.239
Dolichoderus lutosus	Doli luto (1)	Dolichoderinae	arboreal/forest	1.365	-26.024
Dorymyrmex sp.10	Dori sp.10 (1)	Leptomyrmecini	ground/savanna	4.599	-21.605
Tapinoma sp.6	Tapi sp.6 (1)	Dolichoderinae	arboreal/forest	2.935	-25.43
Dorylinae					
Labidus coecus	Labi coec (1)	Dorylinae	ground/savanna	5.382	-22.566
Labidus coecus	Labi coec (2)	Dorylinae	ground/forest	6.057	-22.591
Nomamyrmex esenbeckii	Noma esen (2)	Dorylinae	ground/forest	5.056	-23.326
Ectatomminae					
Ectatomma bruneum	Ecta brun (1)	Ectatommini	ground/savanna	5.422	-21.68
Ectatomma edentantum	Ecta eden (2)	Ectatommini	ground/savanna	5.622	-23.189
Ectatomma edentantum	Ecta eden (3)	Ectatommini	ground/forest	6.945	-24.495
Ectatomma lugens	Ecta lugen (1)	Ectatommini	ground/savanna	7.12	-19.616
Ectatomma lugens	Ecta luge (1)	Ectatommini	ground/forest	5.224	-25.028
Ectatomma opaciventris	Ecta opac (3)	Ectatommini	ground/savanna	5.508	-22.033
Ectatomma permagnum	Ecta perm (1)	Ectatommini	ground/savanna	5.624	-20.77
Ectatomma tuberculatum	Ecta tube (3)	Ectatommini	arboreal/savanna	3.643	-22.937
Ectatomma tuberculatum	Ecta tube (1)	Ectatommini	arboreal/forest	4.409	-25.946
Gnamptogenys sp.7	Gnam sp.7 (1)	Ectatommini	ground/savanna	6.978	-20.602
Formicinae					
Camponotus atriceps	Camp atri (5)	Formicinae	arboreal/savanna	1.472	-23.038
Camponotus atriceps	Camp atri (1)	Formicinae	arboreal/forest	2.466	-25.525
Camponotus balzani	Camp balz (1)	Formicinae	arboreal/savanna	0.943	-23.412
Camponotus blandus	Camp blan (2)	Formicinae	arboreal/savanna	0.819	-26.246
Camponotus blandus	Camp blan (4)	Formicinae	ground/forest	2.477	-25.296
Camponotus bonariensis	Camp bona (3)	Formicinae	arboreal/savanna	0.473	-23.229
Camponotus bonariensis	Camp bona (5)	Formicinae	arboreal/forest	1.417	-26.307
Camponotus cingulatos	Camp cing (4)	Formicinae	arboreal/forest	3.22	-25.315
Camponotus dimorphus	Camp dimo (2)	Formicinae	arboreal/forest	0.842	-27.111
Camponotus lespesii	Camp lesp (2)	Formicinae	arboreal/savanna	2.842	-24.797
Camponotus lespesii	Camp lesp (4)	Formicinae	arboreal/forest	2.414	-25.108
Camponotus melanoticus	Camp mela (3)	Formicinae	arboreal/savanna	0.296	-23.78
Camponotus rengerii	Camp reng (1)	Formicinae	arboreal/savanna	1.853	-24.577
Camponotus senex	Camp sene (5)	Formicinae	arboreal/savanna	1.132	-22.324
Camponotus senex	Camp sene (3)	Formicinae	arboreal/forest	2.302	-25.756

Camponotus sericeiventri	Camp seri (5)	Formicinae	arboreal/savanna	2.133	-24.608
Camponotus sericeiventri	Camp seri (3)	Formicinae	arboreal/forest	2.826	-24.487
Camponotus sp.58	Camp sp.58 (5)	Formicinae	arboreal/savanna	1.609	-24.108
Camponotus sp.74	Camp sp.74 (2)	Formicinae	arboreal/forest	3.219	-24.757
Camponotus sp.75	Camp sp.75 (1)	Formicinae	arboreal/forest	0.772	-26.029
Camponotus sp.77	Camp sp.77 (2)	Formicinae	arboreal/forest	1.642	-26.296
Camponotus sp.78	Camp sp.78 (1)	Formicinae	arboreal/forest	1.183	-28.45
Myrmelachista sp.6	Myrm sp.6 (1)	Formicinae	arboreal/forest	2.667	-28.639
Nylanderia sp.5	Nyla sp.5 (1)	Formicinae	ground/forest	4.704	-25.228
Myrmicinae					
Acromyrmex landolti	Acro land (1)	Attini (fungus-growing)	ground/savanna	0.902	-11.649
Atta laevigata	Atta laev (2)	Attini (fungus-growing)	ground/savanna	-0.093	-25.084
Atta sexdens	Atta sexd (1)	Attini (fungus-growing)	ground/forest	1.884	-24.344
Cephalotes angustus	Ceph angu (1)	Attini (arboreal species)	arboreal/forest	2.008	-27.823
Cephalotes atratus	Ceph atra (3)	Attini (arboreal species)	arboreal/savanna	2.394	-24.504
Cephalotes clypeatus	Ceph clyp (2)	Attini (arboreal species)	arboreal/forest	2.765	-25.609
Cephalotes eduarduli	Ceph edua (2)	Attini (arboreal species)	arboreal/forest	2.328	-27.331
Cephalotes eduarduli	Ceph edua (2)	Attini (arboreal species)	arboreal/savanna	0.58	-25.162
Cephalotes pellans	Ceph pell (2)	Attini (arboreal species)	arboreal/forest	1.982	-27.708
Cephalotes pusillus	Ceph pusi (5)	Attini (arboreal species)	arboreal/savanna	1.129	-25.64
Cephalotes pusillus	Ceph pusi (2)	Attini (arboreal species)	arboreal/forest	1.67	-26.325
Crematogaster ampla	Crem ampl (1)	Crematogastrini	arboreal/savanna	3.473	-25.011
Crematogaster obscura	Crem obsc (2)	Crematogastrini	ground/savanna	4.415	19.0463
Mycetagroicus cerradensis	Myce cerr (1)	Attini (fungus-growing)	ground/savanna	1.386	-20.752
Mycocepurus goeldii	Myco goel (1)	Attini (fungus-growing)	ground/savanna	3.101	-22.96
Pheidole oxyops	Phei oxyo (1)	Attini (ground species)	ground/savanna	5.025	-24.709
Pheidole oxyops	Phei oxyo (1)	Attini (ground species)	ground/forest	7.274	-25.247
Pheidole radowskowisk	Phei rado (1)	Attini (ground species)	ground/forest	4.512	-22.739
Pheidole sp.12	Phei sp.12 (1)	Attini (ground species)	ground/forest	6.345	-25.604
Pheidole subarforest	Phei suba (1)	Attini (ground species)	ground/savanna	6.291	-24.537
Pheidole triconstricta	Phei tric (1)	Attini (ground species)	ground/savanna	5.173	-24.509
Pheidole triconstricta	Phei tric (2)	Attini (ground species)	ground/forest	6.622	-25.295
Pogonomyrmex naegii	Pogo naeg (1)	Pogonomyrmecini	ground/savanna	3.933	-22.008
Sericomyrmex lueuderwaldti	Seri leud (3)	Attini (fungus-growing)	ground/forest	2.476	-23.801
Solenopsis sp.1	Sole sp.1 (1)	Solenopsidini	arboreal/savanna	2.246	-26.183
Solenopsis sp.21	Sole sp.21 (1)	Solenopsidini	ground/forest	6.426	-25.59
Solenopsis sp.23	Sole sp.23 (2)	Solenopsidini	arboreal/forest	4.023	-26.424
Solenopsis substituta	Sole subs (1)	Solenopsidini	ground/savanna	6.549	-23.815
Trachymyrmex holmgreni	Trac holm (1)	Attini (fungus-growing)	ground/savanna	3.294	-19.611
Trachymyrmex sp.15	Trac sp15 (1)	Attini (fungus-growing)	ground/savanna	0.511	-24.31
Trachymyrmex sp.15	Trac sp.15 (1)	Attini (fungus-growing)	ground/forest	3.099	-24.325
Wasmannia auropunctata	Wasm auro (1)	Attini (ground species)	ground/savanna	4.91	-23.505
Pseudomyrmecinae					
Pseudomyrmex curacaensis	Pseu cura (1)	Pseudomyrmecini	arboreal/savanna	1.061	-25.022
Pseudomyrmex gracillis	Pseu grac (5)	Pseudomyrmecini	arboreal/savanna	1.221	-24.407
Pseudomyrmex gracillis	Pseu grac (3)	Pseudomyrmecini	arboreal/forest	3.549	-26.875

CAPÍTULO 2

Using morphological traits to predict the trophic position of Neotropical ants

Abstract

Morphology reflects the way in which organisms physically interact with their environment and it might influence their capability in exploit food resources. Many morphological traits of ants have hypothesized functions related to their feeding habits; however, few studies have integrated morphology and diet to provide insights into the trophic ecology of ant communities. In this study, I evaluated the relationship between the morphological traits of ants and their relative trophic position (RTP) using linear regressions with and without phylogenetic adjustment. It allowed me to determine if the patterns detected in morphology and diet are independent of the phylogenetic relationship among species. I also used multivariate regression models in order to select models that best predicted the variation in RTP among ant species. I collected ground-dwellers and tree-dwellers ant species from savannas and forests and measured their morphology and relative trophic position [using nitrogen isotopic signature ($\delta^{15}N$)]. Although weak, regression analyses showed many associations between individual traits and RTP. Ants with higher RTP values tended to be larger with relatively longer mandibles and longer petioles, but relatively smaller clypeus and heads, smaller eyes and eyes positioned less laterally, and had less spines and were less hairy than were the species with lower RTP values. Multivariate regression models explained a considerable part of the observed variation in RTP. Using data from all species combined, morphological traits explained 48% of the variance in RTP while by performing regression models taking into account the nesting/foraging strata and/or the taxonomic affinities of the species in separate, as much as 94% of the observed variation in RTP could be explained. These results indicate that morphological traits, individually, seem to be of little use in predicting the trophic positions of different ant species. However, the predictive power of these traits increased substantially when they were used in combination.

Key-words: Morphology, Phylogeny, Stable isotope, Trophic Position.

Introduction

The use of food resources by organisms is a result of the interaction between the availability of the resource in the environment and their individual capacity to exploit the resource. This individual's ability of organisms has a strong association with their morphology, which can facilitate or constrain their capability to perform specific tasks (e.g. to capture prey) (Wainwright 1994). Body size, for instance, is a morphological trait frequently associated with diet, and while some studies have indicated that trophic position within a given food web increases with body size (Cohen et al. 1993, Linzmaier et al. 2018), others have shown a negative relationship or even no association between trophic position and size (Burness et al. 2001, Hutchins et al. 2014).

In addition to body size, other morphological traits are likely to be important in determining the diet of a species. Mouthpart morphology, for example, was found to be correlated with diet preference in mites (Perdomo et al. 2012) and with the trophic position of amphipods (Hutchins et al. 2014). Among insects, and particularly among ants, many morphological traits have known or putative ecological functions, and these traits have been widely used in studies about the functional structure of communities and their responses various types of disturbance (Gibb and Parr 2013, Gibb et al. 2018, Liu et al. 2016). Although many morphological traits of ants have hypothesized functions related to feeding habits, few studies have evaluated whether ant morphology is a good predictor of trophic position (but see Gibb et al. 2015, Hanish et al. 2019).

Ants are a diverse and abundant group of insects and a useful taxon for the study of relationship between diet and morphology (Hölldobler and Wilson 1990, Feldhaar et al. 2010). Most ants can utilize a large variety of food resources, including nectar, seeds and arthropods, and the relative importance of the different type of resources to their diet as well as the ability to obtain these resources can be related to their morphology

(Traniello 1989, Pearce-Duvet et al. 2011, Blüthgen and Feldhaar 2010). For exemple, species with relatively longer legs tend to be faster than species with shorter legs, and thus can arrive earlier at freshly available food sources (Oster and Wilson 1978, Kaspari and Weiser 1999). Moreover, the size of food items collected by individual ant workers may be constrained by their body size (Blüthgen and Feldhaar 2010). Other morphological traits, as such head width, eye size and mandible size are often used as a measure of feeding mode (Fowler et al. 1991, Kaspari and Weiser 1999, Weiser and Kaspari 2006). However, it is not clear the extent to which variation in these traits are related to variations in the diet and trophic position of ants (Gibb et al. 2015).

Stable isotopic analyses have strongly improved our knowledge about the feeding ecology of ants (Davidson et al. 2003, Blüthgen et al. 2003, Fiedler et al. 2007, Gibb and Cunningham 2011, Pfeiffer et al. 2014, Vieira et al. unpublished). For instance, based on the relative proportion of the heavy ^{15}N to light ^{14}N isotopes ($\delta^{15}N$) in the body mass of different ant species, one is able to estimate the trophic position of these species in the community into which they are embedded (Ponsard and Arditi 2000, Hood-Nowotny and Knols 2007). Based on these kind of analyses, recent studies have evaluated the degree to which individual morphological traits of different ant species correlate with their delta ^{15}N signature (Gibb et al. 2015). Although significant correlations have been found for some traits at some communities (Gibb et al. 2015, Hanish et al. 2019), these correlations were not strong enough to be of any use in predicting the trophic position of a species whose delta N^{15} signature is unknown. Improving the predictive power of the relationship between ant morphology and trophic position would be of ultimate importance given that ant communities are often highly diverse and because many of the species that compose these communities are rare. For these latter species, as well for small-sized species, obtaining the minimum mass of ants required to perform the analyses can be difficult. Similarly, performing analyses for a large number of species can be both costly and time consuming.

In this study, I link morphological traits of Neotropical ant species to their relative trophic position (RTP) to determine in what extent morphological variation among species can be used to explain relative trophic position. I achieved this based on the estimation of the RTP of 70 species of ants (including species from forests and savannas and both arboreal and ground-dwelling species) and the measurement of 11 morphological traits assumed to be of relevance for the feeding ecology or behavior of ants (Table 1). I first examined the relationships between individual traits and RTP. Since traits are also a product of phylogenetic history (Felsenstein 1985), I also tested the relationship between morphology and RTP using phylogenetic adjustment. This allowed me to evaluate if the patterns detected in morphological traits and diet are independent of the phylogenetic relationship among species. Finally, using multivariate regression models I evaluated the models that best explained the observed variation in RTP among ant species based on the 11 morphological traits I measured. The resulting models were found to explain a substantial part of the observed variation in RTP, indicating that they have a relatively high predictive power.

Material and Methods

Study area

This study was performed in the Panga Ecological Reserve (PER), a 409-hectare protected area located 35 km south of the city of Uberlândia (MG), in southeastern Brazil (19°10’S, 48°24’O). The region presents a tropical climate characterized by rainy summers and dry winters, with an annual mean temperature between 20ºC and 25ºC, and an annual mean rainfall of 1600 mm (Rosa et al. 1991). The reserve is situated within the Cerrado biome and presents a variety of vegetation types, including savannas (which occupy around 71% of the area of the reserve) and semideciduos forests (which occupy 9% of the reserve). The savannas (locally known as cerrado *stricto sensu*) have scattered trees of up to 8 m in height and a ground layer covered with grasses, herbs and small shrubs. Semidecidual forests, have a relatively closed canopy composed of trees up to 12 m in height, and are found on the lower parts of the hillsides and are frequently bordered by gallery forests or typical savanna (Cardoso et al. 2009).

Pitfall sampling

Ants were collected in March and April 2016 along six transects, three in the savannas and three in the semideciduous forests. The transects were at located least 600 meters apart from each other and contained ten sampling points each. All points had a minimum distance of 40 meters from each other and were set with four pitfall traps (in a 2x2 m grid). These traps consisted of 250 ml plastic cups half-filled with water and detergent and buried into the ground with the rim at ground level. I also collected 1 m^2 of litter at each point, sifted this material in a 0.8 cm mesh which was then placed it in Winkler extractors for 48 hours.

Four other pitfall traps were taped onto the branches of the closest tree to each sampling point. Traps were between 2.5-3.5 m high in the savanna areas and between 6.0-8.5 m high in forests. Traps on trees were baited with a solution of urine (33%), detergent, and water (Powell et al. 2011). Caterpillars and spiders were actively collected along all transects (and each stratum) to provide a parameter of the isotopic composition of the local herbivores and predators. I collected at least three individuals of herbivores and three others of predators from each transect.

All traps remained active for 48 hours before being removed. After this, the collected ants were immediately water-washed to eliminate possible urine or detergent contaminations. The samples were then kept in alcohol and identified at the genus, morphospecies and, whenever possible, species level, through comparison with specimens deposited in the Zoological Collection of the Federal University of Uberlândia.

Stable isotope analyses

I obtained the nitrogen isotopic ratio of the most abundant ant species in each habitat, totaling 70 species. The number of samples per species varied from one to five (see chapter 1). Each of the collected ants had their gasters removed to eliminate any possible effect from recently ingested food items on the analysis (Blüthgen et al. 2003, Tillberg et al. 2006). Following this, the ants, herbivores, and predators were dried in an oven at 60 ºC for 48 hours and crushed with an agate mortar and pestle. The dried samples were put into small tin capsules in precisely weighed amounts (1.25-1.5 mg for arthropods). These capsules were then molded into a spherical shape, put on ELISA dishes and sent for analysis in a specialized laboratory (UC Davis Stable Isotope Facility, Davis, California, USA). The obtained results were expressed in delta (δ) notation per thousand, with an internationally acknowledged standard as reference. The equation for the isotopic signatures is defined as $\delta^{15}N$ (‰) = (Rsample – Rstandard) / Rstandard x 1.000, with R representing the molar ratio of the heavy/light isotope of the samples and the atmospheric air is the standard used for nitrogen (Rstandard = 0.0036765).

I used the mean $\delta^{15}N$ values to determine the relative trophic position of each ant species ants taking into account the habitat (savanna or forest) in which it was collected and the foraging stratum (ground or trees) were it is predominantly found (cf.

Vasconcelos et al. 2018). Then, I assessed the relative trophic position of each ant species based on δ^{15}N data of the ants, herbivores and predators collected in different habitats and strata. For this I first calculated the proportion of the dietary inputs to the ant species (ρ1) derived from different trophic levels. This was done following the equation provided by Tillberg et al. (2007) in which ΔN (the difference in δ^{15}N between two subsequent trophic levels) was assumed to be equal to 3.4‰ (cf. Deniro and Epstein 1981, Post et al. 2002), and where:

$\rho 1 = (\delta^{15}\text{Nants} - \delta^{15}\text{Npredators} - \Delta N)/(\delta^{15}\text{Nants} - \delta^{15}\text{Npredators} - \Delta N + \delta^{15}\text{Nherbivores} + \Delta N - \delta^{15}\text{Nants})$,

Mean values of δ^{15}N herbivores differed between forest and savanna habitats and thus the value used in the above equation was different depending on which habitat the species was found (see supplementary information in the first chapter). Values δ^{15}Npredators differed not only between habitats but also between strata (ground or arboreal) and so the values used in the equation depended both on the habitat in which the species was found and the foraging stratum (ground or trees) were it is predominantly found (cf. Vasconcelos et al. 2018). For species with mixed foraging habits (i.e. that forage at similar frequencies on ground and inn the arboreal vegetation) (Table S1) the δ^{15}Npredators was defined as the mean between the values for predators collected in the ground and those collected in the vegetation. Finally, to estimate the relative trophic position (RTP) of each ant species I used the following equation:

$$\text{TPants} = \text{TPpredators} + 1 - (\text{TPpredators} - \text{TPherbivores})\rho 1,$$

where TPpredators= 3 and TPherbivores= 2.

Morphometric ant measurements

Five workers per species were randomly selected to carry out a set of nine continuous morphometric measures and two ordinal measures selected to describe species traits. I considered only minor workers for morphologically dimorphic or polymorphic species. The list of traits and their putative ecological or physiological roles are presented in Table 1. Measurements of pinned specimens (± 0.01 mm) were taken using an ocular micrometer mounted on a Leica M80 stereomicroscope.

Data analysis

For statistical analysis, I used the average of individual trait values per species as a single value per morphological trait per species. Continuous trait measures (*head across eyes, mandible length, clypeus length, petiole length, femur length, scape length*) were standardized by Weber's length (trait value/ Weber's length) to obtain the value of the trait relative to the body size of the ant species. I subsequently $\log_{10}$ transformed the Weber's length values to approximate a normal distribution.

To test for associations between ant species and morphological traits, a principal component analysis (PCA) was performed using data on the six size-corrected traits, eye position, pilosity, number of spines and the log-transformed Weber's length of mean traits of each species. PCA reduces the number of variables while still retaining much of the information in the original dataset (Jolliffe 2005).

To assess the relationship between individual morphological traits and the RTP, I first performed simple linear regressions using data from all 70 species for which I had on the isotopic signature. I performed phylogenetic independent contrasts (PICs) (Felsenstein 1985, Garland and Ives 2000) using the package 'ape" (Paradis et al. 2004) in R version 3.6.1 (R Development Core Team, 2019). This method computes the differences between the character values of sister pairs of species, resulting in n-1(n= number of nodes) contrasts which are independent of each other in terms of evolutionary changes that occurred to produce differences between the two members of a single contrast (Garland et al. 1992). An ant phylogeny that included the same species presented in this study (Neves et al, unpublished data) was used to perform PICs between morphological traits and trophic position. Standard (i.e. without phylogenetic adjustment) regression analyses were conducted using the 'lm' function in R. Eventual differences in the magnitude of the relationship when using different regression methods are indicative of the relative importance of deeper versus recent divergences in trait evolution in explaining the observed patterns (Gibb et al. 2015).

In order to find a model (or models) that best predicted the RTP of the 70 ant species, I used stepwise multiple regression analyses, in which the nine continuous and the two ordinal traits I measured were included as predictor variables. I assessed collinearity among the predictor variables using Pearson simple correlations and since the predictors were not strongly correlated ($r > 0.8$) all were maintained in the analyses. The residuals of all models were also analyzed to verify the homoscedasticity of the data. Considering the large number of morphological traits, I adopted the "Backward elimination" as the method to select a set of variables that provide the best adequate model. In backward selection I started with all morphological measures and decided which variables would be eliminated based on the smallest t-value, lowest partial F and highest p-value. Each time a variable was removed I refitted the model. This procedure stopped the selection when all predictor variables that were included in the model presented a P-value < 0.15.

A total of seven regression models (each using a different set of species as described in the Results section) were performed and the relationship I found between the dependent variable (RTP) and the predictor variables (morphological traits) were represented by a regression equation for each model. I used theses equations to calculate the predicted RTP of the ants for each model. To test the accuracy of the models, I plotted the observed and estimated values, eventually calculating a new coefficient of determination (R^2) when values estimated for different species were based on more than one regression equation.

In order to validate my model, I utilized the observed RTP of other five ant species which were not included in these analyses (F.C. Camarota, unpublished data), as a parameter of the accuracy of the model. For that, I calculated the estimated RTP using the regression equations derived from the present study and compared the resulting estimated values with the observed values.

Results

Principal component analysis

Principal components one (PC1) and two (PC2) described, respectively, 21.7% and 20.1% of the morphological trait variation of the 70 ant species (Table 2). PC1 was positively associated with three traits (relative clypeus length, relative size of the head across eyes, and number of spines) and negatively related with body size. PC2 was negatively related to relative eye length and with eye position and positively with relative mandible and femur lengths. Most arboreal species presented relatively larger eyes or eyes that were positioned more dorsally than the species that nest and forage on ground. Most Myrmicinae had relatively larger clypeus, whereas the poneromorphs and most Camponotini had larger body sizes. The fungus-growing ants differed from most other ants by presenting more spines and relatively longer femurs (Fig. 1).

Relationship with individual traits

Using standard regressions, I found that five morphological traits were significant related with relative trophic position (RTP), including eye position, relative mandible length, relative petiole length, relative eye length and pilosity (Table 3). For three of these traits (eye length, mandible length and petiole length) the relationship with RTP remained significant after adjustment for phylogeny. In addition, a weak, though significant, relationship with Weber's length, head across eyes, clypeus length and number of spines was detected using phylogenetic regressions (Table 3).

Multiple regressions

Using data from all 70 species combined I found that morphological traits explained 48% of the variance in RTP. Only four traits were included in the selected model, the one including clypeus and mandible length, pilosity and number of spines (Table 4). Plotting the observed and estimated trophic position values, I found that the multiple regression equation tended to overestimate the trophic position of the species with a more herbivorous diet and underestimate that of the more predatory species (Fig. 2). I then performed two regression models in separate: one with the species that have a predominantly arboreal habit (and thus with a more herbivorous diet) and one with the ground-dwelling species. The model for the arboreal ants included five traits and explained 68.2% of the variance in relative trophic position whereas that for the ground-dwelling species also included five traits and explained 70.6% of the variance (Table 4). When I plotted the observed and estimated values from these two models, it was clear the predictive power to predict the RTP of the ant species in general increased substantially (Fig. 3); however the trend towards under or overestimating the trophic position of some species was still evident, notably for those of the tribes Attini and

Camponotini. This problem was minimized by building models for the species from these tribes in separate (Table 4), and when this was done the coefficient of determination between the observed and estimated values for all species became very high ($r^2 = 0.94$, Fig. 4).

These last models showed to be effective in predicting the RTP of five ant species that were not included in these multiple regression analyses, with estimated trophic position values very similar to the observed ones (Table 5).

Discussion

Morphology and diet have been integrated to provide insights into the trophic ecology of many aquatic species, including fishes and invertebrates (Lujan et al 2011, Hutchins et al. 2014, Linzmaier 2018), but few studies have applied this approach to insects (but see Barton et al. 2011, Gibb et al. 2015, Hanish et al. 2019). Here, I evaluated the relationship between the morphological traits of ants (a dominant insect group in most terrestrial ecosystems) and their relative trophic position (RTP) using linear regressions with and without phylogenetic adjustment. I also used multivariate regression models with the specific goal of selecting models that best predicted the observed variation in RTP among ant species. This was accomplished by using data on the nitrogen isotopic signature ($\delta^{15}N$) of 70 Neotropical ant species and by measuring 11 morphological traits – with known or presumed ecological functions in food retrieval and feeding habits (Feener et al. 1988, Fowler et al. 1991, Weiser and Kaspari 2006, Wittlinger et al. 2007) – of these same species. Both phylogenic and standard regressions showed weak associations between individual traits and RTP. In contrast, multivariate regression models explained a considerable part of the observed variation in RTP. Moreover, four regression models, each including different sets of species showed high levels of accuracy in estimating the RTP of Neotropical ant species.

A number of morphological traits were significantly correlated with RTP. In particular, I found that species with higher RTP values tended to be larger and have relatively longer mandibles and longer petioles, but relatively smaller clypeus and heads, smaller eyes and eyes positioned more laterally, and had less spines and were less hairy than were the species with lower RTP values (Table 3). Among the species with the highest RTP values are some poneromorph species, such as *Neoponera marginata*, *Ectatomma lugens*, *Gnamptogenys sp.*7 and *Pachycondyla harpax*, all of which are considered predatory and which, consequently, are reported to have elevated nitrogen isotopic signatures (Hanish et al. 2019). Those with low RTP values, included ant species that obtain most part of their diet from plant fluids or insects' exudates, as is the case for many arboreal species (Davidson et al. 2003) and species of attine fungus-growing ants, notably the higher attines, which cultivate their fungus on plant substrates (Hölldobler and Wilson 1990).

In their study of Australian ants, Gibb et al. (2015) also found that several morphological traits were significant correlates of trophic position (as measured by δ^{15}N values). They also stated that similar patterns were found when using regressions with or without phylogenetic adjustment. Similarly, here, the simple linear regression coefficients presented the same sign for all the traits I analyzed, except one, in both the adjusted and unadjusted regressions. However, for only three traits the coefficients were significant in the two types of regression, indicating that both recent and distant evolutionary divergences were important in determining the relationship between morphology and trophic position (cf. Gibb et al. 2015). Among the other six traits, four (Weber's length, relative head size, relative clypeus length and number of spines) showed a significant relationship only when using the adjusted regression and two (pilosity and relative eye position) only when using the unadjusted one. In the latter case deeper as opposed to recent trait divergences in the phylogeny seem to have been more important in determining the relationship between diet (RTP) and morphology, whereas in the former the opposite seems to be true. Previous studies indicate that several morphological traits of ants have a strong phylogenetic signal (Liu et al. 2016), but our results suggest that phylogenetic conservatism helps to explain the relationship between morphology and diet for only some of these traits.

Regardless of the importance of phylogenetic conservatism in driving the patterns we detected, it is clear that, overall, the relationships between individual, morphological traits analyzed and RTP were weak (Table 2). Similarly, among the 13 morphological traits analyzed by Gibb et al. (2015), only four showed a significant relationship with $\delta^{15}N$ and, in all these cases, the trait explained only 17% or less of the variation in $\delta^{15}N$. Together these results suggest that morphological traits, individually, seem to be of little use in predicting the trophic positions of different ant species. Nevertheless, I showed here that the predictive power of these traits increased substantially when they were used in combination. A multiple regression model using data from all species retained four traits, which together explained 48% of the variation in RTP. Furthermore, I found that the predictor power of multiple regression models improved substantially when taking into account the nesting/foraging strata and/or the taxonomic affinities of the species included in the model. Arboreal and ground-dwelling species tend to have both distinct feeding preferences and morphologies (Yanoviak and Kaspari 2000, Kaspari and Yanoviak 2001, Vieira et al. unpublished, Fig. 2) and so by building a separate model for each of these two ant groups we increased our predictive power in 72%. However, the use of these two models still resulted in the over or underestimation of the true RTPs of some species, notably among the attines and the

Camponotini. Attines and Camponotini have a low RTP but they have some morphological characteristics similar to that of predatory species including relatively large mandibles (among attines) or large body sizes (among Camponotini). By building four separate models (one with all arboreal species, except the Camponotini, one with all ground-dwellers, except the attines, and the attines only, and one with the Camponotini only) as much as 94% of the observed variation in RTP could be explained. Although more rigorous tests about the adequacy of these models are needed, our preliminary tests indicate that it is possible to infer the trophic position of ants using morphological data with certain precision.

In conclusion, I have found that although several morphological traits were correlated with the trophic position of ants, in general these correlations were weak. Nevertheless, by combining data from different traits in multiple regression models I found that morphology has a strong potential to predict the relative trophic position of ants, notably when one takes into the account the nesting preferences and morphological peculiarities of certain ant groups. Thus, morphological traits have the potential to increase our understanding about the trophic structure of ant communities in different ecosystems.

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Tables

Table1. List of eleven morphological traits measured and the abbreviations given to these traits and their hypothesized ecological functions. All lengths were measured in millimeters (mm).

Morphological trait	**Hypothesized functional significance**
Continuous measures	
Weber's length (WL)	Indicative of body size (Weber, 1938), correlates with metabolic characteristics and habitat complexity
Head across eyes (HAE)	Indicative of the size of spaces through which ant can pass and indicate of mandibular musculature
Mandible length (ML)	Indicative of diet; longer mandibles could allow predation of larger prey (Fowler et al. 1991)
Clypeus length (CL)	Clypeus indicates sugar feeding, related to liquid absorption abilities (Davidson et al. 2004)
Petiole length (PL)	Correlated to behavior of predatory species and their performance in prey capture
Femur length (FL)	Indicative of foraging speed (Feener et al. 1988)
Eye position (EP)	Related to hunting method (Fowler et al. 1991) or the component of the habitat occupied (Gibb and Parr 2013)
Scape length (SL)	Indicative of sensory abilities; longer scape facilitates the following of pheromone trails (Weiser and Kaspari 2006)
Eye length (EL)	Indicative of foraging period, food-searching behavior and habitat type (Bauer et al. 1998)
Count measures	
Spines (alitrunk) (0= No spine; 1= one to five spines, 2= five to nine spines; 3= more than ten spines)	Spines may act as an anti-predation mechanism (Michaud and Grant 2003)
Pilosity (0 = No or very few hairs; 1 = a sparse but regular covering of hairs; 2 = a consistent, moderate covering of hair; 3 = very dense hair covering	Hairs may increase tolerance to dehydration or may relate to mechanoreception (Wittlinger et al. 2007)

Table 2. Loadings of the first three axes of the principal component analysis for the eleven morphological traits and the percentage of variance for which each axis accounted. Correlation values > 0.3 are highlighted in bold.

Morphological trait	**PC1**	**PC2**	**PC3**
Weber's length	**-0.41**	0.22	-0.1
Relative clypeus length	**0.47**	-0.17	-0.25
Pilosity	-0.19	-0.1	-0.27
Relative petiole length	-0.29	-0.1	-0.14
Relative femur length	0.21	**0.37**	-0.29
Relative eye length	0.16	**-0.50**	-0.01
Relative scape length	0.26	0.22	**-0.54**
Relative mandible length	0.08	**0.38**	-0.05
Relative head across eyes	**0.39**	-0.24	**0.35**
Eye position	0.02	**-0.38**	**-0.47**
Spine	**0.33**	0.3	0.28
Cumulative variance explained	27%	41%	59%

Table 3. *R^2*, standardized coefficients and significance for regressions with adjustment for phylogeny using PICs and linear regressions testing the relationship between the morphological trait predictor variables and the diet based on relative trophic position response variable for 70 ant species collected in savanna and forest. Statistical significance * P < 0.05, ** P < 0.01, *** P < 0.001.

Trait	**Unadjusted R^2**	**Unadjusted Coefficient**	**Adjusted R^2**	**Adjusted Coefficient**
Weber's length	0.00	0.021	0.10**	0.310
Relative head Across Eyes	0.03	-0.186	0.19**	-0.460
Relative clypeus length	0.03	-0.185	0.13**	-0.370
Eye position	0.04*	-0.262	0.01	-0.104
Relative mandible length	0.30***	0.593	0.12**	0.350
Relative petiole length	0.10*	0.306	0.19**	0.454
Relative femur length	0.00	0.008	0.02	-0.181
Relative scape length	0.00	0.095	0.00	-0.063
Spine	0.01	-0.073	0.19***	-0.374
Pilosity	0.04*	-0.234	0.02	-0.142
Relative eye length	0.10**	-0.358	0.11**	-0.347

Table 4. Regression models, and their regression coefficients, intercept and coefficient of determination (R^2), evaluating the relationship between morphological traits and the relative trophic position of Neotropical ant species. Shown are the seven models and the variables which were included. (Model 1: all 70 species; Model 2: arboreal species only; Model 3: ground-dwelling species only ; Model 4: only species of fungus-growing ants ('attine'); Model 5: arboreal species (except for species of Camponotini), Model 6: only species of Camponotini tribe and Model 7: ground-dwelling species (except the attine and Camponotini species).

Model	**Intercept**	**Weber's length ($\log_{10}$)**	**Relative head-across-eyes**	**Relative mandible length**	**Relative clypeus length**	**Relative petiole length**	**Relative femur length**	**Eye-position**	**Relative scape length**	**Relative eye length**	**Spines**	**Pilosity**	R^2
1	2.304	-	-	2.572	-1.093	-	-	-	-	-	-0.148	-0.111	0.480
2	2.556	-	-	2.150	-	-2.234	0.592	-	-0.633	-1.187	-	-	0.682
3	3.844	-0.766	-1.109	-	-1.799	3.090	-	-	-	-	-	-0.191	0.706
4	2.807	-0.710	-	-	-	-	-	-	-	-	-	-	0.416
5	2.975	-0.259	-0.353	1.623	-	-2.261	0.937	-	-0.762	-1.299	-	-	0.955
6	1.290	1.566	-	-	-	-	-	-	-	3.221	-	-	0.706
7	4.184	-0.506	-1.624	0.979	-	1.017	-	-	-0.736	1.453	-	-0.053	0.710

Table 5. Observed and estimated relative trophic position (RTP) for five ant species not included in the multiple regression analyses.

Species	**Group**	**RTP observed**	**RTP estimated (mean ±SE)**
Camponotus sp.37	Camponotini	2.409	2.285 (0.705)
Cephalotes maculatus	Arboreal	2.178	2.175 (0.542)
Cephalotes persimilis	Arboreal	2.428	2.426 (0.568)
Cephalotes grandinosus	Arboreal	2.295	2.325(0.562)
Pseudomyrmex urbanus	Arboreal	2.480	2.449 (0.251)

Figures

Figure 1. Principal Component Analysis ordination (PCA) for 70 species collected in forest and savanna using the eleven selected traits (Table1). Colors represent species collected on the ground (red) or vegetation (for full species names, see Supplementary information).

Figure 2. Comparison between the observed and predicted relative trophic position (RTP) according to multivariate regression model # 1 (see Table 4) which included data for all 70 ant species. The line represents the 1:1 equivalence line.

Figure 3. Comparison between the observed and predicted relative trophic position (RTP) according to multivariate regression model # 2 and model # 3 (see Table 4) which included data for arboreal species only and ground-dwelling species only, respectively. The line represents the 1:1 equivalence line.

Figure 4. Comparison between the observed and predicted relative trophic position (RTP) according to multivariate regression model # 4, model # 5, model # 6 and model #7 (see Table 4) which included data for only species of fungus-growing ants ('attine'), arboreal species (except for species of Camponotini), Camponotini species and ground-dwelling species (except the attine and Camponotini species), respectively. The line represents the 1:1 equivalence line.

Figures

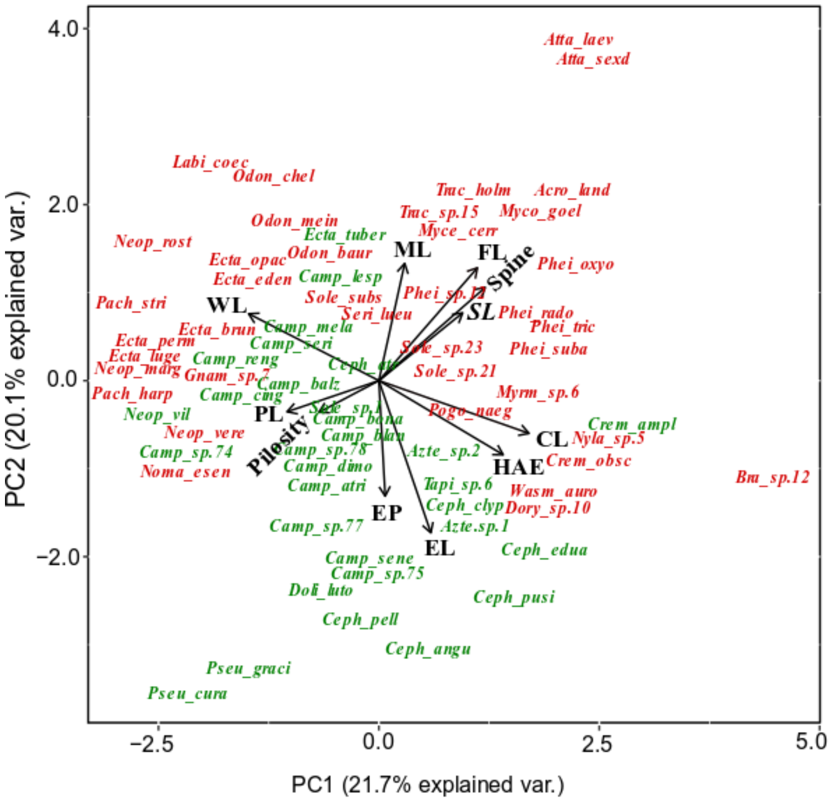

Figure 1.

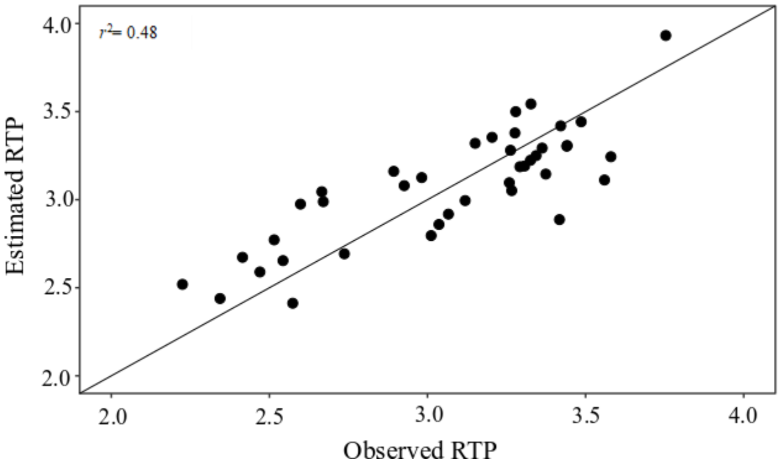

Figure 2.

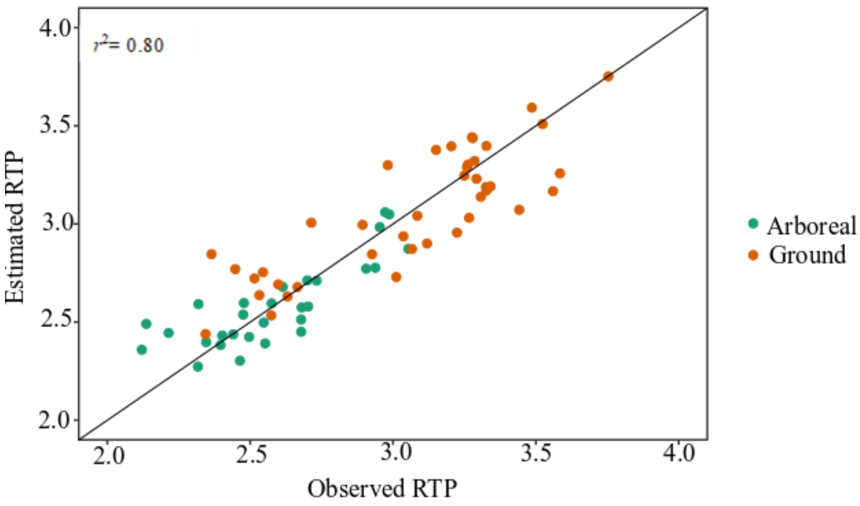

Figure 3.

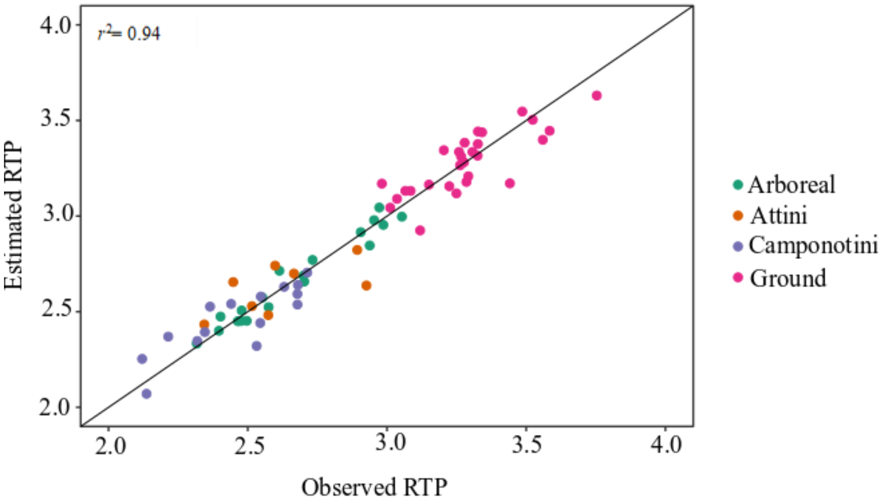

Figure 4.

Supplementary information

Table S1. List of the ant species/morphospecies collected in forest and/or savanna, the nesting/foraging affinities, the stratum which they were found, the habitat and tribe used in the models and their relative trophic position.

Species/Morphospecies	Specie code	Habitat (Vasconcelos et al. 2018)	Habitat	Habitat/Tribe	Relative Trophic Position
Dolichoderinae					
Azteca sp.1	Azte_sp.1	Arboreal	Arboreal	Arboreal	2.937
Azteca sp.2	Azte_sp.2	Arboreal	Arboreal	Arboreal	3.053
Dolichoderus lutosus	Doli_luto	Arboreal	Arboreal	Arboreal	2.317
Dorymyrmex sp.10	Dory_sp.10	Ground	Ground	Ground	3.15
Dorylinae					
Labidus coecus	Labi_coec	Ground	Ground	Ground	3.285
Nomamyrmex esenbeckii	Noma_esen	Ground	Ground	Ground	3.066
Ectatomminae					
Ectatomma bruneum	Ecta_brun	Ground	Ground	Ground	3.292
Ectatomma edentantum	Ecta_eden	Ground	Ground	Ground	3.326
Ectatomma lugens	Ecta_luge	Ground	Ground	Ground	3.584
Ectatomma opaciventris	Ecta_opac	Ground	Ground	Ground	3.307
Ectatomma permagnum	Ecta_perm	Ground	Ground	Ground	3.327
Ectatomma tuberculatum	Ecta_tube	Mixed	Arboreal	Arboreal	2.972
Gnamptogenys sp.7	Gnam_sp.7	Ground	Ground	Ground	3.559
Formicinae					
Brachymyrmex sp. 12	Brac_sp. 12	Ground	Ground	Ground	3.084
Camponotus atriceps	Camp_atri	Arboreal	Arboreal	Camponotini	2.546
Camponotus balzani	Camp_balz	Arboreal	Arboreal	Camponotini	2.44
Camponotus blandus	Camp_blan	Mixed	Ground	Camponotini	2.531
Camponotus bonariensis	Camp_bona	Arboreal	Arboreal	Camponotini	2.345
Camponotus cingulatos	Camp_cing	Ground	Arboreal	Camponotini	2.678
Camponotus dimorphus	Camp_dimo	Arboreal	Arboreal	Camponotini	2.136
Camponotus lespesii	Camp_lesp	Mixed	Ground	Camponotini	2.713
Camponotus melanoticus	Camp_mela	Mixed	Ground	Camponotini	2.364
Camponotus rengerii	Camp_reng	Mixed	Ground	Camponotini	2.63
Camponotus senex	Camp_sene	Mixed	Ground	Camponotini	2.544
Camponotus sericeiventri	Camp_seri	Arboreal	Arboreal	Camponotini	2.68
Camponotus sp.37	Camp_sp37	Arboreal	Arboreal	Camponotini	2.409
Camponotus sp.74	Camp_sp.74	Arboreal	Arboreal	Camponotini	2.678
Camponotus sp.75	Camp_sp.75	Arboreal	Arboreal	Camponotini	2.12
Camponotus sp.77	Camp_sp.77	Arboreal	Arboreal	Camponotini	2.318

Camponotus sp.78	Camp_sp.78	Arboreal	Arboreal	Camponotini	2.214
Myrmelachista sp.6	Myrm_sp.6	Arboreal	Arboreal	Arboreal	2.552
Nylanderia sp.5	Nyla_sp.5	Ground	Ground	Ground	3.011
Tapinoma sp.6	Tapi_sp.6	Arboreal	Arboreal	Arboreal	2.613
Myrmicinae					
Acromyrmex landolti	Acro_land	Ground	Ground	Attini	2.515
Atta laevigata	Atta_laev	Ground	Ground	Attini	2.343
Atta sexdens	Atta_sexd	Ground	Ground	Attini	2.573
Cephalotes angulatus	Ceph_angu	Arboreal	Arboreal	Arboreal	2.402
Cephalotes atratus	Ceph_atra	Arboreal	Arboreal	Arboreal	2.732
Cephalotes clypeatus	Ceph_clyp	Arboreal	Arboreal	Arboreal	2.574
Cephalotes eduarduli	Ceph_edua	Arboreal	Arboreal	Arboreal	2.475
Cephalotes grandinosus	Ceph_gran	Arboreal	Arboreal	Arboreal	2.295
Cephalotes maculatus	Ceph_macu	Arboreal	Arboreal	Arboreal	2.178
Cephalotes pellans	Ceph_pell	Arboreal	Arboreal	Arboreal	2.396
Cephalotes persimilis	Ceph_pers	Arboreal	Arboreal	Arboreal	2.428
Cephalotes pusillus	Ceph_pusi	Arboreal	Arboreal	Arboreal	2.47
Crematogaster ampla	Crem_ampl	Mixed	Arboreal	Arboreal	2.95
Crematogaster obscura	Crem_obsc	Ground	Ground	Ground	3.11
Mycetagroicus cerradensis	Myce_cerr	Ground	Ground	Attini	2.598
Mycocepurus goeldii	Myco_goel	Ground	Ground	Attini	2.893
Pheidole oxyops	Phei_oxyo	Ground	Ground	Ground	3.223
Pheidole radowskowisk	Phei_rado	Ground	Ground	Ground	2.981
Pheidole sp.12	Phei_sp.12	Ground	Ground	Ground	3.266
Pheidole subarmata	Phei_suba	Ground	Ground	Ground	3.441
Pheidole triconstricta	Phei_tric	Ground	Ground	Ground	3.249
Pogonomyrmex naegii	Pogo_naeg	Ground	Ground	Ground	3.036
Sericomyrmex lueuderwaldti	Seri_lueu	Ground	Ground	Attini	2.665
Solenopsis sp.1	Sole_sp.1	Arboreal	Arboreal	Arboreal	2.702
Solenopsis sp.21	Sole_sp.21	Ground	Ground	Ground	3.278
Solenopsis sp.23	Sole_sp.23	Arboreal	Arboreal	Arboreal	2.905
Solenopsis substituta	Sole_subs	Ground	Ground	Ground	3.485
Trachymyrmex holmgreni	Trac_holm	Ground	Ground	Attini	2.926
Trachymyrmex sp.15	Trac_sp.15	Ground	Ground	Attini	2.447
Wasmannia auropunctata	Wasm_auro	Ground	Ground	Ground	3.204
Ponerinae					
Neoponera marginata	Neop_marg	Ground	Ground	Ground	3.753
Neoponera rostrata	Neop_rost	Arboreal	Arboreal	Arboreal	2.986
Neoponera verenae	Neop_vere	Ground	Ground	Ground	3.341
Neoponera villosa	Neop_vill	Arboreal	Arboreal	Arboreal	2.7
Odontomachus bauri	Odon_baur	Ground	Ground	Ground	3.262
Odontomachus chelifer	Odon_chel	Ground	Ground	Ground	3.325
Odontomachus meinerti	Odon_mein	Ground	Ground	Ground	3.276

Pachycondyla harpax	Pach_harp	Ground	Ground	Ground	3.523
Pachycondyla striata	Pach_stri	Ground	Ground	Ground	3.258
Pseudomyrmecinae					
Pseudomyrmex curacaensis	Pseu_cura	Arboreal	Arboreal	Arboreal	2.464
Pseudomyrmex gracillis	Pseu_grac	Arboreal	Arboreal	Arboreal	2.496
Pseudomyrmex urbanus	Pseu_urba	Arboreal	Arboreal	Arboreal	2.48

CAPÍTULO 3

Effects of land-use change on the trophic structure and morphological trait composition of Neotropical ant assemblages

Abstract

Anthropogenic disturbances have been increasingly modifying the structure of natural ecosystems, with cascading effects on their component species and the ecological services they provide. Many studies have used taxonomic diversity as the sole indicator of the effects of habitat disturbance on plant and animal communities, even though in many cases information on the morphological traits of species can help better understand these responses. The Brazilian Savanna (Cerrado) is one of the most threatened biomes of the world, particularly due to the rapid expansion of agriculture. In this study, I evaluated the extent to which changes in land-use and land cover in the Cerrado affects the trophic and morphological structure of ant communities. I sampled ants in five habitats representing a gradient of tree woody cover: semideciduous forests, eucalyptus plantations, savannas, planted pastures, and soy plantations. Ground-dwelling ants were sampled along line transects using pitfall traps. I then selected six continuous morphometric measures and two ordinal measures to describe species traits. Moreover, I used data on ant morphology to calculate their relative trophic position. In total, I recorded 163 species of ants belonging to 42 genera across all land-use types. Soy plantations presented the lowest species richness, whereas savannas the highest. Pasture, eucalyptus plantations and forests had similar species richness. The morphological and trophic structure of ant assemblages were affected by land-use changes and certain morphological traits were strongly correlated with the features of the habitat in which they occurred. Ants in habitats with greater tree cover tended to be larger and presented relatively smaller eyes and dorsally-positioned eyes compared to ants in more open habitats. Furthermore, extremes in morphological traits were most strongly associated with soy plantations, which were dominated by small, hairless, long-legged ants with laterally positioned eyes. Mean relative trophic position was significantly higher in the assemblages from soy plantations and pastures than in those from forest, savanna or eucalyptus plantations.

Key-Words: *Cerrado*, functional traits, morphology, trophic position

Introduction

Understanding the mechanisms that shape communities in different ecosystems, in terms of both species composition and functional structure, has been a central goal in community ecology and biological conservation (McGill et al. 2006). However, a widely recognized process that affects both the diversity and composition of communities is the habitat modification resulting from natural or anthropogenic disturbances (Dornelas 2010). Anthropogenic disturbances are increasingly modifying the structure of natural ecosystems leading to a drastic biodiversity loss (Foley et al. 2005). The replacement of forests, savannas and other natural habitats by agroecosystems (e.g., crops, pastures) can lead to cascading effects on their component species and the ecological services they provide (Matson et al. 1997, Foley et al. 2005, Walther 2010, Pacheco et al. 2013, Solar et al. 2016). Therefore, a better understanding of the impacts of these rapid changes in land use and land cover on biodiversity is urgently needed (Nock et al. 2016).

Many studies have used taxonomic diversity as the sole indicator of the effects of habitat disturbance on plant and animal communities (Austrheim1999, Vellend et al. 2007, Pacheco et al. 2013, Martello et al. 2016). However, it has been suggested that a trait-based approach is also necessary for a better understanding of the effects of anthropogenic disturbance on the structure of ecological communities and the functioning of ecosystems (McGill et al. 2006, Nock et al. 2016). Functional traits are defined as any measurable features (e.g., morphological, structural, or phenological) at the individual level that influence species performance (McGill et al. 2006) and their response to environmental changes (Violle et al. 2007). Many functional traits can be useful to increase our understanding of how species traits interact with the environment (Gibb et al. 2015, McGill et al. 2006, Gibb and Parr 2013). Among insects, and particularly among ants, morphological traits provide the greatest potential, as they can be easily measured even in cryptic and poorly known species (Gibb and Parr et al. 2013). Moreover, morphological traits present relationships with many ecological functions and have been successfully employed in studies about the functional structure of ant communities and their responses to various types of disturbance (Gibb et al. 2015, Liu et al. 2016, Silva and Brandão 2010, Nooten et al. 2019).

Many of these studies have shown that disturbance act as an important filter that can affect the morphological structure of ant communities. As the structural complexity of habitats is a key factor for the anatomical traits of ants (Nooten et al. 2019), the reduction in vegetative structure due to disturbance might select for species with certain traits. The "size-grain hypothesis" (Kaspari and Weiser 1999) predicts that in more complex environments, ants would have a smaller size and proportionally smaller legs than ants in planar environments. Several studies in habitats with different degrees of complexity have corroborated with this hypothesis (Arnan et al. 2013, Gibb and Parr 2013, Gibb et al. 2015). Nevertheless, other studies have found different results. For example, ants collected in a vegetation gradient with different levels of complexity presented smaller size in structurally less complex habitats and larger size in more complex habitats (Guilherme et al. 2019, Nooten et al. 2019). Based on these inconsistent results, the link between morphological traits and the environment still needs to be better explored.

Morphological traits can also be used as a proxy to determine the trophic position of ant species, which is another important functional trait (Gibb et al. 2015, Hanish et al. 2019, Vieira et al. unpublished). There is evidence that habitat disturbance, notably land-use changes, can alter trophic interactions, the availability of food resources and the feeding behavior of consumers (Alley 1982, Catillo-Guevara et al. 2019, Price et al. 2019). Generalist species, for exemple, may survive in simpler environmental conditions while more complex habitats may support more specialized species due the abundance of prey (Guilherme et al. 2019). A recent study compiled body size measures from 333 ant assemblages and found that both large and small predators are more vulnerable to habitat disturbance, with the former being replaced by generalist species (Gibb et al. 2018). Even so, little is known about the extent to which land-use changes affect the trophic structure of ant assemblages (but see Gibb and Cunningham 2011, 2013), as most studies on the trophic structure of ant communities have been conducted in relatively pristine habitats (Fiedler et al. 2007, Pfeiffer et al. 2014, Gibb et al. 2015, Vieira et al. unpublished).

Until a few decades ago, savannas, and seasonal forests covered most of central Brazil (Ratter et al. 1997). However, much of this natural vegetation has been replaced by cattle pastures and more recently by soy or eucalyptus plantations (Furley 1999, Klink and Machado 2005). This current mosaic of native and non-native vegetation with different degrees of structural complexity allowed me to evaluate the extent to which changes in land-use and land-cover in the Cerrado can affect the trophic and morphological structure of ant communities. I addressed the following questions: (1) Does the morphological and trophic structure of ant communities differ across land-use types? (2) If so, to what extent these differences are correlated with variations in tree cover between land-uses?

Material and Methods

Study site

The study was conducted in the western region of Minas Gerais state, in Brazil (Fig.1). This region has a tropical climate characterized by a dry winter and a rainy summer. The mean annual temperature and mean annual rainfall are around 22ºC and

1,650 mm, respectively (Alvares et al. 2013). Sampling took place between October and December 2017 (i.e., during the local rainy season).

I sampled ground-dwelling ants in the most predominant types of land-use in the study region (Fig. 1). These were: soy plantations, cattle pastures, eucalyptus plantations, woodland savannas (locally known as cerrado *stricto sensu*), and semideciduous forests. These land-uses represent a gradient of canopy cover and vegetation complexity as follows: 1-Soy plantations were the less complex habitat, characterized as an open habitat covered with ~15-cm tall soybean plants, whose seeds were planted directly in the bare soil (i.e., there was no soil tillage before seeding); 2- Cattle pastures were characterized by >80% grass cover (*Urochloa sp*., an introduced African grass) and the presence of scattered trees; 3-Woodland savannas, the most common type of savanna vegetation in the region, which are characterized by a 50–60% coverage of herbaceous vegetation and a tree cover of 30–50%; 4- Eucalyptus plantations were five to six years old and had trees 20-25 m in height, forming a nearly closed canopy; 5- Semideciduous forests were characterized with trees up to 15 m in height forming a continuous canopy, <10% grass cover and > 80% litter cover.

Ant Sampling

A total of eight sampling sites per land-use type were selected (Fig. 1). In each site, we established a 500-m long, linear transect in which 10 traps were installed at 50-m intervals with the first trap located ~100-m from the edge of any other type of habitat. We collected ants using pitfall traps that consisted of plastic recipients (400 traps, 19 cm in diameter and 11 cm in height), buried so that the opening of the trap was leveled with the soil surface and filled to one-third of their volume with water and detergent. Pitfall traps were protected from direct rainfall with a plastic cover (20 cm diameter) that was fixed *ca*. 10 cm above the ground level using bamboo sticks. The traps remained in operation for 48 hours.

All ants collected were sorted to morphospecies and, whenever possible, identified to species using available taxonomic keys or through comparison with specimens previously identified by experts. Voucher specimens of all species were deposited at the Zoological Collection of the Federal University of Uberlandia (MG) in Brazil.

Morphological traits measurements

Eight morphological traits were measured (Table 1) in all the 197 species collected. These traits were selected because of their putative ecological functions (Table 1). For each species, we measured from one to five specimens, depending of the abundance of the species in the samples. For the most abundant species, we sampled individuals from different types of habitat to encompass the natural variation that might exist in functional traits across habitats. I considered only minor workers for morphologically dimorphic or polymorphic species. Measurements of pinned specimens (± 0.01 mm) were made using an ocular micrometer mounted on a Leica M80 stereomicroscope.

I used the average of individual trait values as a single value per morphological trait per species. Prior to all statistical analyses, measurements of the scape length, femur length, eye length, mandible length and eye position were relativized by dividing their values by Weber's length (trait value/Weber's length) and thus representing five size-corrected traits of the ant species. I subsequently $\log_{10}$-transformed Weber's length values to approximate a normal distribution.

Relative trophic position

Stable isotope analyses have been frequently used to assess the trophic position of ant species (Duyck et al. 2011, Fiedler et al. 2007, Gibb and Cunningham 2011, Pfeiffer et al. 2014, Vieira et al. unpublished). A disadvantage of this approach is that performing these analyses for a large number of species can be both costly and time consuming. An alternative approach is to use the morphology of species to estimate their trophic position, since morphological traits can be easily recorded (Vieira et al. unpublished, Gibb et al. 2015). My previous study has showed that by combining data from different morphological traits in multiple regression models it is possible to predict the trophic position of ants with certain precision. Thus, to estimate the relative trophic position (RTP) of the species collected across all the land-use types I used four regression equations presented in the second chapter of this thesis. These equations were derived from models that used morphological traits as predictors of the RTP. To increase model accuracy (and thus its predictive power), four separate models were built, one for each of the following ant groups: a) fungus-growing ants, b) Camponotini ants, c) arboreal ants (except Camponotini), d) ground-dwelling ants (except the fungus-growers). So, I first classified each of the 163 species collected into one of the four above described group and then I calculated the predicted RTP of the species using the respective regression model (Table S1).

Trait-environment relationships

To determine the relationship between the functional traits and the land-use types at the assemblage level I used two approaches. First, I calculated the community-weighted mean (CWM) for the estimated trophic position and for each morphological trait (size-correction was applied to all continuous measures, except body size). CWM utilize the average of trait values weighted by the relative abundances of species (Garnier et al. 2004) in order to measure the shifts in mean trait values due to environmental selection for a given trait (Ricotta and Moretti 2011). As a measure of abundance, I used the number of occurrences of ant species in each sample, which are related to the density of nests (Schlick-Steiner et al. 2006). CWM was calculated using the "dbFD" function of the package *FD* (Laliberté and Legendre 2010). Further, to assess the effect of land-use type on functional traits, I conducted a one-way ANOVA followed by Tukey's post hoc analysis.

In addition, I used the fourth-corner analysis, which also relates traits and site-level environmental variables using data on assemblage composition (Brown et al. 2014). However, unlike the CWM, the fourth-corner analysis takes into account the non-independence of data among sites, and thus has a better statistical power than the CWM (Miller et al. 2014). The fourth-corner analysis fits a predictive model for species abundances as a function of environmental variables, species traits, and their interactions (Brown et al. 2014). It provides information not only about the association between environmental variables and functional traits, but also presents coefficients that quantify the strength and direction of the associations. This fourth-corner analysis was run using the "trait.mod" function in the package *mvabund* (Wang et al. 2012), which relates a matrix of environmental variables (R; sites × habitat type) to a matrix of species traits (Q; species × traits) via a matrix of species occurrences at the different sites (L; species × site) (Brown et al. 2014). For this analysis, we used a negative binomial regression because the count data (for species abundances) was overdispersed. I also used the least absolute shrinkage and the selection operator penalty, which endow high predictive performance in species distribution models (Renner and Warton 2013). Both the CWM and the fourth corner analyses were performed in R, version 3.5.1 (R Core Team 2013).

Results

A total of 3,653 species-occurrences were recorded across all land-use types, for 163 species of ants from 42 genera. Overall, the most frequent genera were *Pheidole*, *Camponotus* and *Brachymyrmex*, occurring in 28%, 15% and 7% of the samples, respectively. All other genera were found in less than 5% of samples. The most frequent species in our samples were *Pheidole oxyops* (Forel, 1908), *Pheidole subarmata* (Mayr, 1884), *Brachymyrmex sp. 5* and *Dorymyrmex brunneus* (Forel, 1908) (Table S1, Supplementary material). In total, 110, 86, 80, 68 and 37 species were recorded, respectively, in savanna, forest, eucalyptus, pasture and soy plantation. There were significant differences in mean species richness between land-uses ($F_{4,35=}$ 31.2, $P < 0.001$). Tukey's pairwise *post hoc* comparisons showed that ant communities in soy plantations were the least diverse whereas those in savannas were the most diverse. Pastures, eucalyptus plantations and forests were not significantly different from each other in terms of mean species richness.

Morphological structure

Community weighted mean (CWM) values differed significantly among land uses for all morphological traits I measured (ANOVA, df=4,35, $p < 0.002$ in all cases). I observed a nearly linear increase in body size and a decrease in relative eye length as one move from the more open habitats (soy plantations and pastures) to those with a high density of trees (eucalyptus plantations and forests) (Fig. 2). Eye position changed similarly along this gradient, becoming more dorsally-positioned as tree cover increased (Fig. 2).

Variation in the CWM of the remaining morphological traits were also noted but only between the most distinct land-uses. I observed that ant communities in soy plantations differed significantly from those in all remaining land uses with regard to mean number of spines, and relative femur length, whereas communities in soy plantations and pasture differed from those in other land uses with respect to pilosity (Fig. 2). The same was true with regard to relative trophic position whose CWM was significantly greater in soy plantations and pastures than in savannas, forests and eucalyptus plantations (ANOVA: $F_{4,35}$= 17.35, $p < 0.0001$). (Fig. 2).

The fourth-corner analysis showed greater domination by ants with particular traits in soy plantations (Fig.3). Soy plantations were dominated by ants with smaller bodies (shorter Weber's length), shorter antennae, longer legs, with fewer spines and hairs, and by ants feeding relatively higher in the food chain. The other land uses also showed significant correlations with morphological traits, but those were much weaker. For instance, ants with larger body size and relatively longer scape dominated in woody habitats such as eucalyptus plantations and forests (Fig. 3).

Analysis of the frequency in which species with different relative trophic positions (RTP) occurred in the different land-uses (Fig. 4), revealed that in savannas, eucalyptus plantations and forests most species belong either to the group of species with RTP between 2.5 to 2.8 (i.e., of species with a more herbivorous diet) or the group with RTP > 3 (i.e. of species with predominantly predatory habits). Soy plantations were very distinct from the remaining land uses by having very few species with a RTP lower than 3 (Fig. 4).

Discussion

In this study I evaluated the effects of changes in land use and land cover on the morphological and trophic structure of ground-dwelling ant communities. Overall, my findings indicate that both the morphological and the trophic structure of ant communities are affected by land-use changes and that the variation observed in certain traits were correlated with variations in habitat structure. I found that with increasing tree cover, community-weighted mean ant body size increased, whereas eyes become relatively smaller and more dorsally-positioned. Moreover, ant communities in the most structurally simpler habitat (soy plantations), were very distinct from the remaining land uses in terms of species richness, relative trophic position and morphology.

Morphological structure of ant communities

Community weighted mean (CWM) and fourth corner analysis revealed a range of relationships between morphological traits and land-use types at the assemblage level. Some of these associations clearly followed a gradient of increasing tree cover and selected for species with particular morphological traits. Density of vegetation often modifies the structural complexity of the ground substrate (Arnan et al. 2007) which, in turn, influences the locomotory ability of ants (Kaspari and Weiser 1999). The "size-grain hypothesis", for exemple, predicts that smaller ants with relatively smaller legs would have better access to rugose substrates, such as litter interstices (Kaspari and Weiser 1999, Farji-Brener et al. 2004). The fact that body size increased with tree cover, contrasts with a range of studies showing that smaller ants are prevalent in more complex habitats (in this study, forest) and that species living in structurally simple habitats are larger (Kaspari and Weiser 1999, Gibb and Parr 2010, Arnan et al. 2013). However, this is in agreement with findings for the Amazon Basin, for which ants in more complex environments had larger size while less complex habitats harbored more species of smaller ants (Guilherme et al. 2019). Decreasing of relative eye size with the increasing of vegetation cover might be associated with availability of light, once visual orientation becomes less relevant in places with lower luminosity (Schofield et al. 2016). Furthermore, small eyes are associated with more predaceous genera (Weiser and Kaspari 2006, Gibb at al. 2015, Liu et al. 2019), such as *Pachycondyla* and *Neoponera*, that were abundant mainly in forests. Eye position is an indicator of habitat complexity (Gibb and Parr 2013), but different from the expected, CWM showed that ants from woody habitats had eyes more dorsally-positioned which contrasts the idea that complex habitats require organisms with lateral eyes to be more capable of seeing obstacles around them, for example moving under leaf litter. In contrast, the fourth corner analysis showed a greater prevalence of species with more dorsally-positioned eyes in soy plantations. It is unclear why these two analyses gave opposing results.

Mandible length and pilosity differed only between ant communities from open habitats (soy plantations and pastures) and more closed habitats (savanna, eucalyptus plantation and forest). Longer mandibles might favour the occurrence of predatory species (Yates et al. 2014) and the fact that ants inhabiting open habitats had relatively longer mandibles is consistent with the relative trophic position of communities in these habitats, which was higher than in the remaining land uses. The high prevalence of species with few hairs in open habitats does not support the hypothesis that hairs increase tolerance to dehydration due hotter temperatures (Wittlinger et al. 2007). Lastly, ant communities in soy plantations presented the prevalence of certain traits different from all other land-uses: they had longer legs and almost no spines. Although species in this habitat were smaller, they had relatively long legs which might be related to the longer distances that ants in open habitats have to walk to foraging for food (Yates et al. 2014) compared to ants found in complex habitats which usually do not walk long distances (Silva and Brandão 2010). Additionally, temperature is usually higher in the surface of open habitats and might favor smaller ants with relative longer legs by increasing the distance between the ant body and the heat-radiating surface (Cerdá and Retana 2000, Wiescher et al. 2012, Guilherme et al. 2019). The number of spines, which might be related with predation risk, was associated with canopy cover in Australian ants (Gibb et al. 2015), and the absence of spine in ant communities from soy plantations suggests that the risk of predation is lower in simpler habitats. However, little is known about the assemblages of predator of ants in agroecosystems.

Trophic structure of ant communities

I found marked differences in the trophic structure of ant communities across land-use types. In general, RTP was greater in soy plantations followed by pastures, indicating that the average species in these habitats are more 'predatory' than in the remaining land uses. However, in these same habitats (especially in soy plantations), I found almost no species with a trophic position similar to that of herbivores. The trophic structure of ant communities is strongly influenced by the availability of food resources and it is known that the quantity and quality of these resources varies according to the structure of the vegetation (Arnan et al. 2007). Here, soy plantations are the simplest habitat and the significant reduction of trees, grasses and consequently leaf-litter probably reduced some types of food resources available for ants in this habitat. For exemple, many species of ants use trees as a source of nesting and/or food (i.e. floral nectar) thus, the lack of trees in such habitats may not support species specialized in this kind of resource (Armbrecht and Perfecto 2003, Frizzo and Vasconcelos 2013, Camarota et al. 2015). Besides nest site and food source limitation, the interactions with other species (such as competition or predation) may have led to a narrow trophic structure of ants in this land use. Ant communities from soy plantations were dominated by generalist species such as, *Dorymyrmex brunneus* and *Pheidole oxyops*, which are often better succeeded in disturbed habitats due their superior competitive abilities against other species (Holldobler and Wilson 1990, Pacheco et al. 2013, Andersen 2000, 2018). Ant communities from pastures were also dominated by generalist species with higher trophic position, however, they also presented species with a more herbivorous diet (RTP between 2.5 to 2.8) and species with more predatory habits (RTP > 3). This might be explained by the relatively greater availability of honeydew, extra-floral nectar and prey resources provided by the presence of scattered trees in pastures sites (Gibb and Cunningham 2011, Frizzo and Vasconcelos 2013, Carvalho et al. 2020).

Trophic diversity was higher in eucalyptus plantations and in the native habitats (savanna and forest), reflecting an increasing of dietary breath. The increasing of vegetation cover affects the degree of ground cover, which produces more litter, dead wood and creating microclimatic conditions different from those in open habitats (Andersen 1990, Folkerts et al. 1993). These modifications can determine changes in the abundance and composition of food resources and consequently may harbor more species occupying different niches (Arnan et al. 2007). Although there is a simplification of the vegetation structure and an impoverishment of the leaf litter layer in eucalyptus plantations (Winck et al. 2017), this monoculture appears to maintain not only a relatively high number of ant species, but also species with a variety of feeding modes. Still, it is clear that forests and savannas have greater structural complexity and variety of resources than the other land-uses, as well as more microclimates and microhabitats, which allows for the coexistence of more species in the community with specialized requirements of nesting and food. For instance, strictly arboreal ants belonging to the genera *Cephalotes* occurred only in savanna habitats while highly predatory species from Ponerinae occurred only in forests. Moreover, previous study showed that despite of the structural differences between these habitats, the trophic structure of ant communities is similar with a wide range of trophic modes in the food chain (Vieira et al. unpublished).

Concluding remarks

The present study is the first one to assess the impacts of land use and land cover on both morphological and trophic structure of ant assemblages in a Brazilian savanna. Taken as a whole, the conversion of forests and savannas into monocultures altered the morphological trait composition and the trophic structure of ant communities, but these changes were mainly regulated by vegetation structure of habitats. Changes in trait composition occurred mainly between open habitats (soy plantations and pastures) and between habitats with higher canopy cover (eucalyptus and forests). Possibly their similar environmental conditions, as well as the availability of nesting and food sources in these habitats filtered for species functionally equivalents. Furthermore, I found evidence that planted pastures and eucalyptus plantations had both trophic and morphological diversity as high as the one found in native habitats. On the other hand, the greater simplification of vegetation structure in soy plantations has led to a greater decline on morphological and trophic diversity of ants.

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Tables

Table 1. Morphological traits of ants analyzed in this study, their hypothesized function and a description of how it was measured.

Trait hypothesized function	How it was measured (in millimeters)
Weber's length: indicative of worker body size (Weber 1938), which correlates with metabolic characteristics, and many life history traits such as resource use	Distance from the anterodorsal margin of the pronotum to the posteroventral margin of the propodeum
Eye position: related to hunting method (Fowler et al. 1991) or the component of the habitat occupied (Gibb and Parr 2013)	Head width across the eyes minus head width between the eyes–higher eye position indicates more dorsal eyes
Scape length: sensory abilities—longer scapes facilitate following of pheromone trails (Weiser and Kaspari 2006)	Length of the antennal scape
Eyes length: indicator of feeding behavior: predatory ants have smaller eyes (Weiser and Kaspari 2006)	Length of the largest eye diameter
Mandible length: Indicative of diet: longer mandibles could allow predation of larger prey (Fowler et al. 1991)	Straight-line distance from the insertion to the tip of the mandible
Femur length: indicative of foraging speed, which reflects the complexity of the habitat (Feener et al. 1988)	Length of the femur of the hind leg
Number of spines: spines might act as an anti-predation mechanism (Michaud and Grant 2003)	Count of spines on propodeum and petioles
Pilosity: hairs might increase tolerance to dehydration or might relate to mechanoreception (Wittlinger et al. 2007)	0 = No or very few hairs; 1 = a sparse but regular covering of hairs; 2 = a consistent, moderate covering of hair; 3 = very dense hair covering (Gibb et al. 2015)

Figures

Figure 1: Map showing the location of the study area in central Brazil with the distribution of the sampling sites and the five land-use types following a gradient of tree cover: (a) soy plantation, (b) cattle pasture, (c) woodland savanna, (d) eucalyptus plantation and (e) semideciduous forest.

Figure 2. Box plots of community weighted means for nine functional traits of the ant communities found in five land-uses representing a gradient of increased canopy cover. Letters above boxes indicate differences among mean values.

Figure 3. Fourth corner plot with the interaction coefficients between ant species traits (y-axis) and land-use types (x-axis), accounting for species abundances. Negative associations are shown in red, while positive ones in blue. Color intensity represents the strength of the interaction (coefficient values are on a log scale).

Figure 4. Histograms showing the number of species found in each land-use according to their estimated relative trophic position.

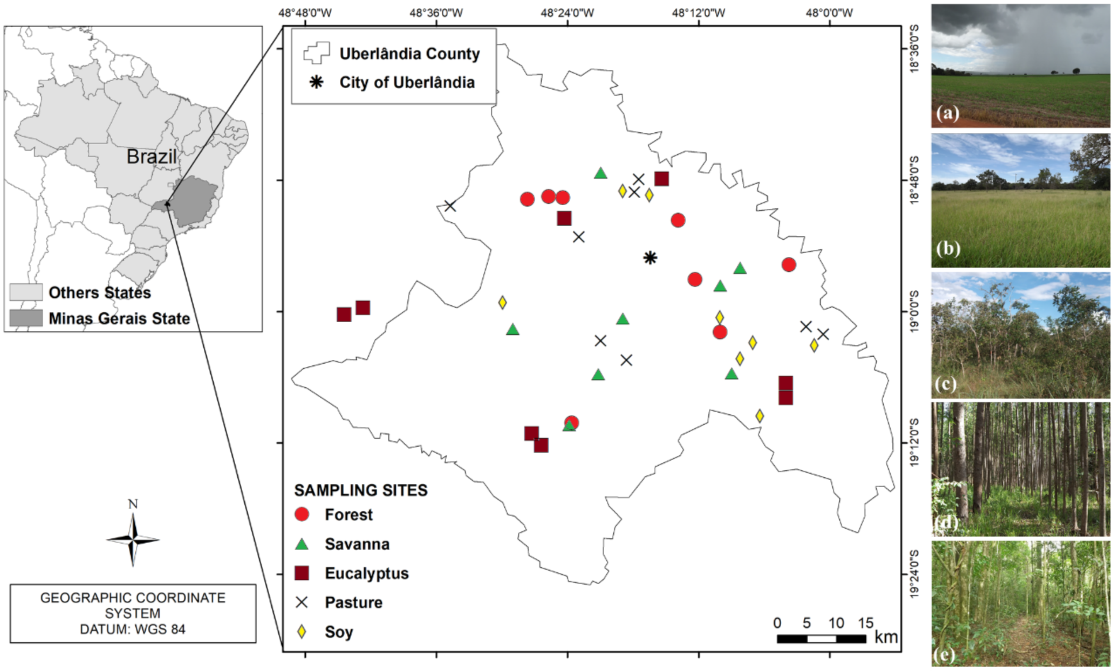

48°48'0"W
48°36'0"W
48°24'0"W
48°12'0"W
48°0'0"W
18°36'0"S
18°48'0"S
19°0'0"S
19°12'0"S
19°24'0"S
Uberlândia County
City of Uberlândia
Brazil
Others States
Minas Gerais State
N
GEOGRAPHIC COORDINATE SYSTEM
DATUM: WGS 84
SAMPLING SITES
Forest
Savanna
Eucalyptus
Pasture
Soy
0 5 10 15
km
(a)
(b)
(c)
(d)
(e)

Figure 1.

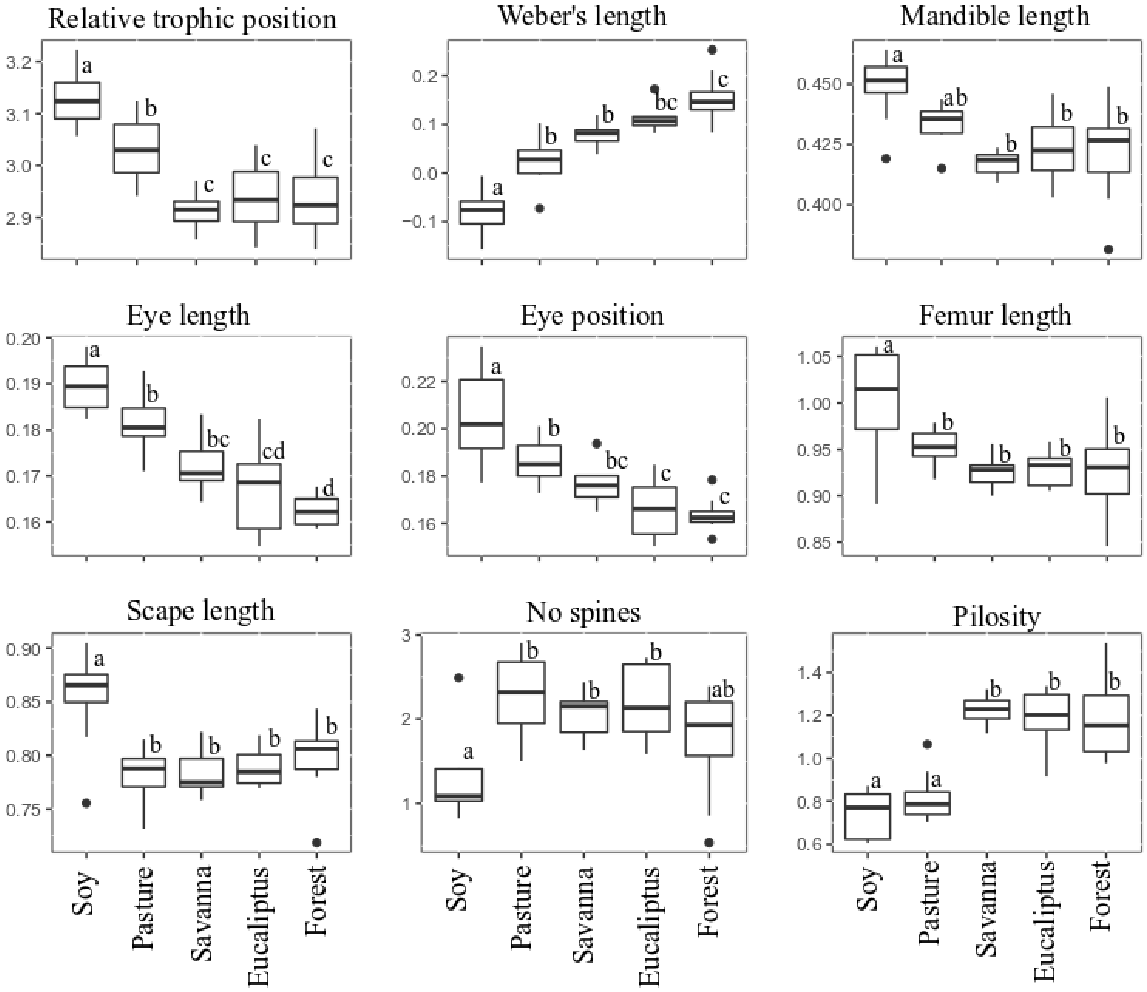

Relative trophic position
3.2
3.1
3.0
2.9
a
b
c
c
c
Weber's length
0.2
0.1
0.0
-0.1
a
b
b
bc
c
Mandible length
0.450
0.425
0.400
a
ab
b
b
b
Eye length
0.20
0.19
0.18
0.17
0.16
a
b
bc
cd
d
Eye position
0.22
0.20
0.18
0.16
a
b
bc
c
c
Femur length
1.05
1.00
0.95
0.90
0.85
a
b
b
b
b
Scape length
0.90
0.85
0.80
0.75
a
b
b
b
b
No spines
3
2
1
a
b
b
b
ab
Pilosity
1.4
1.2
1.0
0.8
0.6
a
a
b
b
b
Soy
Pasture
Savanna
Eucaliptus
Forest

Figure 2.

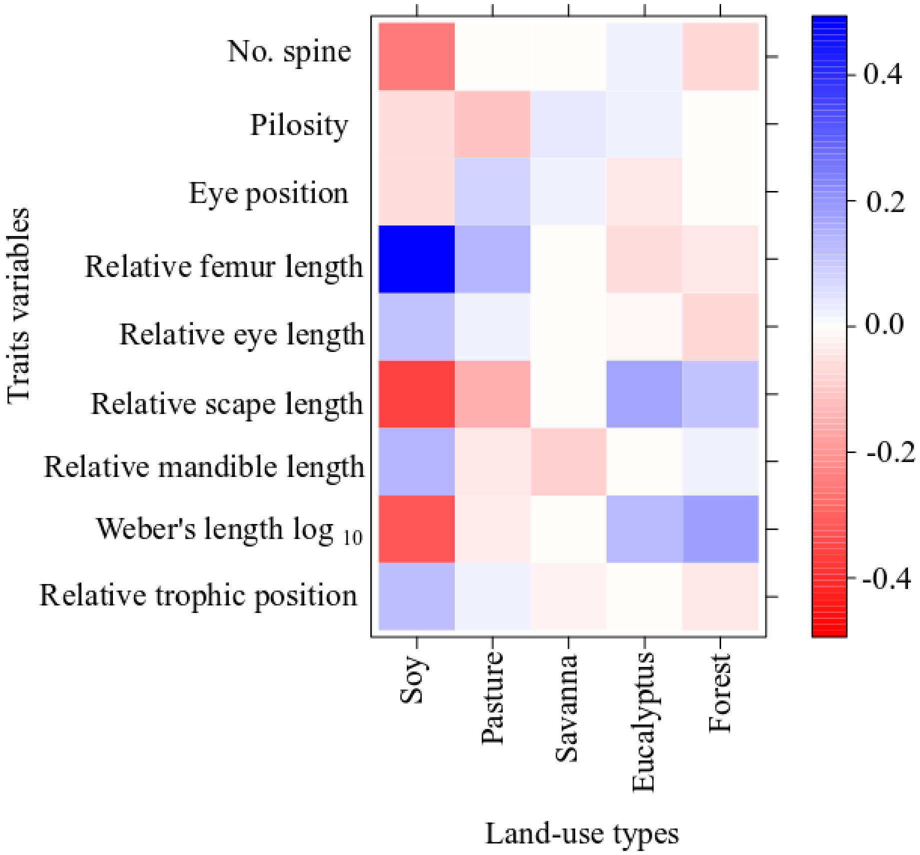
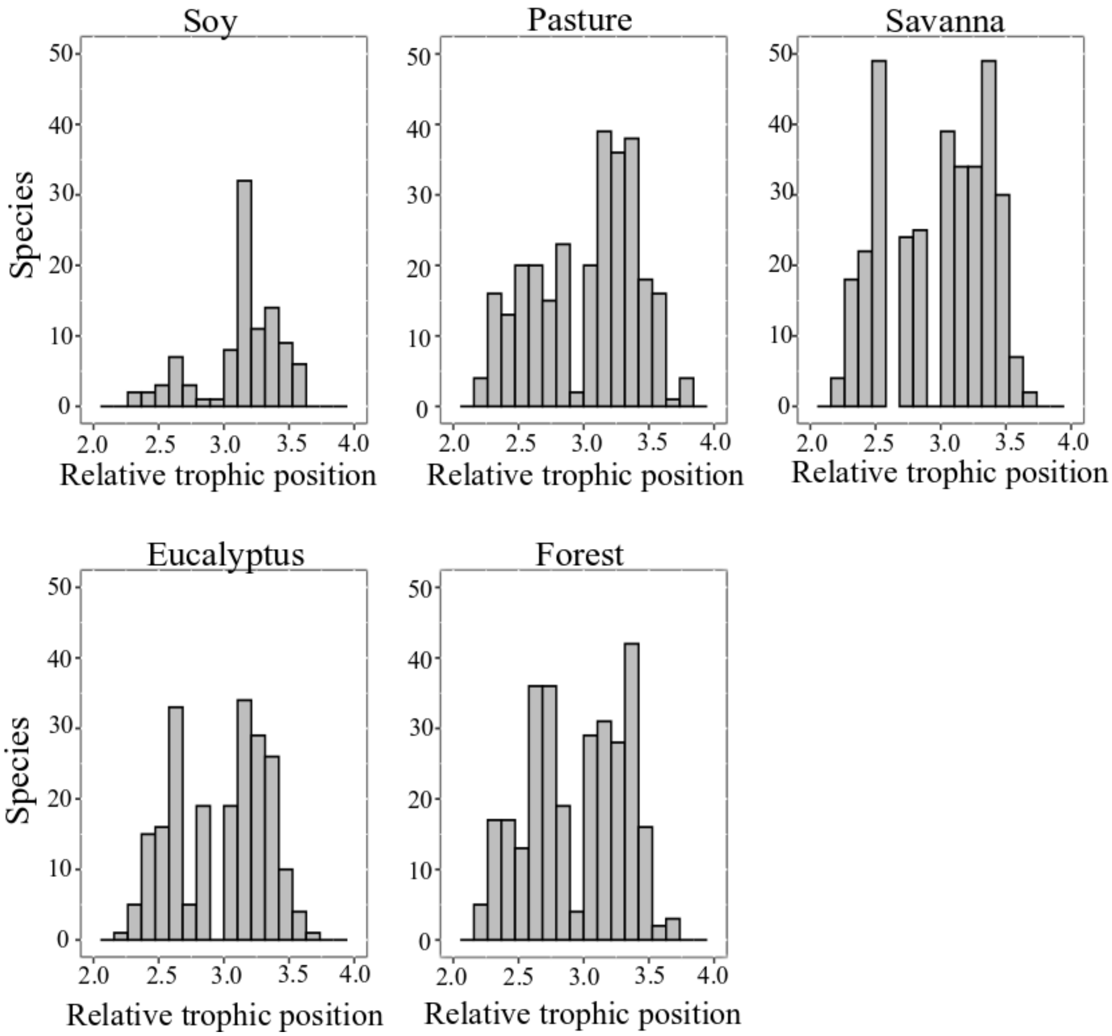

No. spine
Pilosity
Eye position
Relative femur length
Relative eye length
Relative scape length
Relative mandible length
Weber's length log 10
Relative trophic position
Traits variables
Soy
Pasture
Savanna
Eucalyptus
Forest
Land-use types
0.4
0.2
0.0
-0.2
-0.4

Figure 3.


Soy

Pasture

Savanna

Eucalyptus

Forest

Figure 4.

Supplementary information

Table S1. List of the ant species/morphospecies, divided by the genera and the subfamily they belong to, the frequency of occurrence they were collected across all land-use types and their estimated relative trophic position.

Species	Soy	Pasture	Savanna	Eucalyptus	Forest	Relative trophic position (RTP)
Dolichoderinae						
Azteca sp.02	0	0	0	0	2	3.00
Dorymyrmex brunneus	57	57	2	9	0	2.95
Dorymyrmex goeldii	2	9	6	2	1	3.14
Dorymyrmex pyramicus	7	23	21	2	0	2.90
Dorymyrmex sp.10	0	3	0	0	0	3.16
Dorymyrmex sp.21	0	17	0	0	0	3.12
Forelius brasiliensis	1	6	3	0	0	
Linepithema angulatum	0	1	8	0	4	3.30
Linepithema aztecoides	1	0	23	14	1	3.11
Linepithema cerradense	0	0	12	0	0	3.25
Linepithema sp.12	0	0	0	0	4	2.97
Dorylinae						
Eciton quadriglume	0	0	0	1	0	3.01
Neivamyrmex sp.	0	1	0	0	0	3.24
Ectatomminae						
Ectatomma brunneum	0	18	3	4	0	3.29
Ectatomma edentatum	0	20	15	28	4	3.38
Ectatomma lugens	0	0	0	0	10	3.45
Ectatomma opaciventre	0	7	17	1	0	3.34
Ectatomma permagnum	0	0	6	0	2	3.44
Ectatomma tuberculatum	0	0	8	0	2	3.09
Gnamptogenys acuminata	1	2	3	5	4	3.56
Gnamptogenys sp.06	1	2	1	0	0	3.45
Gnamptogenys sp.07	0	0	9	0	0	3.40
Gnamptogenys sp.09	1	37	8	1	0	3.53
Gnamptogenys striatula	0	0	0	0	4	3.61
Gnamptogenys sulcata	7	17	10	0	1	3.29
Formicinae						
Brachymyrmex coactus	1	0	0	0	0	3.13
Brachymyrmex sp.05	53	44	11	9	2	2.94
Brachymyrmex sp.12	2	18	34	19	32	3.13
Brachymyrmex sp.21	0	0	0	0	3	3.19
Camponotus arboreus	0	0	1	0	0	2.44

Camponotus atriceps	0	2	6	4	3	2.58
Camponotus balzani	0	0	4	9	0	2.54
Camponotus blandus	1	18	37	7	15	2.32
Camponotus bonariensis	0	0	2	0	0	2.39
Camponotus cingulatus	0	0	10	0	25	2.54
Camponotus fatigatus	0	0	2	0	0	2.30
Camponotus lespesii	0	0	13	18	58	2.70
Camponotus leydigi	0	3	14	0	0	2.53
Camponotus melanoticus	0	15	27	37	0	2.53
Camponotus novogranadensis	0	3	2	0	2	2.17
Camponotus personatus	0	8	3	0	0	2.26
Camponotus renggeri	0	1	33	22	2	2.63
Camponotus rufipes	0	0	0	7	0	2.64
Camponotus senex	0	3	41	31	5	2.44
Camponotus sericeiventris	0	0	0	0	3	2.64
Camponotus sp.09	0	0	1	0	2	2.30
Camponotus sp.10	0	1	4	0	0	2.36
Camponotus sp.33	0	0	0	0	2	2.36
Camponotus sp.35	0	4	8	0	1	2.50
Camponotus sp.44	0	0	1	0	0	2.39
Camponotus sp.72	0	2	6	1	10	2.19
Camponotus sp.74	0	0	0	0	1	2.62
Camponotus sp.75	0	0	0	0	1	2.25
Camponotus sp.80	0	0	0	0	14	2.32
Camponotus substitutus	0	2	2	0	0	2.52
Nylanderia sp.04	0	0	11	2	10	3.22
Nylanderia sp.05	0	0	18	0	10	3.04
Nylanderia sp.09	0	0	0	0	6	3.08
Tapinoma sp.03	1	2	0	0	0	2.61
Myrmicinae						
Acromyrmex brunneus	1	0	0	0	19	2.50
Acromyrmex crassispinus	2	11	0	1	8	2.72
Acromyrmex landolti	0	26	16	0	0	2.53
Acromyrmex rugosus rochai	0	0	0	7	0	2.55
Apterostigma sp.01	0	0	1	0	0	2.69
Apterostigma sp.02	0	0	4	0	6	2.75
Atta spp.	11	37	46	18	32	2.46
Cardiocondyla emergyi	12	43	1	5	1	3.70
Carebara brevipilosa	0	0	0	0	6	2.01
Carebara urichi	0	0	0	0	1	1.97
Cephalotes atratus	0	0	2	0	0	2.77
Cephalotes eduarduli	0	0	0	0	1	2.45
Cephalotes persimilis	0	0	1	0	0	2.33

Cephalotes pusillus	0	1	3	1	0	2.51
Crematogaster limata	0	0	0	0	2	2.93
Crematogaster obscurata	0	6	1	2	0	2.93
Crematogaster sp.18	0	0	4	0	0	2.98
Cyphomyrmex rimosus	0	23	8	0	1	2.88
Cyphomyrmex sp.38	0	0	0	0	2	2.76
Cyphomyrmex transversus	0	8	8	6	9	2.88
Hylomyrma reiterri	0	0	1	0	1	3.96
Megalomyrmex silvestrii	0	0	1	0	0	3.75
Megalomyrmex symmetochus	0	0	1	0	1	3.50
Mycetagroicus cerradensis	0	0	9	0	0	2.74
Mycetarotes parallelus	0	12	2	0	0	2.78
Mycocepurus goeldii	0	21	32	8	7	2.82
Mycocepurus smithii	0	1	3	4	2	2.90
Myrmicocrypta camargoi	0	2	1	0	0	2.73
Myrmicocrypta squamosa	2	13	14	5	4	2.73
Ochetomyrmex semipolitus	0	0	1	0	2	3.40
Pheidole ambigua	3	0	10	2	1	2.95
Pheidole cyrtostela	0	0	7	0	0	2.81
Pheidole fimbriata	0	0	1	1	9	2.79
Pheidole fracticeps	9	9	42	22	22	3.26
Pheidole gertrudae	0	2	0	0	0	2.89
Pheidole obscurithorax	0	6	0	3	1	3.30
Pheidole oxyops	69	71	64	38	42	3.16
Pheidole radoszkowskii	22	29	25	31	1	3.17
Pheidole rufipilis	0	5	0	3	0	3.04
Pheidole schwaezmaieri	0	1	3	7	10	3.08
Pheidole sp.01	0	1	0	0	0	3.03
Pheidole sp.03	0	0	0	2	0	2.96
Pheidole sp.08	0	0	6	0	15	3.01
Pheidole sp.103	1	0	0	0	0	2.88
Pheidole sp.12	0	0	1	0	0	3.23
Pheidole sp.135	0	0	0	2	3	3.14
Pheidole sp.14	0	0	1	0	0	3.20
Pheidole sp.15	1	0	11	19	9	3.03
Pheidole sp.40	0	0	6	0	0	3.34
Pheidole sp.41	0	0	0	0	17	3.21
Pheidole sp.70	0	1	0	1	0	3.16
Pheidole sp.76	0	0	0	1	0	3.30
Pheidole sp.83	0	1	0	0	0	2.98
Pheidole sp.84	1	2	0	0	0	3.03
Pheidole sp.88	0	0	1	0	0	3.17
Pheidole sp.94	0	0	0	7	5	3.11

Pheidole sp.97	0	0	8	0	0	2.93
Pheidole sp.98	1	0	0	0	0	3.15
Pheidole sp.j	9	2	0	2	0	3.00
Pheidole spnova	9	0	0	1	0	3.03
Pheidole subarmata	8	43	23	35	26	3.17
Pheidole susannae	0	0	5	0	0	3.11
Pheidole synarmata	23	21	14	16	7	3.23
Pheidole triconstricta	0	25	14	11	24	3.12
Pheidole vafra	0	3	2	0	0	3.37
Pogonomyrmex naegelli	0	2	8	0	0	3.09
Rogeria sp.01	0	0	1	1	0	3.10
Sericomyrmex mayri	0	0	0	1	17	2.81
Sericomyrmex parvulus	0	0	0	0	25	2.78
Sericomyrmex scrobifer	0	0	8	0	0	3.57
Solenopsis globularia	0	1	0	0	0	3.57
Solenopsis iheringi	16	5	1	2	0	3.61
Solenopsis loretana	1	4	10	2	0	3.68
Solenopsis sp.01	3	5	22	7	14	2.66
Solenopsis sp.21	1	6	9	5	1	3.38
Solenopsis sp.23	0	4	0	0	0	2.92
Solenopsis sp.30	0	0	1	0	0	3.65
Solenopsis substituta	7	5	17	0	0	3.55
Strumigenys sp.06	0	4	1	0	0	3.89
Trachymyrmex bugnioni	0	0	0	0	31	2.75
Trachymyrmex dichrous	0	0	6	0	0	2.68
Trachymyrmex holmgreni	0	11	5	7	1	2.61
Trachymyrmex homlmgreni	0	2	2	0	0	2.64
Trachymyrmex sp.01	0	0	5	0	0	2.67
Trachymyrmex sp.09	0	0	1	0	0	2.73
Trachymyrmex sp.15	0	8	36	54	11	2.65
Trachymyrmex sp.36	0	1	5	0	10	2.82
Trachymyrmex sp.45	0	4	1	0	0	2.74
Trachymyrmex urichi	0	0	1	0	0	2.62
Wasmannia auropunctata	0	2	10	5	16	3.34
Ponerinae						
Anochetus inermis	0	12	0	2	0	3.07
Anochetus sp.05	0	0	0	0	3	3.18
Dinoponera australis	0	0	0	0	2	3.08
Leptogenys bohlsi	0	0	0	0	2	3.81
Neoponera marginata	0	1	1	1	2	3.63
Neoponera verenae	0	1	0	0	12	3.44
Neoponera villosa	0	0	1	0	1	2.69
Odontomachus bauri	0	5	2	6	0	3.27

Odontomachus chelifer	0	0	2	3	19	3.32
Odontomachus meinerti	0	0	1	1	9	3.28
Pachycondyla harpax	0	2	11	5	11	3.50
Pachycondyla striata	0	0	0	7	24	3.34
Pseudomyrmycinae						
Pseudomyrmex gracilis	0	0	3	0	3	2.45
Pseudomyrmex termitarius	6	20	5	2	0	2.30

Considerações gerais

No primeiro capítulo, comparei a estrutura trófica de formigas arborícolas e de solo em dois ambientes estruturalmente contrastantes. Uma vez que a disponibilidade de recursos alimentares varia de acordo com as características físicas do hábitat e suas condições abióticas, as diferenças estruturais entre cerrado e floresta poderiam influenciar a demanda e a disponibilidade de nutrientes, assim como a maneira em que as espécies iriam explorá-los. No entanto, encontrei uma similaridade na estrutura trófica das comunidades de floresta e de solo. Nos dois hábitats as formigas arborícolas possuem uma dieta mais herbívora enquanto as formigas de solo tem uma dieta mais predadora. Esses resultados são explicados ao menos em parte pelas diferenças na composição da fauna que foram muito mais marcadas entre estratos do que entre hábitats. Além disso, as formigas arborícolas no cerrado tiveram, em média, mais carbono originado a partir de plantas C_3 do que as formigas de solo. Ainda assim, poucas espécies obtiveram carbono de gramíneas C_4, apesar da abundância das gramíneas nesse hábitat.

No segundo capítulo, eu avaliei se os caracteres morfológicos das formigas podem ser utilizados para fazer predições sobre seus hábitos alimentares. Mais especificamente, criei um modelo de regressão múltipla para estimar a posição trófica relativa das espécies de formigas. Individualmente, alguns caracteres morfológicos tiveram associações com a posição trófica das espécies. Por exemplo, formigas com posição trófica mais alta (mais predadoras) tendem a ser maiores, com tamanho relativo da mandíbula maior e pecíolo mais alto. Já as formigas em uma posição trófica mais baixa (mais herbívoras) possuem tamanho relativo do clípeo e do olho maiores, além de terem mais espinhos e mais pelos. No entanto, essas relações explicaram muito pouco da variação na posição trófica das espécies. Por outro lado, quando combinei todos os caracteres morfológicos no modelo de regressão múltipla, o poder em explicar essa variação aumentou significativamente, principalmente quando considerei o hábito de forrageamento/nidificação e afinidades taxonômicas de alguns grupos em modelos separados.

No terceiro capítulo, eu avaliei se a estrutura morfológica e a estrutura trófica das comunidades de formigas variam entre diferentes usos da terra e se essa variação está relacionada com a complexidade da cobertura arbórea de cada hábitat. Eu encontrei um forte efeito da estrutura do hábitat em determinar alguns traços morfológicos, assim como a estrutura trófica dessas comunidades. Com o aumento da cobertura vegetal as comunidades apresentaram tamanho médio do corpo maior, olhos relativamente menores e posicionados dorsalmente. Além disso, houve uma maior similaridade nos traços das comunidades de formigas nos hábitats com uma maior cobertura vegetal (eucalipto e floresta) do que entre os hábitats mais abertos (plantação de soja e pastagem). A comunidade de formigas nas plantações de soja e nas pastagens tiveram posição trófica mais alta comparado com as comunidades nos outros usos da terra, indicando uma maior abundância de formigas com hábitos alimentares predadores. Por outro lado, os hábitats com vegetação nativa (cerrado e floresta) tiveram uma maior diversidade trófica, apresentando espécies de formigas com dieta herbívora e predadoras especialistas.

De maneira geral, esta tese fornece evidências sobre como o ambiente e suas características estruturais influenciam a prevalência de certos traços funcionais na comunidade de formigas. A morfologia e a posição trófica das espécies parecem ser afetados pelas mudanças no hábitat, uma vez que juntas elas refletem a maneira com que as espécies interagem e exploram o ambiente. Além disso, esse estudo elucida a importância da complexidade estrutural da vegetação para manter uma alta diversidade de traços funcionais entre as espécies, visto que a conversão de hábitats naturais em monoculturas e pastagens levou a uma simplificação tanto na estrutura trófica quanto na estrutura morfológica das comunidades.