



ICARO WILKER GONZAGA DE CARVALHO

**LAND USE CHANGES AFFECT ANT ASSEMBLAGES,
RESOURCE PREFERENCE, AND ECOSYSTEM FUNCTIONS
IN NEOTROPICAL BIOMES**

**LAVRAS - MG
2025**

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Tese apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Ecologia Aplicada, área de concentração em Ecologia Conservação de Recursos em Paisagens Fragmentadas e Agrossistemas, para a obtenção do título de Doutor.

Profa. Dra. Carla Rodrigues Ribas
Orientadora

Dr. Chaim José Lasmar
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Dr. Tom Rhys Bishop
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**MUDANÇAS NO USO DO SOLO AFETAM ASSEMBLEIAS DE FORMIGAS,
PREFERÊNCIA POR RECURSOS E FUNÇÕES ECOSSISTÊMICAS EM BIOMAS
NEOTROPICAIS**

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2025**

*Dedico este trabalho à minha mãe, Lediene,
ao meu pai, Ademilson, à minha irmã, Ágatha, ao
meu irmão, Kaique, e à minha namorada, Enggel.*

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RESUMO GERAL

As conversões no uso do solo são a principal causa da perda de biodiversidade em ambientes tropicais terrestres. Nessas regiões, essas alterações modificam drasticamente a estrutura e composição da vegetação, afetando o microclima e a disponibilidade de recursos alimentares. Apesar de muitos estudos avaliarem os impactos das mudanças no uso do solo, ainda há necessidade de sínteses e revisões e de uma abordagem mais ampla que vá além da ecologia taxonômica (*e.g.*, riqueza de espécies), incluindo efeitos na preferência de recursos e nas funções ecossistêmicas, que têm ligações diretas com o funcionamento dos ecossistemas e pode auxiliar em estratégias de conservação. Nesta tese de doutorado, busquei avaliar nesta tese como as mudanças no uso do solo e as variações microclimáticas afetam em assembleias de formigas a riqueza de espécies, preferência por nutrientes e predação de insetos. Além disso, fiz uma revisão sistemática com meta-análise sobre os efeitos do uso do solo nas assembleias de formigas no Brasil. Encontrei que no bioma Mata Atlântica as formigas apresentam maior preferência por aminoácidos e maior predação de insetos. Além disso, apesar de formigas predadoras terem a base da sua alimentação com proteínas e aminoácidos, aumentam a sua preferência por recursos energéticos devidos limitações nutricionais por carboidratos e lipídeos. Encontrei também que o microclima afeta a preferência nutricional em formigas, onde o aumento da temperatura tende a diminuir a preferência por recursos ricos em aminoácidos em relação a carboidratos e lipídios. Além disso, encontrei que as mudanças no uso do solo afetam direta e indiretamente as assembleias de formigas. A redução na predação de insetos causada pelas alterações no uso do solo é mediada pela perda da riqueza de espécies de formigas e, especificamente, das espécies predadoras. Por fim, na revisão e meta-análise, evidenciei que alterações muito contrastantes no uso do solo (*e.g.*, conversão de floresta para pastagem) reduzem a riqueza de espécies e alteram a composição das assembleias de formigas, provavelmente devido à perda de espécies sensíveis e especialistas. Dessa forma, concluo que alterações nos usos do solo podem desencadear efeitos negativos em diferentes aspectos das comunidades terrestres, como número e composição de espécies e funções ecossistêmicas, principalmente em conversões de habitat mais contrastantes. Assim, sugiro que, sempre que possível, habitats antropizados sejam mantidos o mais próximo possível do ambiente original, a fim de favorecer a conservação das espécies e das funções ecossistêmicas.

Palavras-chave: Ecologia Nutricional; Função Ecossistêmica; Formicidae; Brasil; Tropical.

GENERAL ABSTRACT

Land-use changes are the primary cause of biodiversity loss in terrestrial tropical environments. In these regions, such changes drastically alter vegetation structure and composition, affecting the microclimate and the availability of food resources. Despite numerous studies assessing the impacts of land-use changes, there is still a need for syntheses, reviews, and a broader approach that goes beyond taxonomic ecology (e.g., *species* richness), including effects on resource preference and ecosystem functions. These aspects are directly linked to ecosystem functioning and can help guide conservation strategies. In this PhD thesis, I aimed to evaluate how land-use changes and microclimatic variations affect ant assemblages, specifically species richness, nutrient preference, and insect predation. Additionally, I conducted a systematic review with a meta-analysis on the effects of land use on ant assemblages in Brazil. I found that in the Atlantic Forest biome, ants show a greater preference for amino acids and higher predation on insects. Furthermore, although predatory ants have a diet primarily based on proteins and amino acids, they increase their preference for energetic resources due to nutritional limitations in carbohydrates and lipids. I also found that the microclimate affects the nutritional preference in ants, where an increase in temperature tends to reduce the preference for amino acid-rich resources compared to carbohydrates and lipids. Furthermore, I found that land-use changes affect ant assemblages both directly and indirectly. The reduction in insect predation caused by land-use changes is mediated by the loss of ant species richness, particularly predatory species. Finally, in my review and meta-analysis, I demonstrated that highly contrasting land-use changes (e.g., from forest to pasture conversion) reduce species richness and alter the composition of ant assemblages, likely due to the loss of sensitive and specialist species. Thus, I conclude that land-use changes can cause negative effects on various aspects of terrestrial communities, such as species richness, composition, and ecosystem functions, particularly in more extreme habitat conversions. Therefore, I suggest that, whenever possible, anthropized habitats should be maintained as close as possible to their original environment to promote species conservation and ecosystem functions.

Keywords: Nutritional Ecology; Ecosystem Function; Formicidae; Brazil; Tropical.

INDICADORES DE IMPACTO

O Brasil abriga grande parte da biodiversidade global. Entretanto, as constantes e crescentes ameaças aos ambientes naturais vêm colocando a biodiversidade brasileira em risco. Diversos estudos ecológicos buscam avaliar os impactos antrópicos na biodiversidade, mas frequentemente de maneira limitada, como acessando apenas o número de espécies e identidade delas. Nessa tese, composta por três capítulos, foram encontrados resultados relevantes a respeito de impactos antrópicos na biodiversidade brasileira, mais especificamente dos efeitos das conversões dos usos do solo na riqueza, composição e função ecossistêmica em formigas. Esses resultados podem impactar de forma científica e social, com avanços no conhecimento ecológico e identificação de efeitos negativos na biodiversidade causadas por atividade humanas frequentes como agricultura e pecuária. Além disso, alguns resultados dessa tese têm caráter extensionista, divulgando os achados de artigo científico para um público adulto, e criando um jogo de cartas didático para crianças a partir de 8 anos. Essas atividades foram desenvolvidas com a colaboração de uma docente e um pós-doutorado interno, uma pós-doutoranda externa, dois discentes de doutorado e uma discente de mestrado. Dentro da Política Nacional de Extensão, essa tese compreende as áreas temáticas de Cultura e Meio ambiente, onde foi identificado que ações humanas afetam a biodiversidade de diferentes maneiras, e as áreas temáticas Comunicação e Educação com as Mídias de Divulgação geradas. Por fim, os impactos da pesquisa e se estão alinhados com quatro dos 17 (dezessete) Objetivos de Desenvolvimento Sustentável (ODS) da Organização das Nações Unidas (ONU): ODS 2 – Fome zero e agricultura sustentável: com resultados que auxiliam na busca pela agricultura que impactam menos o meio ambiente; ODS 4 – Educação de qualidade: com as Mídias de Divulgação voltada ao público não acadêmico; ODS 13 – Ação contra a mudança global do clima: identificando que alterações dos usos do solo podem afetar o clima local, e servir de base para estudos em escalas maiores; e ODS 15 – Vida terrestre: identificando impactos antrópicos que alteram a biodiversidade terrestre, além de discutir e sugerir alternativas.

IMPACT INDICATORS

Brazil harbours a large portion of global biodiversity. However, the constant and growing threats to natural environments have been putting Brazilian biodiversity at risk. Several ecological studies aim to assess the anthropogenic impacts on biodiversity, but often in a limited way, such as only assessing the number of species and their identity. In this thesis, composed of three chapters, relevant results regarding anthropogenic impacts on Brazilian biodiversity were found, specifically the effects of land-use conversions on species richness, composition, and ecosystem function in ants. These results can impact both scientifically and socially, with advances in ecological knowledge and the identification of negative effects on biodiversity caused by frequent human activities such as agriculture and livestock farming. Furthermore, some results from this thesis have an extensionist nature, disseminating the findings of scientific articles to an adult audience and creating an educational card game for children aged 8 and above. These activities were developed with the collaboration of a faculty member, an internal postdoctoral researcher, an external postdoctoral researcher, two doctoral students, and a master's student. Within the National Extension Policy, this thesis encompasses the thematic areas of Culture and Environment, where it was identified that human actions affect biodiversity in different ways, and the thematic areas of Communication and Education, with the Outreach Media generated. Finally, the research impacts are aligned with four of the 17 Sustainable Development Goals (SDGs) of the United Nations (UN): SDG 2 – Zero Hunger and Sustainable Agriculture: with results that assist in the search for agriculture that impacts the environment less; SDG 4 – Quality Education: with Outreach Media aimed at a non-academic audience; SDG 13 – Climate Action: identifying that land-use changes can affect the local climate and serve as a basis for studies on larger scales; and SDG 15 – Life on Land: identifying anthropogenic impacts that alter terrestrial biodiversity, in addition to discussing and suggesting alternatives.

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PRIMEIRA PARTE

INTRODUÇÃO GERAL

Os ambientes tropicais abrigam a maior parte da biodiversidade do planeta, mas enfrentam ameaças crescentes devido às ações humanas, especialmente a conversão do uso do solo (Newbold *et al.*, 2020). Esse processo ocorre quando um habitat natural é transformado em outro, como no desmatamento de florestas tropicais para expansão agrícola. Isso pode causar grandes alterações nas condições ambientais e na disponibilidade de recursos (Stein; Gerstner; Kreft, 2014; Machado *et al.*, 2020), o que por sua vez, impactam as comunidades biológicas, levando à perda de espécies sensíveis e à redução da biodiversidade local (Filgueiras *et al.*, 2021). Embora os estudos frequentemente abordem essas perdas do ponto de vista taxonômico, aspectos relacionados às preferências por recursos e à ecologia funcional, áreas ainda emergentes (Luza *et al.*, 2023), são pouco estudados. Assim, investigar os efeitos da conversão do uso do solo além da diversidade taxonômica pode contribuir para uma compreensão mais ampla dos impactos antrópicos em ambientes tropicais, relacionada ao ecossistema como um todo.

Na região Neotropical, a conversão do uso do solo ocorre principalmente pela substituição de florestas e savanas por áreas agrícolas e pastagens (Fao, 2016). No Brasil, esse processo tem sido historicamente intenso, gerando dois *hotspots* de biodiversidade: o Cerrado e a Mata Atlântica (Kong; Zhou; Jiao, 2021). A substituição da vegetação nativa por cultivos pode provocar mudanças drásticas na estrutura e composição da vegetação, incluindo a redução da cobertura vegetal e da diversidade de espécies de plantas (Castillo-Campos *et al.*, 2024). Como consequência, ocorrem modificações no microclima e na disponibilidade de recursos (Stein; Gerstner; Kreft, 2014; Machado *et al.*, 2020), afetando a fauna local e levando à perda de espécies especializadas e termossensíveis.

Além de afetar a riqueza e diversidade de espécies, as alterações no uso do solo podem modificar a atividade das espécies remanescentes. Ambientes mais extremos, com temperaturas elevadas, tendem a ter menor riqueza e redução da atividade das espécies devido aos riscos de dissecação (Parr; Bishop, 2022). No entanto, algumas espécies ajustam seu comportamento para lidar com essas mudanças. Por exemplo, temperaturas mais altas podem aumentar o metabolismo, elevando a busca por recursos energéticos (Riemer *et al.*, 2018). Da mesma forma, a limitação de certos nutrientes pode intensificar o esforço de forrageamento e alterar a preferência pelos nutrientes mais escassos (Kaspari *et al.*, 2012). Assim, compreender como o uso do solo altera as condições ambientais e a oferta de recursos é fundamental para avaliar a

dinâmica das comunidades ecológicas em áreas antropizadas, além das avaliações microclimáticas poderem auxiliar estudos sobre mudanças climáticas em escalas mais amplas.

Essas mudanças na disponibilidade de recursos e no comportamento das espécies podem ter consequências diretas sobre as funções ecossistêmicas. Alguns mecanismos alternativos podem explicar esses impactos. Primeiro, a perda de espécies pode comprometer determinadas funções ecossistêmicas, uma vez que a redução do número de espécies e indivíduos pode diminuir a realização de determinada função (Biggs *et al.*, 2020). Segundo, a perda de muitas espécies sensíveis e ganho de poucas generalistas (“*few winners, many losers*”; Mckinney; Lockwood, 1999) pode, em alguns casos, intensificar certas funções ecossistêmicas, já que espécies generalistas podem ser mais ativas em ambientes antropizados e ocupar o nicho das espécies perdidas (Manlick; Newsome, 2021). Terceiro, a substituição de espécies, especialmente com a predominância de espécies dominantes, pode levar à homogeneização das funções ecossistêmicas (Wong; Guénard; Lewis, 2020). Assim, avaliar como as alterações nos usos do solo modificam as funções ecossistêmicas se torna relevante para estratégias de conservação, como o planejamento de paisagens multifuncionais, incluindo sistemas agrícolas e áreas naturais e/ou corredores ecológicos, propiciando conservação das espécies e suas funções.

Apesar dos esforços crescentes para compreender os impactos antrópicos na biodiversidade, a maioria dos estudos foca principalmente na riqueza e diversidade taxonômica, deixando outras áreas ainda pouco exploradas, como preferências por recursos e funções ecossistêmicas (Moses *et al.*, 2023). Investigar esses aspectos pode ser crucial para entender como as comunidades se ajustam a ambientes antropizados, especialmente diante das alterações na atividade de forrageio resultantes da redução de recursos e das mudanças microclimáticas. Além disso, essas modificações no forrageio podem afetar diretamente a realização de funções ecossistêmicas, um tema que também é pouco avaliado em relação a ecologia taxonômica, mas essencial para dinâmicas ecológicas em ambientes naturais e serviços ecossistêmicos em áreas antropizadas (Luza *et al.*, 2023).

Para compreender como os usos do solo impactam a biodiversidade terrestre tropical, levando em consideração aspectos taxonômicos (riqueza e composição), preferências por recursos e funções ecossistêmicas, utilizei as formigas como modelo de estudo. As formigas são um grupo megadiverso, especialmente em regiões tropicais como o Brasil (Feitosa *et al.*, 2022). Além de sua vasta diversidade de espécies e grupos funcionais, elas forrageiam por diferentes tipos de alimento e desempenham funções ecológicas essenciais, como predação,

herbivoria e proteção de plantas (Folgarait, 1998). Por outro lado, as formigas são altamente sensíveis a impactos antrópicos, como a conversão do uso do solo, o que pode reduzir a riqueza de espécies e alterar os padrões de forrageio e as funções ecossistêmicas (Moses *et al.*, 2023; Wilker *et al.*, 2023). Embora já exista uma grande quantidade de estudos sobre efeitos dos usos do solo nas formigas no Brasil, ainda há uma necessidade de uma revisão abrangente que sintetize os resultados existentes e identifique lacunas no conhecimento da área da mirmecologia (Wilker *et al.*, 2024).

Assim, meu objetivo geral nesta tese foi avaliar como as alterações no uso do solo e as mudanças microclimáticas afetam a diversidade de formigas, suas preferências alimentares e a função ecológica de predação, além de realizar uma revisão sistemática com meta-análise sobre os efeitos do uso do solo sobre as formigas no Brasil. Para isso, dividi a tese em três capítulos:

1) *Land use and microclimate changes alter ant foraging in Neotropical biomes*

No primeiro capítulo da tese, atualmente na segunda rodada de revisão na revista *Ecological Entomology*, avaliamos como a conversão de florestas para plantações de café nos biomas Cerrado e Mata Atlântica afeta o forrageio de formigas por nutrientes (aminoácidos, carboidratos, lipídios e sódio) e larvas de insetos (*Tenebrio molitor* Linnaeus, 1758).

2) *Land use changes have direct and indirect negative effects on ant species richness and predation*

No segundo capítulo, formatado conforme as normas da *Biodiversity and Conservation*, avaliamos os efeitos diretos e indiretos da conversão de áreas de floresta para plantações de café sobre o microclima, a riqueza de espécies de formigas e, consequentemente, sobre a predação de insetos.

3) *A systematic review of the land use change effects on ant diversity in Neotropics*

No terceiro capítulo, publicado na revista *Biological Conservation*, realizamos uma revisão sistemática com meta-análise sobre os estudos de caso que investigam os efeitos do uso do solo sobre as formigas no Brasil.

Além dos artigos científicos, a tese também inclui duas mídias de divulgação científica: uma notícia publicada no Portal da Ciência da Universidade Federal de Lavras, voltada para o público adulto, sobre os efeitos do uso do solo nas formigas no Brasil, um jogo de cartas com livro ilustrado, ainda em desenvolvimento, destinado a adultos e crianças acima de 8 anos, sobre interações tróficas e os impactos antrópicos na biodiversidade do Cerrado.

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SEGUNDA PARTE

ARTIGO 1 - The preference for energetic resources is positively associated with predatory activity in ants

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1 ABSTRACT

2 1. Land use changes can alter resource availability and microclimate variables in tropical
3 ecosystems, generally altering community structure by decreasing species richness and
4 changing its composition. These changes affect foraging activity, nutrient preferences, and
5 consequently ecosystem functions.

6 2. Our aim was to assess how foraging activity and nutrient preference is influenced by
7 changes in land use and microclimate.

8 3. We sampled ants (Formicidae) at 32 sites undergoing conversion from natural habitats
9 to coffee systems in two Neotropical biomes: the Atlantic rainforest and the Cerrado. We
10 assessed nutrient preference (amino acids, carbohydrates, lipids, and sodium) and predation
11 using mealworm larvae, while also measuring temperature and humidity.

12 4. We found the same ants foraged for different resources, likely because generalist species
13 can perform these activities on the ground. Furthermore, foraging for energetic resources
14 (carbohydrates and lipids) positively correlated with foraging for larvae. This indicates that the
15 limitation of energetic resources can contribute to an increase in foraging and predatory activity.
16 Moreover, ant preference for amino acids decreases with increasing temperature, indicating that
17 ants prefer to consume energetic resources to support metabolic processes.

18 5. In conclusion, foraging is primarily carried out by generalist species. In addition, the
19 preference for energetic nutrients, driven by energetic limitations, is linked to predatory
20 activity. Moreover, ant species richness increases foraging for larvae, while rising temperatures
21 decrease the preference for amino acids. Thus, conserving species richness and mitigating
22 temperature increases may enhance larval foraging and support the insect predation function in
23 Neotropical habitats.

24 **Keywords:** Disturbance, ecosystem function, macronutrients, nutritional ecology, nutrient
25 preference, temperature, tropical biodiversity

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INTRODUCTION

Land use changes drive tropical biodiversity loss primarily through the conversion of forest to agriculture (Jayathilake et al., 2021; Williams & Newbold, 2020). This conversion alters environmental conditions (Machado et al., 2023) and decrease the resources that are available to resident species (Stein et al., 2014; Tews et al., 2004). This can decrease species richness (McKinney & Lockwood, 1999; Wilker et al., 2024) and select for organisms with different ecological adaptations, such as modifications in their foraging activity and diet (Castillo-Guevara et al., 2019; Manlick & Newsome, 2021). In turn, changes in foraging activity and nutrient preference can alter ecosystem functions (Dudley et al., 2012; Maisey et al., 2021). Consequently, understanding how land use in the tropics affects foraging activity and nutrient preference would provide a better comprehension of the impacts of land use beyond community structure (e.g., species richness), laying the groundwork for future conservation practices.

The foraging activity of animals can be altered by microclimate alterations resulting from land use changes. For example, as forest vegetation is converted to open vegetation land uses, there is a reduction in available shade and an increase in solar radiation (Machado et al., 2023). This leads to an increase in maximum temperature and a decrease in minimum temperature and humidity (Alkama & Cescatti, 2016; Trancoso et al., 2022). Consequently, many animals tend to reduce their foraging activity to minimize thermal and desiccation risks (Parr & Bishop, 2022). On the other hand, increased temperatures may enhance foraging activity on average, especially in ectotherms. This happens because higher temperatures raise animals' metabolic rates, thus allowing them to forage for greater durations relative to when it is cooler (Riemer et al., 2018). Therefore, changes in foraging due to microclimatic changes can have opposite effects in tropical habitats.

The other way in which land use change impacts foraging activity and nutrient preference is by decreasing the quantity and variety of resources provided by plants and animals (Adkins et al.,

2023; Tilman et al., 1996). This occurs because, according to the compensation hypothesis, animals tend to increase their foraging activity for nutrients that are scarce in their environment or diet (Kaspari et al., 2012; Kaspari & Yanoviak, 2001). In this sense, as agricultural systems reduce the productivity of native plant resources (Barnes et al., 2017), a scarcity of energetic nutrients occurs. This can lead both to a decrease in overall foraging activity due to smaller population sizes and to an increase in the search for specific limiting energetic nutrients (e.g., carbohydrates and lipids) compared to non-energetic nutrients (e.g., amino acids and sodium; Lasmar et al., 2021; Peters et al., 2014). Moreover, the decline in productivity commonly associated with anthropogenic land uses may lead to increased foraging for energetic resources (Lasmar et al., 2021), including a greater preference for lipids over amino acids among predatory groups due to energetic limitations (Lasmar et al., 2023; Mayntz et al., 2005). In contrast, species that forage on the ground in natural tropical environments are typically not constrained by sodium availability (Lasmar et al., 2021). Additionally, sodium availability may rise through practices such as fertilization and irrigation (Hopmans et al., 2021), which could reduce the preference for this nutrient. Thus, despite an expected decrease in foraging activity due to the low population sizes in agricultural land uses, animals may alter nutrient preference, focusing primarily on energetic resources, due to there being a greater number of limiting nutrients caused by the land use change.

Despite the negative impacts of land use on community structure, the effects on foraging activity and nutrient preference are still poorly evaluated (but see Lasmar et al., 2023; Moses et al., 2023). Several studies have identified a decline in species richness due to the local extinction of sensitive species and the survival of generalist species (e.g., Tabarelli et al., 2012). This may lead to a reduction in overall foraging activity due to the positive relationship between species richness and the intensity of foraging (Lasmar et al., 2021; Noriega et al., 2021). On the other hand, generalist species can forage for a variety of resources in anthropogenic land uses

(Dehling et al., 2021; Manlick & Newsome, 2021), changing their patterns of nutrient preference. Additionally, the impact of land use changes can vary in magnitude depending on the type of natural habitat (Carvalho et al., 2022; López-Bedoya et al., 2022; Wilker et al., 2024). For example, land use changes in different biomes may select for different species based on the original species pool (Corbelli et al., 2015). Consequently, these species may alter their foraging patterns in various ways, influenced by their response to changes in the microclimate and resource availability, as well as by the impacts of land use modifications on foraging activity and nutrient preferences. Thus, assessing the effects of land use changes on nutrient preference, considering the biome context and microclimatic variables, may contribute to the conservation in both natural and anthropized habitats.

Ants (Hymenoptera: Formicidae) are excellent models for assessing the effects of land use changes (Andersen, 2019; Ribas et al., 2012) on foraging effort and nutrient preference (Lasmar et al., 2021, 2023; Peters et al., 2024). This is because ants exhibit a high diversity of species and life histories among animals (Feitosa et al., 2022). They also exhibit decreases in species richness and changes in community composition in response to anthropogenic impacts, including land use change (Andersen, 2019; Ribas et al., 2012). Furthermore, ants forage for various nutrients such as carbohydrates and lipids as energy sources, amino acids for body growth, and sodium for metabolic processes (Riemer et al., 2018). For example, ants may exhibit increased predatory activity in anthropogenic land uses, driven by the heightened activity of generalist groups (Wilker et al., 2023). Moreover, the consumption of lipids has been linked to predatory activity in ants and ground-dwelling communities (Lasmar et al., 2023). Consequently, in predatory behaviour, which is most exhibited by generalist ants (Cerdá & Dejean, 2011), these arthropods may forage more for carbohydrates and lipids due to their limited availability at the trophic level (Kaspari et al., 2012; Lasmar et al., 2023; Wilder et al., 2013). Alternatively, the scarcity of these nutrients in their diet can lead to increased lipid intake

from prey bodies (Mayntz et al., 2005). However, ant foraging activity and nutrient preferences may be affected by changes in land use. Due to ants being thermosensitive, microclimate changes in anthropogenic land uses can decrease their foraging activity (Parr & Bishop, 2022). Additionally, a lower number of species associated with intensified land use is linked to reduced foraging activity, likely due to a smaller number of foraging ants (Lasmar et al., 2021). Thus, ants may exhibit changes in foraging patterns with alterations in land uses in tropical ecosystems.

Here, our aim was to assess whether changes in land use and microclimate explain the foraging activity and nutrient preference of ants. We considered foraging activity for the following resources: nutrients (lipids, carbohydrates, amino acids, sodium) and mealworm larvae (*Tenebrio molitor* Linnaeus, 1758). More specifically, we asked: (i) How similar is the species composition across land uses and resources? We expected that ant composition would differ across land uses due to species turnover but would be similar among ants that forage for larvae, carbohydrates, and lipids, indicating limiting resources for predatory ants; (ii) Is foraging for larvae explained by nutrient preference? We expected that foraging for larvae would be positively associated with foraging for carbohydrates and lipids, as predatory ants should increase their foraging for energy sources; (iii) How are changes in foraging activity (foraging for larvae and nutrient preference) explained by ant species richness, land use, and microclimate changes? We expected that foraging activity would be positively associated with increases in ant species richness and temperature but negatively associated with extreme temperatures and low humidity in agricultural systems. Moreover, we expected that foraging for lipids, carbohydrates (energetic resources), and larvae would increase in anthropogenic land uses due to resource limitations.

METHODS

Study site

We collected data on ant foraging activity in the state of Minas Gerais, Brazil. Minas Gerais has a territory of 586,528 km², mainly composed of the Atlantic rainforest (40%) and the Cerrado (54%) (Figure 1; Biomas, 2019). The Atlantic rainforest and Cerrado are considered global biodiversity hotspots due to their high species numbers, endemism, and the significant threat by land use changes (Trew & Maclean, 2021). The Atlantic rainforest (tropical forest) extends into tropical and subtropical regions, generating diverse rainforest environments. On the other hand, the Cerrado (Brazilian savannah) features various vegetation types, ranging from open vegetation habitats to closed forests, including grasslands, shrublands, typical savannas, and woodland savannah (cerradão). These regions are characterized by a wet summer (October to March) and a dry winter (April to September). In the winter, Cerrado has an average precipitation of 23.50 mm and average temperature of 18.25 °C, while the Atlantic rainforest has an average precipitation of 26.75 mm and average temperature of 18.97 °C. In the summer, Cerrado has an average precipitation of 212.87 mm and average temperature of 22.16 °C, while Atlantic rainforest has an average precipitation of 134.54 mm and an average temperature of 20.41 °C (INMET, 2024).

Experimental design

We sampled between January and March of 2022 and 2023. In total, we sampled 32 sites (n = 32). The sites are composed of six woodland savannahs (cerradão), six tropical forests in Atlantic rainforest, eight coffee plantations in Cerrado and 12 coffee plantations in Atlantic rainforest (Figure 1; Table S1). The collections in the Cerrado were conducted in the rural areas of the municipality of Patrocínio (14 sites), while the collections in the Atlantic rainforest were conducted in the rural areas in the municipalities of Lavras (4 sites) and Santo Antônio do Amparo (SAA) (14 sites). Each site had only one transect per sampling, and the sites were spaced at least 322 m apart.

We collected data from coffee plantations of the species *Coffea arabica* L. All plantations were unshaded and mechanized (e.g., use of tractors). In the Atlantic rainforest, all coffee plantations were conventional (12 sites). In the Cerrado, four sites were conventional coffee (with the use of fertilizers and insecticides), and four sites were organic coffee (without the use of fertilizers and insecticides). Before conducting our hypothesis tests, we assessed the possible influence of these variables on our analyses and found that the type of coffee management (conventional or organic) did not affect the results, allowing us to combine the data and disregard management type in the analyses.

Foraging activity for resources

In each transect, we assessed ant foraging activity for resources, including nutrients (amino acids, carbohydrates, lipid, and sodium) and larvae. Nutrients were offered in the liquid form, and we used water as control. In each site, we created a transect with 25 sampling points spaced 10 meters apart (totalling 240 m). In each transect, we sampled ants, between 7 a.m. and 8 a.m., using the nutrients in Fisher 50 mL tubes. Each tube contained 10 ml of an aqueous solution of each type of nutrient. The nutrients included 20% amino acids (AA, made with Whey Protein Isolate and unflavoured containing L-glutamine and other amino acids such as leucine, isoleucine, and valine), 20% carbohydrates (CHO, made with sucrose), lipids (100% extra virgin olive oil, without water), 1% sodium solution (NaCl, made with salt), and tap water (Lasmar et al. 2021; 2023). The tubes were placed horizontally on the ground and closed at the end of sampling, with the ants inside collected and stored in 70% alcohol for preservation.

After the nutrient experiment, in the same transect but only at five sampling points spaced 50 m apart (totalling 200 m), we assessed foraging for larvae as a proxy measure for insect predation by ants. At each sampling point, we installed two beetle larvae (*Tenebrio molitor*). The larvae were attached with Velcro to an ethylene-vinyl acetate (EVA) surface to prevent them from escaping. At each sampling point, between 8 a.m. and 12 p.m., we observed foraging

activity in four rounds of five minutes each. First, we attached the larvae to the ground at the first sampling point and immediately observed the foraging for larvae for five minutes. Then, we attached larvae at the second sampling point and observed the foraging for larvae for five minutes. We repeated this process until completing the transect and then started again for the second, third, and fourth rounds. This totaled 20 minutes per sampling point and 100 minutes per transect. We considered the foraging activity by ants when they attacked the larvae, either by stinging or biting (Wilker et al., 2023). The ants that engaged in predation were collected and stored in 70% alcohol for later identification.

Microclimate measurements

We measured temperature and humidity alongside the larvae experiment. Using a digital thermo-hygrometer, we measured air temperature (°C) and humidity (%) at 5 cm from the ground at the sampling point. We took 20 temperature and humidity measurements per transect (five sampling points x four rounds) and used the average of them in our analyses.

Ant species richness and composition

After the larvae experiment, in the same transect with five sampling points spaced 50 meters apart (totalling 200 m), we installed pitfall traps to assess ant species richness and composition. The traps consisted of plastic pots with a diameter of 12 cm and a depth of 11 cm, installed at ground level. We added an aqueous solution composed of 200 ml of water mixed with salt and detergent to capture and preserve the collected ants. Each trap was left sampling for a period of 48 hours. After this period, the captured ants were stored in 70% alcohol.

Ant species identification

We identified to the genus level based on Baccaro et al. (2015) and morphotyped them based on external morphological characters. Identification and confirmation of species and morphospecies were made by Rodrigo M. Feitosa and Ana Carolina A. Neundorff at the Laboratório de Sistemática e Biologia de Formigas at the Universidade Federal do Paraná

(UFPR). Specific published descriptions were used to identify species in the genera *Acromyrmex* (Gonçalves, 1961), *Acropyga* (LaPolla, 2004), *Apterostigma* (Lattke, 1997), *Basiceros* (Probst & Brandão, 2022), *Brachymyrmex* (Ortiz-Sepúlveda et al., 2019), *Carebara* (Fernández, 2004), *Ectatomma* (Kugler & Brown, 1982), *Gnamptogenys* (Camacho et al., 2020), *Labidus* (Watkins, 1976), *Linepithema* (Wild, 2007), *Neivamyrmex* (Watkins, 1976), *Odontomachus* (Brown, 1976), *Pheidole* (Wilson, 2003), *Strumigenys* (Bolton, 2000), and *Wasmannia* (Longino & Fernández, 2007). Voucher specimens were deposited in the reference collection of Laboratório de Ecologia de Formigas at UFLA and the Coleção Entomológica Padre Jesus Santiago Moure at UFPR (DZUP).

Data analysis

Foraging activity for resources was computed in two distinct ways for nutrients and larvae. For nutrients, we used a measure nutrient preference at each transect (relative resource use; Lasmar et al., 2021). As we are primarily interested in the preference between energy nutrients (carbohydrates and lipids) compared to amino acids, to calculate the nutrient preference, we excluded water (control) and sodium (NaCl) from compute nutrient preference. Moreover, as expected, the control and sodium tubes had lower ant occurrence (Figure S2). Nutrient preference was calculated as the number of tubes visited for a given nutrient at a transect, divided by the total number of tubes visited per transect. Thus, nutrient preference indicates the foraging for a specific nutrient in relation to all others. A nutrient foraging value of 1 indicates that all occurrences were on a single nutrient, and a nutrient foraging value of 0 means that no ant occurrences were recorded for a nutrient (Lasmar et al., 2021). To do this, we measured the nutrient preference between energy and AA, with energy being the combination of carbohydrates and lipids data. We transformed these proportional values using a logit transformation to meet Gaussian assumptions in our analyses (Lasmar et al., 2021; Warton &

Hui, 2011). For larvae, foraging was calculated by the number of attacks on larvae, being a count data, and we used the Poisson family (Wilker et al., 2023).

To assess (i) whether the species composition is similar across land uses and resources, we calculated Sørensen dissimilarity using the betapart package version 1.6 (Baselga, 2010; Baselga et al., 2023). Sørensen dissimilarity ranges from 0 to 1, where 0 indicates assemblages with identical compositions and 1 indicates assemblages with completely different compositions. We had 32 sites with five resources (amino acids, carbohydrates, lipids, sodium, and larvae), totaling 160 “assemblages”. However, in several sites, we collected only one or two ant species per assemblage. Due to the low number of species in each assemblage, we could not compute the dissimilarity between them. As an alternative, we merged the assemblages within the same land use type (woodland savannah, tropical forest, coffee plantation in Atlantic rainforest, and coffee plantation in Cerrado). This reduced our sample size to 20 (five resources X four land use types) but increased the number of species for each sample unit. Moreover, we partitioned β sør-diversity into turnover (β sim) and nestedness (β sne). We used β sør, β sim and β sne to perform three non-metric multidimensional scaling (NMDS) analyses, using the function *metaMDS* (vegan package version 2.6-6; Oksanen et al., 2024). We then tested the difference in community dissimilarity with three permutational analyses of variance (PERMANOVA), using the function *adonis2* (vegan package version 2.6-6; Oksanen et al., 2024) with 9999 permutations. In all models, we used the predictor variables of resources and land use type. As a response variable, we used β sør, β sim and β sne, one for each model. When we found a significant result in PERMANOVA, we used the function *pairwise.adonis2* (pairwiseAdonis package version 0.4; Martinez Arbizu, 2020) to understand which pairs of assemblages were different.

To assess (ii) whether foraging for larvae is explained by nutrient preferences, we built two generalized linear model (GLM). As the response variable, we used the number of foraging for

larvae per transect. As predictors we used the nutrient preference per transect (foraging for a specific nutrient in relation to all others). In first model, we used the nutrient preference for energetic nutrients, and in second model the nutrient preference for AA. We considered a result significant if $p < 0.05$. We used the Poisson family because the response variable is count data (number of ants foraging for larvae per transect). We evaluated the normality of the residuals using histograms and quantile-quantile plots and the heteroscedasticity using residuals by fitted value plots. Moreover, because the model was overdispersed, we changed the family to negative binomial, using the MASS package (Venables & Ripley, 2002).

To avoid multicollinearity between microclimate variables, we tested a correlation between temperature and humidity. The Spearman correlation coefficient between these variables was strongly negative ($\rho = -0.86$; $p < 0.001$; Figure S1). For this reason, we used only temperature as a microclimate variable.

To assess (iii) whether changes in foraging activity are explained by ant species richness, land use, and microclimate changes, we calculated three GLMs. In all models, we used ant species richness, land use (natural habitat or coffee plantation) and temperature as predictor variables. We also use biome (Atlantic rainforest and Cerrado) with a predictor variable to assess whether the patterns were consistent across different geographic contexts. In one model, we used foraging for larvae as the response variable. In the other two models, we used nutrient preference for energy and nutrient preference for amino acids. For models with larvae, we used a negative binomial error family because of the overdispersion. For the models with nutrient preference, we used the gaussian family. In all models, we tested the residual normality and homoscedasticity. Moreover, in all models, we used the *dredge* function to select the best models and identified “uninformative parameters” following Leroux (2019).

We used the *dredge* function (MuMIn package version 1.47.5; Bartoń, 2023) to run all possible models. The dredge function ranked the models based on the Akaike information criterion

corrected for small sample sizes (AICc). We considered models to be equivalent if $\Delta\text{AICc} < 2$ (Burnham & Anderson, 2002). However, within our selected models there may be “uninformative parameters”, leading to a Type I error (Leroux, 2019). We followed the approach proposed by Leroux (2019) for detecting these “uninformative parameters”. We compared the log-likelihoods of the top model and those models within $\Delta\text{AICc} < 2$ that had additional parameters not in the top model. If the log likelihoods were different (log-likelihoods > 1), we considered the additional parameters as informative. If the log likelihoods were similar (log-likelihoods < 1), we checked to see if the 95% confidence intervals (CI) of the additional parameters overlapped zero, using the *confint* function (stats package; R Core Team, 2024). If the confidence intervals overlapped zero, we considered the parameters to be uninformative, if they did not overlap zero, we considered them to be informative. When the predictor overlaps zero, it probably does not explain the response variable (Leroux, 2019).

All analyses were completed in R 4.3.3 (R Core Team, 2024). All graphs were made with the ggplot2 package (Wickham, 2016).

RESULTS

We sampled 12,346 ant workers and 138 ant species, belonging to 124 ant species for pitfall data, 28 ant species foraging for larvae, and 51 species for nutrient preference (more details in Tables S2-S6). Concerning nutrient preference, we found that ant foraging was higher for carbohydrates (ant presence in carbohydrate tubes: mean $\pm$ deviation standard = 0.50 ± 0.50) and lipids (ant presence in lipid tubes: 0.45 ± 0.49), intermediate for amino acids (ant presence in amino acid tubes: 0.19 ± 0.39) and sodium (ant presence in sodium tubes: 0.21 ± 0.41), and low for control tubes (ant presence in control tubes: 0.09 ± 0.29) across all transects (Figure S2; Table S6).

Regarding (i) whether the species composition is similar across land uses and resources, we found that the ant species composition differs between land uses (degrees of freedom (d.f.) = 3;

$F = 6.373$; $p < 0.001$), and the principal beta diversity component is turnover ($\beta_{\text{sor}} = 0.918$, $\beta_{\text{sim}} = 0.883$, and $\beta_{\text{sne}} = 0.035$; Figures S3-S4). However, we did not find a different ant composition across different resources (Figure 2 and Table S7).

Regarding (ii) whether foraging for larvae is explained by nutrient preference, we found that an increase in foraging for energy (carbohydrates and lipids combined), relative to amino acids, positively explained the foraging effort for larvae (d.f. = 30; $F = 3.924$; $p = 0.047$; $R^2 = 0.11$; Figure 3). However, we did not find an effect of nutrient preference for amino acids compared to energy (d.f. = 30; $F = 0.956$; $p = 0.328$).

Regarding (iii) whether changes in foraging activity are explained by ant species richness, land use, and microclimate changes, we found predictors for both foraging for larvae and nutrient preference for amino acids (Table 1). As ant species richness increased, so did the number of foraging for larvae. Moreover, both foraging for larvae and preference for amino acids were greater in the Atlantic rainforest than in the Cerrado (Table 1; Figure 4A; Figure 5). Additionally, an increase in temperature ($^{\circ}\text{C}$) reduced the ants' preference for amino acids (Table 1; Figure 4B). On the other hand, we did not find any effect of microclimate or land use on nutrient preference for energetic nutrients (Table 1).

DISCUSSION

In our study, we identified important patterns regarding changes in foraging activity and nutrient preference caused by land use and microclimate changes. We found that ants preferred foraging for carbohydrates and lipids, indicating the ants' preference for energy resources (Lasmar et al., 2021, 2023; Peters et al., 2014). We also found that the ants foraging for different resources had the same species composition, probably due to the presence of generalist ants on the ground. Additionally, we found a positive relationship between ants foraging for energetic nutrients and larvae, suggesting that limitations in energetic resources (carbohydrates and lipids) an increase in ant foraging can contribute to higher insect predation, as it leads to more

frequent foraging on larvae. Moreover, both foraging for larvae and preference for amino acids were higher in the Atlantic rainforest than in the Cerrado, suggesting greater predatory ant activity and amino acid consumption in this biome. Thus, although foraging for larvae was associated with amino acid preference in the same biome, it is possible that nutrient limitation for energetic resources leads to increased foraging activity for these nutrients, thereby enhancing predation events.

In agreement with other studies, we found that the conversion of natural habitats to coffee systems decreases ant diversity (e.g., De la Mora et al., 2013; Escobar-Ramírez et al., 2020) and changes species composition (Perfecto & Snelling, 1995), making the communities more homogeneous in this type of land use. Sun coffee plantations, as observed in our study, tend to have more intense effects on ant assemblages compared to shaded coffee plantations, which has a more negative impact on ant diversity (Urrutia-Escobar & Armbrrecht, 2013). Moreover, ants are important predators in coffee systems, contributing to the reduction of coffee berry borer (Aristizabal & Metzger, 2019; Philpott & Armbrrecht, 2006). However, to the best of our knowledge, this is the first study to assess ant nutrient preference in coffee systems, making significant advances in the field, particularly by linking this nutrient search to insect predation, an important ecosystem function in this type of plantation.

(i) How similar is the species composition across land uses and resources?

We found that ant composition differed across land use types but was similar across all resources. At a regional scale, it was expected that species composition would differ between biomes due to distinct species pools and geographic distance (Schmidt et al., 2017). Moreover, with land use changes, there is a loss of sensitive species and a gain of generalist and resistant ones, resulting in species turnover and changes in composition (Queiroz et al., 2020; Wilker et al., 2023). The similarity in ant composition across different resources is likely due to the presence of omnivorous and opportunistic species. Most ants in our study belonged to the genus

Pheidole (Tables S2-S5), which is dominant in Brazilian biomes and forages broadly on the ground (Feitosa et al., 2022; Sarnat et al., 2015). Thus, while ant composition varies across land use types due to species turnover, it remains similar within each land use type because the same opportunistic species exploit available resources.

(ii) Is foraging for larvae explained by nutrient preference?

We found that an increase in foraging for energetic nutrients (carbohydrates and lipids) positively explained foraging for larvae. Energetic nutrients are scarce in prey, leading predators to increase foraging for carbohydrates and lipids despite the low energy gain from amino acids (Jensen et al., 2012; Lasmar et al., 2023; Wilder et al., 2013). Thus, our results suggest a positive link between the search for energetic nutrients (carbohydrates and lipids) and the predatory activity of ants compared to amino acids. Additionally, the lower correlation coefficient ($R^2 = 0.11$) can be explained by the greater number of generalist ants in our experiments, and this pattern could be stronger for strictly predatory animals.

(iii) How are changes in foraging activity explained by ant species richness, land use, and microclimate changes?

Regionally, foraging for larvae and preference for amino acids were higher in the Atlantic rainforest than in the Cerrado. This may be due to a greater limitation of amino acids in Atlantic rainforest ecosystems compared to the Cerrado, leading predatory ants to seek these nutrients more in the bodies of their prey. Cerrado is known for presenting high levels of amino acids that are present in extrafloral nectaries (Leal et al., 2017; Ribas et al., 2010). Although we collected data only from the ground, and extrafloral nectaries are found in arboreal strata, many ground-dwelling ants forage in both strata to search for resources (Passos & Leal, 2019; Rezende et al., 2024). Thus, ants are more limited by resources from nectaries, including amino acids, in the Atlantic rainforest than in the Cerrado, leading to increased predation in this biome.

Therefore, the predatory activity of animals may depend on the biome context, where nutrient limitations can enhance this function.

We also found a positive effect of ant species richness on foraging for larvae. Several studies indicate a positive relationship between ant species richness and predatory activity (e.g., De la Mora et al., 2015; Philpott & Armbrrecht, 2006). This occurs because ant predatory activity involves various species, including both specialists and generalists (Wilker et al., 2023). Thus, an increase in the number of species elevates foraging activity and, consequently, insect predation (Frizzo et al., 2020). Therefore, strategies aimed at conserving more species may consequently benefit the conservation of ecosystem functions such as predation.

In addition, we found that increasing temperature decreases the preference for amino acids compared to energetic nutrients. This is likely because, in ants and other ectothermic animals, rising temperatures lead to an increase in metabolic processes (Riemer et al., 2018). As metabolism increases, there is a greater demand for energetic resources such as carbohydrates and lipids, which are essential for energy production and metabolic function (Prather et al., 2018). On the other hand, the consumption of amino acids tends to be higher during periods of lower seasonality and cooler temperatures, which are typically associated with reproduction and body growth (Lasmar et al., 2021).

Study limitations and future directions

In our study, there are some methodological limitations and suggestions. The similarity in ant composition foraging for different resources may be due to our collection being limited to above-ground strata. These strata are dominated by omnivorous and opportunistic species that forage for a wide variety of resources. Therefore, it would be important to assess changes in species composition in other habitat strata, such as subterranean and arboreal (Lasmar et al., 2023). Moreover, we collected our data only during the summer, when temperature and

humidity tend to be higher in the Atlantic rainforest and Cerrado biomes. Therefore, we encourage further studies to evaluate seasonal differences, as they may affect ant communities (Queiroz et al., 2022) and consequently influence the search for and use of resources. Additionally, although we found a positive relationship between foraging for energetic nutrients (carbohydrates and lipids) with larvae, we sampled these nutrients separately. However, arthropod prey typically contains these nutrients together in varying concentrations (Wilder et al., 2013; Wilder & Eubanks, 2010). Therefore, it may be important for future studies to evaluate combinations of these nutrients in relation to predation to understand this relationship more comprehensively (Wilder et al., 2019).

CONCLUSION

Here, we found that land use, species richness, biome, and microclimate changes affect ant foraging activity and nutrient preference. Ant species composition varied with land use type but remained similar across different foraging resources. This suggests that generalist ants may forage on a variety of resources, helping to maintain ecosystem functions. More specifically, we observed a positive relationship between foraging for energetic nutrients (carbohydrates and lipids) and foraging for larvae, indicating that predatory ants are limited by energetic nutrients and forage for these nutrients, which can enhance predation. In addition, we found that both foraging for larvae and preference for amino acids were greater in the Atlantic rainforest than in the Cerrado, which may indicate higher predatory activity aimed at consuming amino acids in environments where these nutrients are less available. Moreover, species richness was positively associated with foraging for larvae, while higher temperatures reduced preference for amino acids. Therefore, we suggest that conserving species richness and mitigating high temperatures could help enhance predatory activity in tropical environments.

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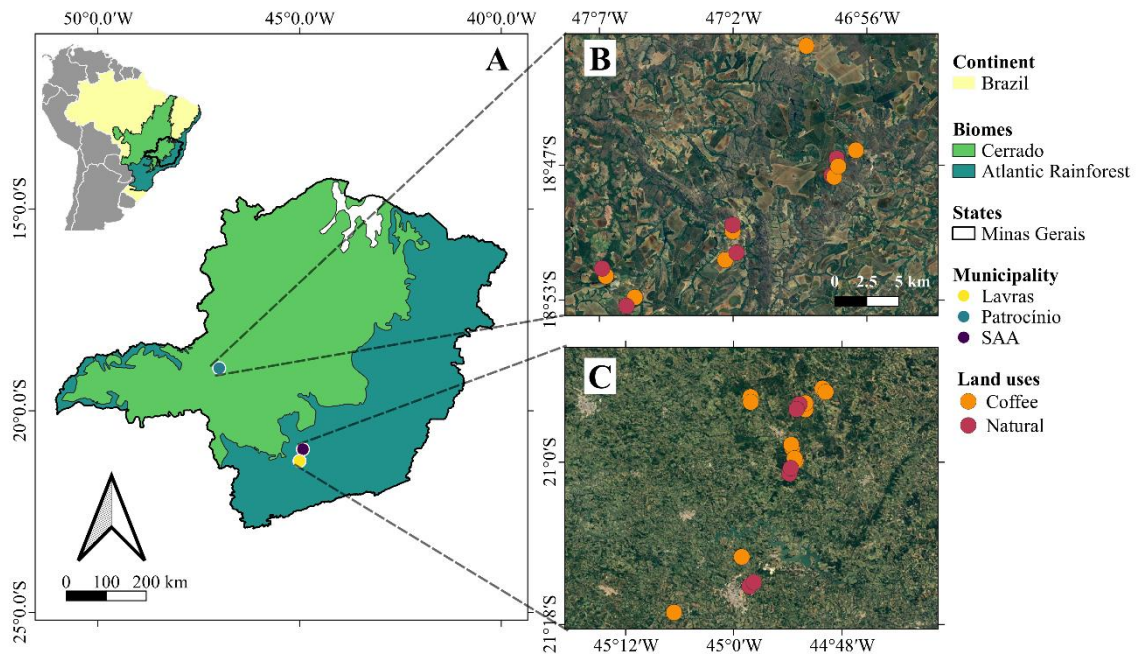


FIGURE 1 The panel A indicates the Brazilian state of Minas Gerais, including its position in South America and the location of the biomes and sampled cities. The panel B indicates some sampling points within the municipality of Patrocínio and panel C indicates the sampling points in municipalities of Lavras and Santo Antônio do Amparo (SAA). The figure was generated using QGIS version 3.32 (QGIS.org, 2023) and adapted biome and state data from Instituto Brasileiro de Geografia e Estatística (IBGE, 2019). The satellite image was from Google Satellite (2024).

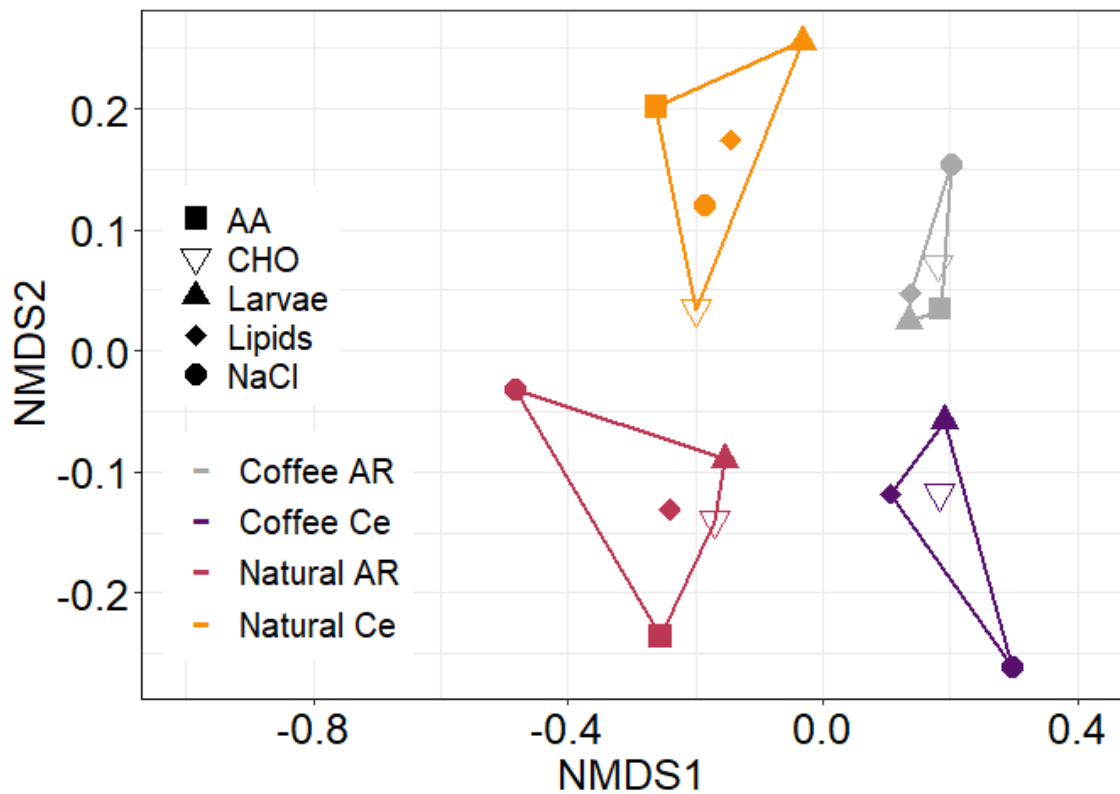


FIGURE 2 Ant species composition differs between land use types: Natural AR (forest in the Atlantic rainforest; medium pink), Natural Ce (woodland savannah in Cerrado; orange), Coffee AR (coffee plantation in the Atlantic rainforest; grey), and Coffee Ce (coffee plantation in Cerrado; purple). However, it does not differ significantly with respect to resource types: AA (amino acids; square), CHO (carbohydrates; empty triangle), Lipids (vegetable oil; diamond), NaCl (sodium; circle) and Larvae (predation experiment; full triangle). Species composition was measured using Sørensen dissimilarity ($\beta_{\text{Sør}}$).

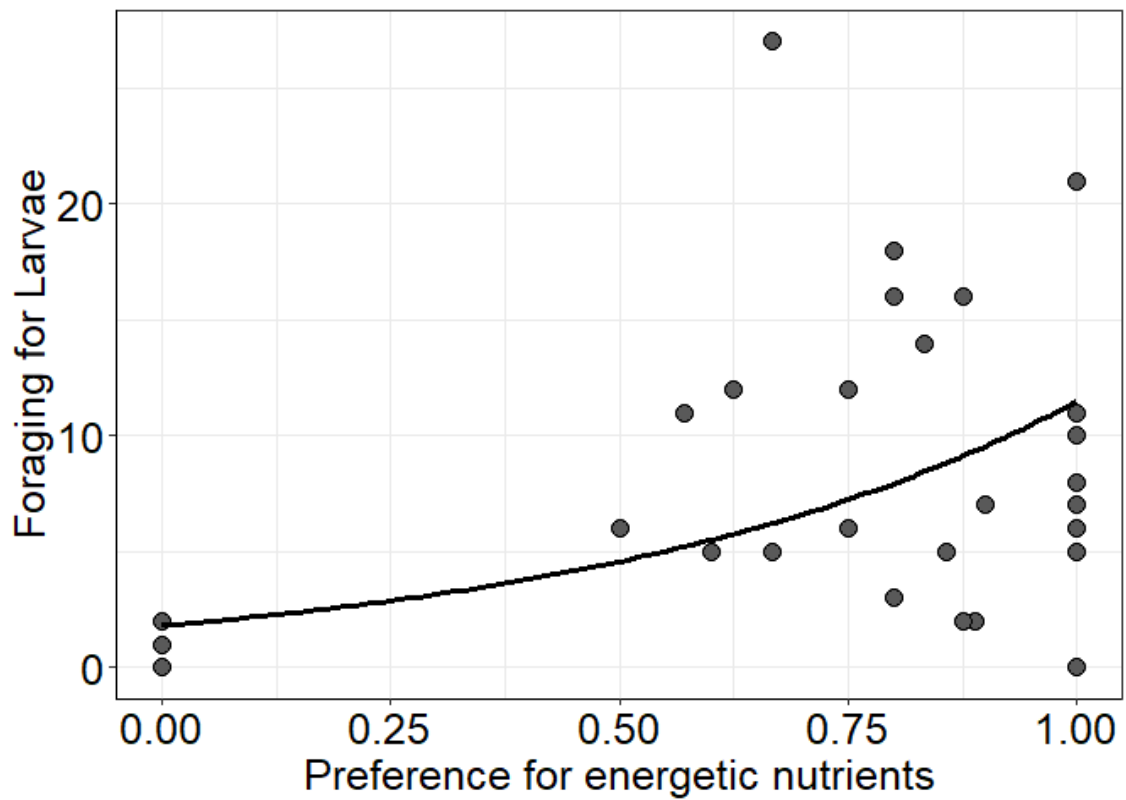


FIGURE 3 The y-axis indicates the number of foraging for larvae. The x-axis indicates the nutrient preference for energetic nutrients (carbohydrates and lipids) compared to amino acids. The increase in foraging for energetic nutrients, and consequently the decrease in foraging for amino acids, increases larvae foraging.

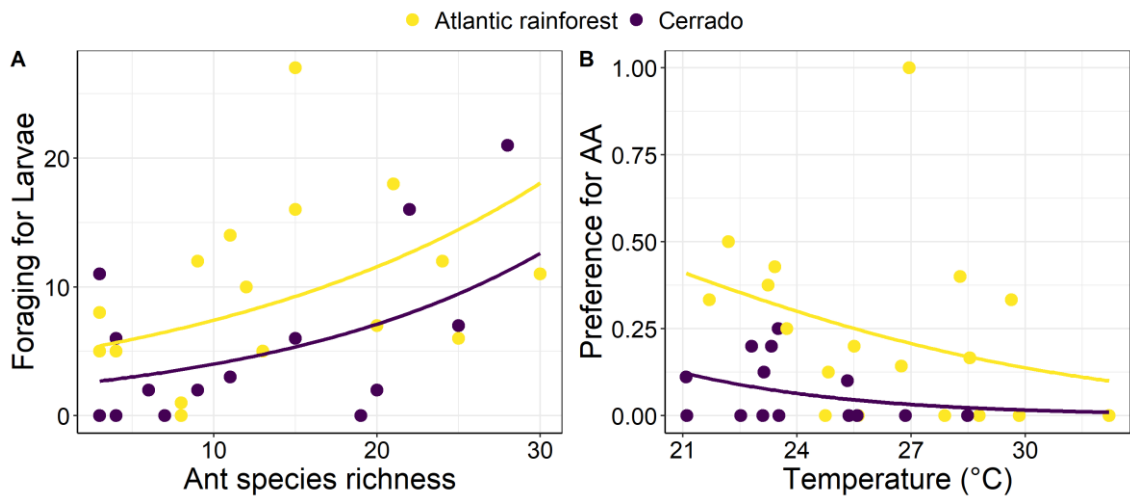


FIGURE 4 Foraging for larvae and preference for amino acids (AA) is greater in Atlantic rainforest than Cerrado. However, ant species richness increases foraging for larvae (panel A), while temperature decreases preference for amino acids (panel B).

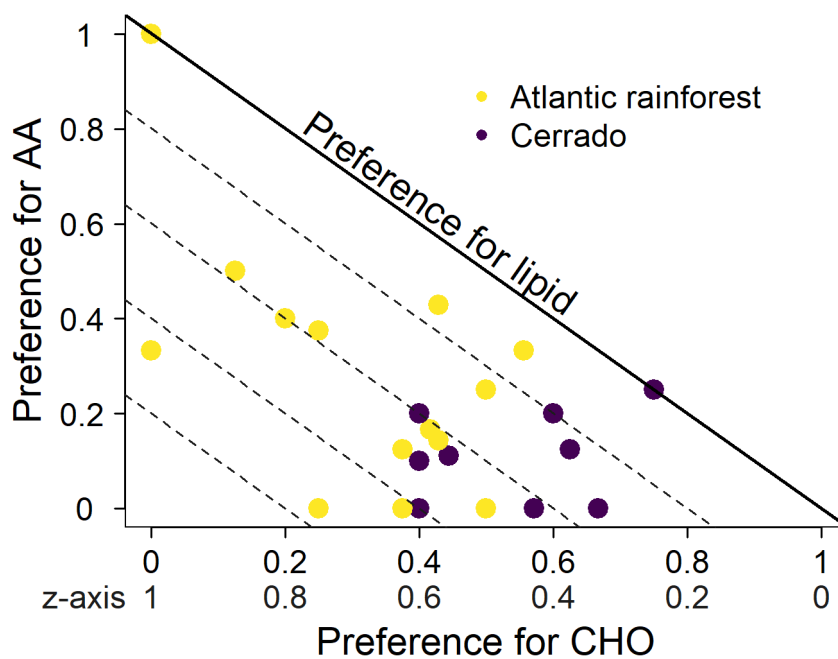


FIGURE 5 Right-angled mixture triangle (Raubenheimer, 2011), for AA (y-axis), carbohydrates (x-axis), and lipids (z-axis). This graph represents relative preference in three nutrients: AA, CHO, and Lipids. For the x-axis, the higher the preference in CHO, the lower the preference in AA and Lipids. For the y-axis, the higher the preference in AA, the lower the preference in CHO and Lipids. For relative lipid preference, the points are graphically represented in relation to the diagonal lines, with the values indicated in relation to the z-axis. The lowest lipid preference occurs when the point touches the diagonal 0, and the highest occurs when the point touches the diagonal 1 for the z-axis. In the Atlantic rainforest, ant assemblages tend to forage more for amino acids than in the Cerrado

TABLE 1 In the table, “preference for AA” represents the preference for amino acids compared to energetic nutrients (CHO + lipids), while “preference for energy” represents the preference for energetic nutrients compared to amino acid, “Land use” are the land uses (natural habitat and coffee plantation), “Temperature” is the mean of temperature in °C, “Richness” is the ant species richness, and “Biome” are the biomes (Atlantic rainforest and Cerrado). Only models with $\Delta\text{AICc} \leq 2$ were considered. Degrees of freedom of the model (d.f.), differences in AICc values (ΔAICc), Akaike weight (ω), Log Likelihood (LogLik), and Adjusted coefficient of determination (Adj-R^2) were evaluated.

Question 3: How are changes in foraging activity explained by ant species richness, land use, and microclimate changes?

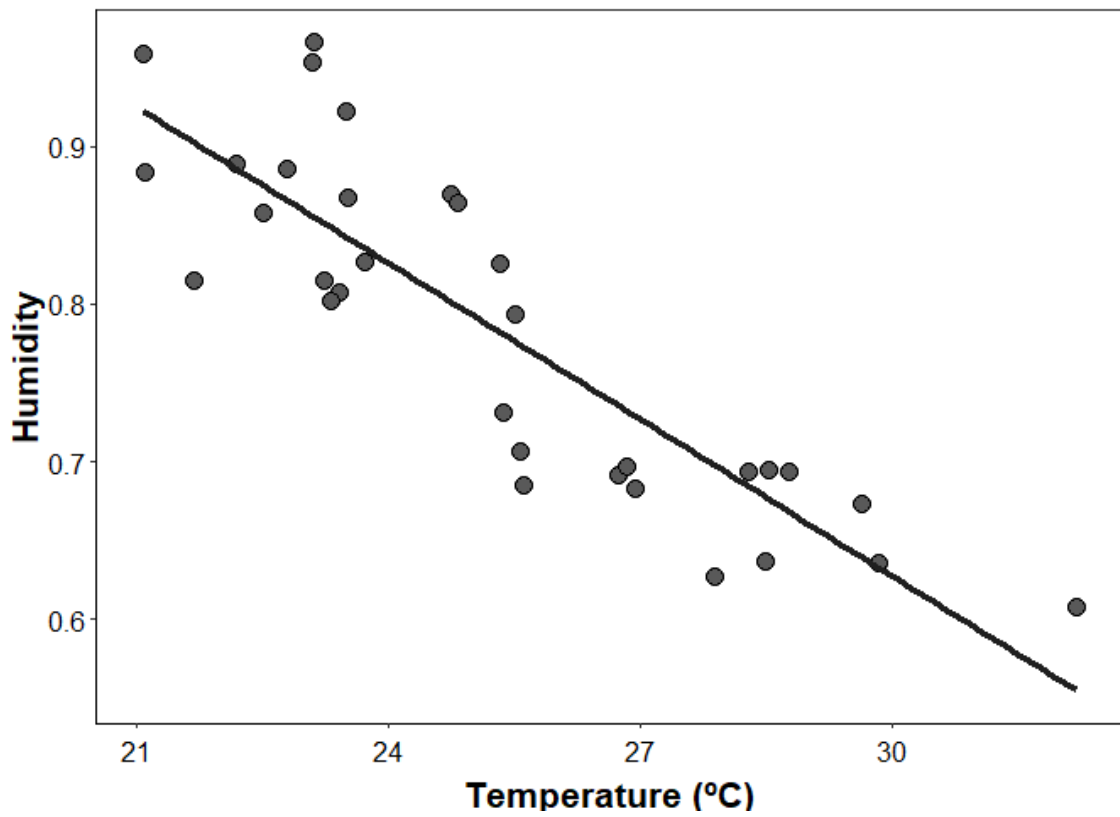
Model (larvae)	d.f.	AICc	ΔAICc	ω	LogLik	Adj-R²
Richness	3	198.0	0.00	0.21	-95.59	0.15
Biome + Richness	4	198.1	0.06	0.21	-94.31	0.21
Model (preference for AA)						
Biome + Temperature	4	125.0	0.00	0.31	-57.73	0.31
Temperature	3	126.4	1.47	0.13	-59.78	0.15
Model (preference for energy)						
<i>Null model</i>	2	151.4	0.00	0.22	-73.49	0.00
Biome	3	152.5	1.14	0.12	-72.84	0.04
Land use	3	152.7	1.28	0.11	-72.91	0.03
Temperature	3	152.8	1.42	0.10	-72.98	0.03
Richness	3	153.1	1.75	0.09	-73.14	0.02

SUPPLEMENTARY MATERIAL

Table S1. Table with transect specifications and localization. “Transect” is the name of transect; “City” is the city of transect (SAA: Santo Antônio do Amparo); “Biome” (AR: Atlantic rainforest; Ce: Cerrado); “Land use” is land use collect, natural (Atlantic Forest and Woodland Savannah) and Coffee (coffee plantation); “Altitude” is in meters above the sea level.

Transect	City	Biome	Land use	Latitude	Longitude	Altitude (m)
a1	SAA	AR	Coffee	20°58'25"S	44°53'31"W	1014
a2	SAA	AR	Coffee	20°58'03"S	44°53'37"W	1000
a3	SAA	AR	Coffee	20°52'45"S	44°58'08"W	994
a4	SAA	AR	Coffee	20°53'19"S	44°58'07"W	1025
a5	SAA	AR	Coffee	20°59'48"S	44°53'07"W	1016
a6	SAA	AR	Coffee	20°59'34"S	44°53'15"W	1002
a7	SAA	AR	Coffee	20°54'08"S	44°52'03"W	1078
a8	SAA	AR	Coffee	20°53'26"S	44°52'03"W	1106
a9	SAA	AR	Coffee	20°51'48"S	44°50'09"W	1025
a10	SAA	AR	Coffee	20°52'12"S	44°49'48"W	1009
a11	SAA	AR	Natural	20°53'33"S	44°52'42"W	1102
a12	SAA	AR	Natural	20°54'07"S	44°53'02"W	1039
a13	SAA	AR	Natural	21°01'15"S	44°53'49"W	1055
a14	SAA	AR	Natural	21°00'39"S	44°53'40"W	1039
a15	Lavras	AR	Coffee	21°10'30"S	44°59'07"W	919
a16	Lavras	AR	Coffee	21°16'40"S	45°06'38"W	924
a17	Lavras	AR	Natural	21°13'44"S	44°58'15"W	936
a18	Lavras	AR	Natural	21°13'19"S	44°57'46"W	929
a19	Patrocínio	Ce	Coffee	18°49'49"S	47°01'31"W	902
a20	Patrocínio	Ce	Coffee	18°51'05"S	47°01'51"W	919
a21	Patrocínio	Ce	Coffee	18°52'45"S	47°05'52"W	937
a22	Patrocínio	Ce	Coffee	18°51'48"S	47°07'09"W	995
a23	Patrocínio	Ce	Coffee	18°41'35"S	46°58'15"W	1130
a24	Patrocínio	Ce	Coffee	18°46'13"S	46°56'03"W	1128
a25	Patrocínio	Ce	Natural	18°51'28"S	47°07'19"W	983
a26	Patrocínio	Ce	Natural	18°53'08"S	47°06'14"W	960
a27	Patrocínio	Ce	Natural	18°46'35"S	46°56'54"W	1126
a28	Patrocínio	Ce	Natural	18°47'20"S	46°57'08"W	1121
a29	Patrocínio	Ce	Natural	18°50'46"S	47°01'21"W	868
a30	Patrocínio	Ce	Natural	18°49'32"S	47°01'31"W	933
a31	Patrocínio	Ce	Coffee	18°47'24"S	46°57'01"W	1129
a32	Patrocínio	Ce	Coffee	18°46'56"S	46°56'50"W	1128

813 Figure S1



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815 Figure S1. High negative Spearman correlation between microclimate variables ($\rho = -0.86$; $p <$
816 0.001).

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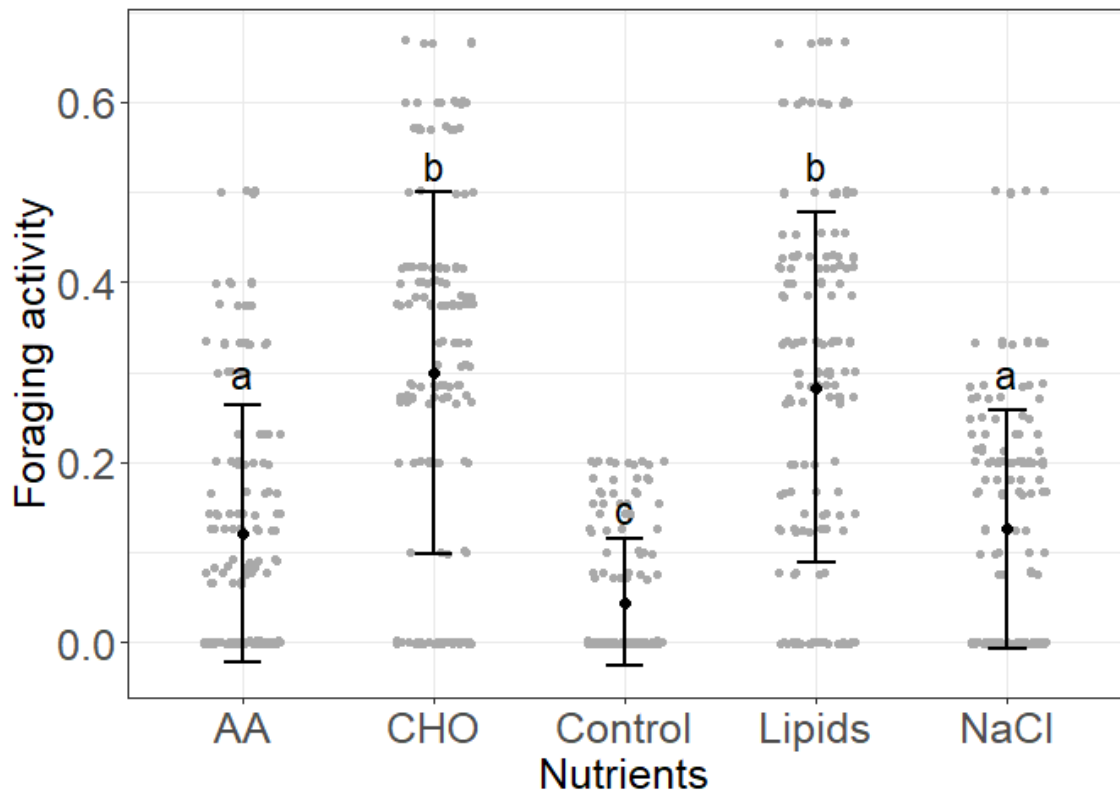
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825 Figure S2



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827 Figure S2. General foraging activity between five nutrients (AA: amino acids; CHO:
 828 carbohydrates; Control: Water; Lipids: Vegetal oil; and NaCl: Salt). The foraging activity for
 829 Control is lower than other nutrients (Gaussian GLM: $df = 795$; $F = 65.091$; $p < 0.001$).

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Table S2. Ant species richness and number of workers sampled in natural habitats (forests) in the Atlantic rainforest. “Pitfall” refers to the ants collected in pitfall traps. “Larvae” refers to ants collected in predation experiments using *Tenebrio molitor* Linnaeus, 1758 larvae (for larvae, we did not compute the number of workers, only the presence or absence of ants). The other columns refer to the nutrients experiment (CHO: carbohydrates, Lipids: vegetable oil, AA: amino acids/whey protein, NaCl: salt, and Water).

Atlantic rainforest: Natural habitat							
Species	Pitfall	CHO	Lipids	AA	NaCl	Water	Larvae
Dolichoderinae							
<i>Linepithema gallardoi</i> (Brèthes, 1914)	1	0	0	0	0	0	0
<i>Linepithema leucomelas</i> (Emery, 1894)	30	0	0	0	0	0	1
<i>Linepithema pulex</i> Wild, 2007	26	1	0	0	0	0	1
<i>Linepithema</i> sp. 2	5	0	0	0	0	0	0
Dorylinae							
<i>Labidus coecus</i> (Latreille, 1802)	2	0	0	0	0	0	0
Ectatomminae							
<i>Ectatomma edentatum</i> Roger, 1863	85	9	2	0	0	0	1
<i>Gnamptogenys sulcata</i> (Smith, 1858)	13	0	0	0	0	0	0
<i>Holcaponera striatula</i> (Mayr, 1884)	48	1	0	0	0	0	1
Formicinae							
<i>Acropyga decedens</i> (Mayr, 1887)	2	0	0	0	0	0	0
<i>Brachymyrmex bruchi</i> Forel, 1912	2	0	0	0	0	0	0
<i>Brachymyrmex cordemoyi</i> Forel, 1895	3	0	0	0	0	0	0
<i>Brachymyrmex minutus</i> Forel, 1893	1	0	0	0	0	0	0
<i>Brachymyrmex pictus</i> Mayr, 1887	1	0	0	0	0	0	0
<i>Brachymyrmex</i> sp. 1	1	0	0	0	0	0	0
<i>Camponotus (Myrmophaenus)</i> sp. 8	1	0	0	0	0	0	0
<i>Camponotus cingulatus</i> Mayr, 1862	140	0	0	0	0	0	1
<i>Camponotus rufipes</i> (Fabricius, 1775)	4	0	0	0	0	0	0
<i>Camponotus lespesii</i> Forel, 1886	37	0	0	0	0	0	0
<i>Camponotus melanoticus</i> Emery, 1894	1	0	0	0	0	0	0
<i>Camponotus (Tanaemyrmex)</i> sp. 1	1	0	0	0	0	0	0
<i>Camponotus (Tanaemyrmex)</i> sp. 4	4	0	0	0	0	0	0
Myrmicinae							
<i>Acromyrmex aspersus</i> (Smith, 1858)	424	0	0	0	0	0	0
<i>Acromyrmex hispidus</i> Santschi, 1925	3	0	0	0	0	0	0
<i>Apterostigma pilosum</i> Mayr, 1865	5	0	0	0	0	0	0
<i>Apterostigma</i> sp. 3	2	0	0	0	0	0	0
<i>Apterostigma wasmannii</i> Forel, 1892	1	0	0	0	0	0	0
<i>Atta sexdens</i> (Linnaeus, 1758)	269	0	0	0	0	0	0

<i>Basiceros disciger</i> (Mayr, 1887)	2	0	0	0	0	0	0
<i>Crematogaster</i> pr. <i>chodati</i> Forel, 1921	1	0	0	0	0	0	0
<i>Crematogaster rochai</i> Forel, 1903	1	0	0	0	0	0	0
<i>Cyphomyrmex minutus</i> Mayr, 1862	2	0	0	0	0	0	0
<i>Hylomyrma reitteri</i> (Mayr, 1887)	1	0	0	0	0	0	0
<i>Mycetomoellerius urichii</i> (Forel, 1893)	39	0	0	0	0	0	0
<i>Myrmicocrypta squamosa</i> Smith, 1860	17	0	0	0	1	0	0
<i>Pheidole aper</i> Forel, 1912	10	0	0	1	0	0	1
<i>Pheidole brevicona</i> Mayr, 1887	8	1	0	0	1	0	0
<i>Pheidole fallax</i> Mayr, 1870	38	0	185	0	0	0	1
<i>Pheidole gertrudae</i> Forel, 1886	0	0	0	0	18	0	0
<i>Pheidole oxyops</i> Forel, 1908	0	1	135	0	0	0	0
<i>Pheidole sigillata</i> Wilson, 2003	5	0	12	0	0	0	0
<i>Pheidole</i> sp. 3	18	32	29	15	0	0	0
<i>Pheidole</i> sp. 4	1	0	0	0	0	0	0
<i>Pheidole</i> sp. 12	47	12	12	3	3	0	1
<i>Pheidole</i> sp. 15	0	0	39	0	0	0	0
<i>Pheidole</i> sp. 16	0	0	0	2	0	0	0
<i>Pheidole</i> sp. 27	0	0	43	0	0	0	0
<i>Pheidole</i> sp. 29	0	0	12	0	0	0	0
<i>Pheidole</i> sp. 30	13	0	0	0	0	0	0
<i>Pheidole</i> sp. 46	0	0	5	0	0	0	0
<i>Pheidole</i> sp. 55	22	0	0	0	0	0	0
<i>Pheidole</i> sp. 69	0	23	2	0	0	0	0
<i>Pheidole</i> sp. 71	0	1	0	0	0	0	0
<i>Pheidole</i> sp. 73	65	35	161	17	0	1	1
<i>Pheidole</i> sp. 77	1	0	0	0	0	0	0
<i>Pheidole transversostriata</i> Mayr, 1887	3	0	0	0	0	0	0
<i>Solenopsis</i> sp. 1	1	0	0	0	0	0	0
<i>Solenopsis</i> sp. 3	1	0	0	2	0	0	0
<i>Solenopsis</i> sp. 4	2	18	7	0	0	0	0
<i>Solenopsis</i> sp. 7	3	0	0	0	0	0	0
<i>Solenopsis</i> sp. 8	10	10	2	5	0	0	1
<i>Solenopsis</i> sp. 10	9	0	13	2	1	0	0
<i>Solenopsis</i> sp. 11	10	0	0	0	1	0	0
<i>Strumigenys appretiata</i> (Borgmeier, 1954)	2	0	0	0	0	0	0
<i>Strumigenys denticulata</i> Mayr, 1887	1	0	0	0	0	0	0
<i>Strumigenys subdentata</i> Mayr, 1887	1	0	0	0	0	0	0
<i>Wasmannia affinis</i> Santschi, 1929	10	0	0	0	0	0	0
<i>Wasmannia auropunctata</i> (Roger, 1863)	0	3	0	0	0	0	0
Ponerinae							
<i>Hypoponera</i> sp. 3	2	0	0	0	0	0	0
<i>Neoponera marginata</i> (Roger, 1861)	1	0	0	0	0	0	0
<i>Odontomachus chelifer</i> (Latreille, 1802)	8	0	0	0	0	0	1
<i>Odontomachus meinerti</i> Forel, 1905	3	0	0	0	0	0	0
<i>Pachycondyla harpax</i> (Fabricius, 1804)	1	0	0	0	0	0	0

<i>Pachycondyla striata</i> Smith, 1858	52	0	0	0	0	0	1
Total of ant workers	1,527	147	659	47	25	1	NA
Total of ant species	63	11	15	8	6	1	12

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Table S3. Ant species richness and number of workers sampled in coffee plantations in the Atlantic rainforest. “Pitfall” refers to the ants collected in pitfall traps. “Larvae” refers to ants collected in predation experiments using *Tenebrio molitor* Linnaeus, 1758 larvae (for larvae, we did not compute the number of workers, only the presence or absence of ants). The other columns refer to the nutrients experiment (CHO: carbohydrates, Lipids: vegetable oil, AA: amino acids/whey protein, NaCl: salt, and Water).

Atlantic rainforest: Coffee plantation							
Species	Pitfall	CHO	Lipids	AA	NaCl	Water	Larvae
Dolichoderinae							
<i>Dorymyrmex brunneus</i> Forel, 1908	17	0	0	0	0	0	0
<i>Linepithema cerradense</i> Wild, 2007	7	4	0	0	1	0	0
<i>Linepithema neotropicum</i> Wild, 2007	359	119	2	130	61	4	1
<i>Linepithema pulex</i> Wild, 2007	25	0	0	0	0	0	0
<i>Linepithema</i> sp. 1	0	0	0	0	2	0	0
<i>Linepithema</i> sp. 4	0	0	0	0	0	0	1
Ectatomminae							
<i>Ectatomma brunneum</i> Smith, 1858	1	0	3	0	0	0	0
<i>Ectatomma permagnum</i> Forel, 1908	2	0	0	0	0	0	0
<i>Holcaponera striatula</i> (Mayr, 1884)	117	1	14	1	0	0	1
Formicinae							
<i>Brachymyrmex cordemoyi</i> Forel, 1895	75	0	0	0	0	0	0
<i>Brachymyrmex pictus</i> Mayr, 1887	4	0	0	0	0	0	0
<i>Brachymyrmex pilipes</i> Mayr, 1887	3	0	0	0	0	0	0
<i>Camponotus melanoticus</i> Emery, 1894	7	4	0	0	25	0	0
<i>Nylanderia</i> sp. 7	2	0	0	0	0	0	0
Myrmicinae							
<i>Atta sexdens</i> (Linnaeus, 1758)	7	0	0	0	0	0	0
<i>Carebara</i> pr. <i>brasiliensis</i> Fernández, 2004	1	0	0	0	0	0	0
<i>Mycetomoellerius</i> sp. 1	1	0	0	0	0	0	0
<i>Mycocepurus smithii</i> (Forel, 1893)	2	0	0	0	0	0	0
<i>Pheidole fallax</i> Mayr, 1870	6	0	2	0	0	0	0
<i>Pheidole obscurithorax</i> Naves, 1985	52	0	0	0	0	0	1
<i>Pheidole oxyops</i> Forel, 1908	1	56	23	0	0	0	1
<i>Pheidole radoszkowskii</i> Mayr, 1884	102	6	96	1	2	0	1
<i>Pheidole risii</i> Forel, 1892	0	0	5	0	0	0	0
<i>Pheidole subarmata</i> Mayr, 1884	96	209	401	2	50	1	1
<i>Pheidole</i> sp. 5	2	2	0	0	0	0	0
<i>Pheidole</i> sp. 6	0	0	0	0	0	0	1
<i>Pheidole</i> sp. 12	2	0	0	0	0	0	0
<i>Pheidole</i> sp. 65	8	0	0	0	0	0	1

<i>Pheidole</i> sp. 73	1	0	0	0	0	0	1
<i>Pheidole</i> sp. 75	8	13	0	0	2	1	0
<i>Pheidole</i> sp. 99	1	0	0	0	0	0	0
<i>Pogonomyrmex naegeli</i> Emery, 1878	2	0	0	0	0	0	0
<i>Solenopsis</i> gr. <i>saevissima</i> sp. 1	112	237	281	6	1	0	1
<i>Solenopsis</i> sp. 2	1	0	0	0	0	0	0
<i>Solenopsis</i> sp. 3	0	3	0	0	0	0	0
<i>Solenopsis</i> sp. 4	1	0	0	0	0	0	0
<i>Solenopsis</i> sp. 8	9	0	0	0	0	0	0
<i>Strumigenys louisianae</i> Roger, 1863	5	0	0	0	0	0	0
Ponerinae							
<i>Hypoponera</i> sp. 1	1	0	0	0	0	0	0
<i>Hypoponera</i> sp. 2	1	0	0	0	0	0	0
<i>Hypoponera</i> sp. 3	1	0	0	0	0	0	0
<i>Hypoponera</i> sp. 4	9	0	0	0	0	0	0
<i>Hypoponera</i> sp. 5	6	0	0	0	0	0	0
<i>Pachycondyla striata</i> Smith, 1858	13	0	0	0	1	0	1
Total of ant workers	1,070	654	827	114	145	6	NA
Total of ant species	39	11	9	5	9	3	12

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Table S4. Ant species richness and number of workers sampled in natural habitat (woodland savannah) in the Cerrado. “Pitfall” refers to the ants collected in pitfall traps. “Larvae” refers to ants collected in predation experiments using *Tenebrio molitor* Linnaeus, 1758 larvae (for larvae, we did not compute the number of workers, only the presence or absence of ants). The other columns refer to the nutrients experiment (CHO: carbohydrates, Lipids: vegetable oil, AA: amino acids/whey protein, NaCl: salt, and Water).

Cerrado: Natural habitat							
Species	Pitfall	CHO	Lipids	AA	NaCl	Water	Larvae
Dolichoderinae							
<i>Linepithema neotropicum</i> Wild, 2007	16	0	0	0	0	0	0
<i>Linepithema pulex</i> Wild, 2007	87	3	0	0	1	0	0
<i>Lenepthema</i> sp. 1	9	0	0	0	0	0	0
<i>Lenepthema</i> sp. 3	1	0	0	0	0	0	0
Dorylinae							
<i>Neivamyrmex</i> sp. 1	1	0	0	0	0	0	0
Ectatomminae							
<i>Ectatomma edentatum</i> Roger, 1863	7	6	0	0	0	0	1
<i>Gnamptogenys sulcata</i> (Smith, 1858)	2	0	0	0	0	0	0
<i>Holcaponera striatula</i> (Mayr, 1884)	17	0	0	0	0	0	0
Formicinae							
<i>Brachymyrmex minutus</i> Forel, 1893	2	0	0	0	0	0	0
<i>Brachymyrmex pictus</i> Mayr, 1887	14	0	0	0	0	0	0
<i>Brachymyrmex</i> sp. 2	3	0	0	0	0	0	0
<i>Brachymyrmex</i> sp. 3	6	0	0	0	0	0	0
<i>Brachymyrmex</i> sp. 4	1	0	0	0	0	0	0
<i>Camponotus crassus</i> Mayr, 1862	4	0	0	0	0	0	0
<i>Camponotus fastigatus</i> Roger, 1863	4	0	0	0	0	0	1
<i>Camponotus atriceps</i> (Smith, 1858)	2	0	0	0	0	0	0
<i>Camponotus cingulatus</i> Mayr, 1862	441	7	0	0	0	0	0
<i>Camponotus ager</i> (Smith, 1858)	19	0	0	0	0	0	0
<i>Camponotus lespeii</i> Forel, 1886	19	0	0	0	0	0	1
<i>Camponotus melanoticus</i> Emery, 1894	0	19	0	0	0	0	0
<i>Camponotus (Tanaemyrmex)</i> sp. 1	2	0	0	0	0	0	0
<i>Nylanderia docilis</i> (Forel, 1908)	18	11	0	1	0	0	0
<i>Nylanderia</i> sp. 7	1	0	0	0	0	0	0
<i>Nylanderia steinheili</i> (Forel, 1893)	35	20	0	1	0	1	0
Myrmicinae							
<i>Acromyrmex aspersus</i> (Smith, 1858)	206	0	0	0	0	0	0
<i>Acromyrmex hispidus</i> Santschi, 1925	19	0	0	0	0	0	0
<i>Acromyrmex subterraneus</i> (Forel, 1893)	716	0	0	0	0	0	0

<i>Atta sexdens</i> (Linnaeus, 1758)	1,196	0	0	0	0	0	0
<i>Carebara brevopilosa</i> Fernández, 2004	4	0	0	0	0	0	0
<i>Crematogaster corticicola</i> Mayr, 1887	0	0	0	0	0	0	1
<i>Cyphomyrmex minutus</i> Mayr, 1862	2	0	0	0	0	0	0
<i>Mycetomoellerius urichii</i> (Forel, 1893)	1	0	0	0	0	0	0
<i>Mycetomoellerius</i> sp. 1	1	0	0	0	0	0	0
<i>Mycetophylax lectus</i> (Forel, 1911)	1	0	0	0	0	0	0
<i>Ochetomyrmex</i> sp. 1	1	0	0	0	0	0	0
<i>Pheidole aberrans</i> Mayr, 1868	2	0	0	0	0	0	0
<i>Pheidole fallax</i> Mayr, 1870	15	16	1	0	9	0	1
<i>Pheidole gertrudae</i> Forel, 1886	0	3	23	0	0	0	0
<i>Pheidole jelskii</i> Mayr, 1884	6	0	8	0	0	0	1
<i>Pheidole oxyops</i> Forel, 1908	2	0	0	0	0	0	1
<i>Pheidole pr. deima</i> Wilson, 2003	1	0	0	0	0	0	0
<i>Pheidole pr. radoszkowskii</i> Mayr, 1884	0	0	2	0	0	0	0
<i>Pheidole radoszkowskii</i> Mayr, 1884	408	158	222	3	74	3	1
<i>Pheidole sarcina</i> Forel, 1912	3	0	0	0	0	0	0
<i>Pheidole sigillata</i> Wilson, 2003	0	0	3	0	0	0	0
<i>Pheidole</i> sp. 12	60	32	3	4	1	2	0
<i>Pheidole</i> sp. 15	4	2	32	0	0	0	0
<i>Pheidole</i> sp. 19	4	0	0	0	0	0	0
<i>Pheidole</i> sp. 22	0	5	10	0	8	0	0
<i>Pheidole</i> sp. 41	5	0	0	0	0	0	0
<i>Pheidole</i> sp. 55	3	0	0	0	0	0	1
<i>Pheidole</i> sp. 65	18	0	0	0	0	0	0
<i>Pheidole</i> sp. 69	0	23	0	0	0	0	0
<i>Pheidole</i> sp. 71	5	1	5	0	0	0	0
<i>Pheidole</i> sp. 73	0	32	0	0	0	0	0
<i>Rogeria lirata</i> Kugler, 1994	1	0	0	0	0	0	0
<i>Sericomyrmex saussurei</i> Emery, 1894	382	0	0	0	0	1	0
<i>Solenopsis</i> sp. 3	1	0	0	0	0	0	0
<i>Solenopsis</i> sp. 4	1	0	0	0	0	0	0
<i>Solenopsis</i> sp. 10	1	0	0	0	0	0	0
<i>Solenopsis</i> sp. 11	5	0	0	0	0	0	0
<i>Solenopsis</i> sp. 21	0	0	0	0	0	1	0
<i>Wasmannia auropunctata</i> (Roger, 1863)	14	15	26	0	0	0	0
Ponerinae							
<i>Hypoponera</i> sp. 2	1	0	0	0	0	0	0
<i>Neoponera</i> sp. 1	1	0	0	0	0	0	0
<i>Odontomachus chelifer</i> (Latreille, 1802)	8	0	0	0	0	0	0
<i>Pachycondyla striata</i> Smith, 1858	51	0	2	0	0	0	1
Pseudomyrmecinae							
<i>Pseudomyrmex gr. pallidus</i> sp. 1	1	0	0	0	0	0	0
<i>Pseudomyrmex phyllophilus</i> (Smith, 1858)	1	0	0	0	0	0	0
Total of ant workers	3,862	353	337	9	93	8	NA
Total of ant species	60	16	12	4	5	5	10

Table S5. Ant species richness and number of workers sampled in coffee plantations in the Cerrado. “Pitfall” refers to the ants collected in pitfall traps. “Larvae” refers to ants collected in predation experiments using *Tenebrio molitor* Linnaeus, 1758 larvae (for larvae, we did not compute the number of workers, only the presence or absence of ants). The other columns refer to the nutrients experiment (CHO: carbohydrates, Lipids: vegetable oil, AA: amino acids/whey protein, NaCl: salt, and Water).

Cerrado: Coffee plantation							
Species	Pitfall	CHO	Lipids	AA	NaCl	Water	Larvae
Dolichoderinae							
<i>Dorymyrmex brunneus</i> Forel, 1908	50	13	0	0	4	0	1
<i>Linepithema neotropicum</i> Wild, 2007	28	2	0	0	1	0	0
Ectatomminae							
<i>Holcaponera striatula</i> (Mayr, 1884)	70	43	12	0	0	0	1
Formicinae							
<i>Brachymyrmex cordemoyi</i> Forel, 1895	28	0	0	0	0	0	0
<i>Brachymyrmex pilipes</i> Mayr, 1887	3	0	0	0	0	0	0
<i>Camponotus cingulatus</i> Mayr, 1862	1	0	0	0	0	0	0
<i>Camponotus melanoticus</i> Emery, 1894	1	0	0	0	1	0	0
Myrmicinae							
<i>Cardiocondyla minutior</i> Forel, 1899	1	0	0	0	0	0	0
<i>Mycocepurus smithii</i> (Forel, 1893)	1	0	0	0	0	0	0
<i>Pheidole aberrans</i> Mayr, 1868	1,491	0	0	0	0	0	0
<i>Pheidole fallax</i> Mayr, 1870	50	5	31	0	0	1	1
<i>Pheidole gertrudae</i> Forel, 1886	12	0	9	0	0	1	0
<i>Pheidole obscurithorax</i> Naves, 1985	0	0	133	0	0	1	0
<i>Pheidole oxyops</i> Forel, 1908	1	0	0	0	0	0	0
<i>Pheidole radoszkowskii</i> Mayr, 1884	35	0	0	0	0	0	0
<i>Pheidole</i> sp. 5	0	0	0	0	0	0	1
<i>Pheidole</i> sp. 6	0	0	0	1	0	0	1
<i>Pheidole</i> sp. 7	0	7	0	0	0	0	0
<i>Pheidole</i> sp. 65	0	0	80	1	0	0	0
<i>Pheidole</i> sp. 75	35	0	0	0	0	0	0
<i>Pheidole subarmata</i> Mayr, 1884	41	25	96	0	0	0	1
<i>Pheidole vallifica</i> Forel, 1901	7	35	5	0	1	0	0
<i>Solenopsis</i> gr. <i>saevissima</i> sp. 1	21	0	0	1	0	0	1
<i>Solenopsis</i> sp. 17	1	0	0	0	0	0	0
<i>Solenopsis</i> sp. 18	76	0	0	0	0	0	0
Total of ant workers	1,953	130	366	3	7	3	NA
Total of ant species	20	7	7	2	4	3	7

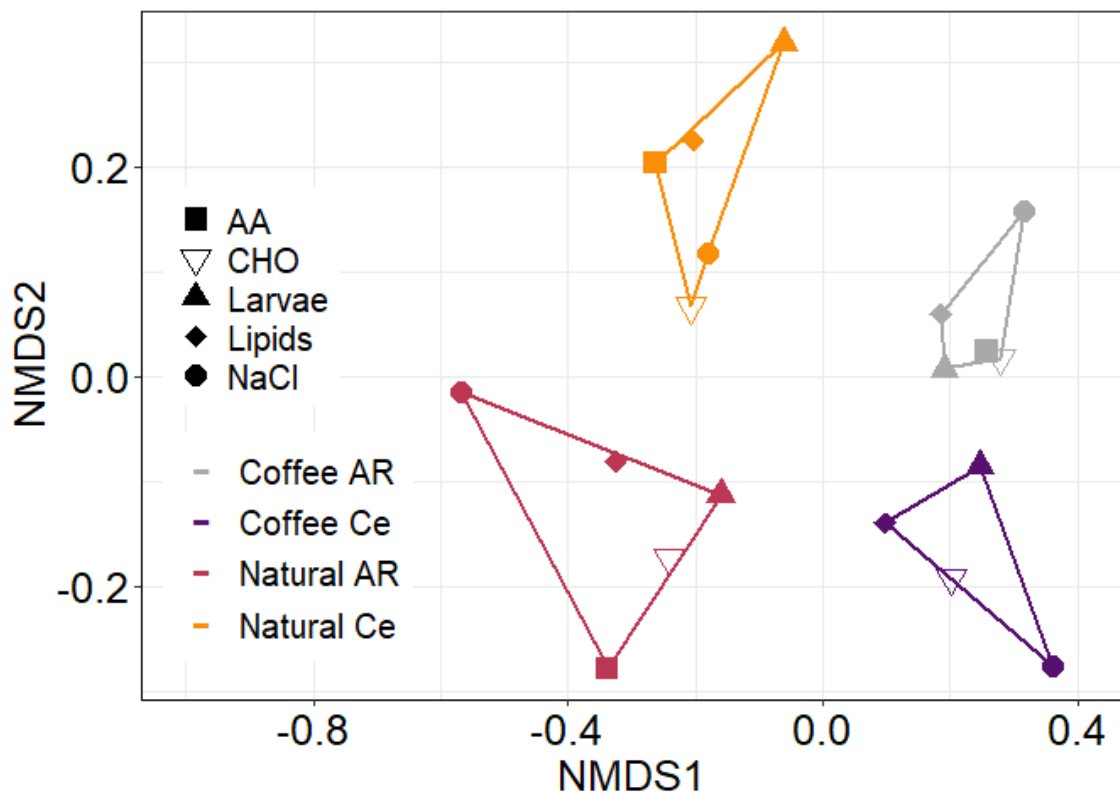
Table S6. Mean and sd (standard deviation) for ant foraging in different resources (presence of ants). “Biome” refers to the biome sampled (AR: Atlantic rainforest and Cerrado); “Habitat” refers to the land use sampled (Natural: Forest in Atlantic rainforest and woodland savannah in Cerrado; Coffee: coffee plantation in both biomes); “n” indicates the number of transects; “Param.” indicates mean and sd parameters; “Pitfall” is the number of ant species. “Larvae” is the number of insect predation by ants; and five nutrients (CHO: carbohydrates, Lipids: vegetable oil, AA: amino acids/whey protein, NaCl: salt, and Water).

Biome	Habitat	n	Param.	Pitfall	Larvae	CHO	Lipids	AA	NaCl	Water
AR	Natural	6	mean	20	11.12	0.53	0.53	0.40	0.20	0.03
AR	Natural	6	sd	6.54	4.79	0.50	0.50	0.49	0.40	0.18
AR	Coffee	12	mean	11.68	9.06	0.35	0.38	0.20	0.23	0.08
AR	Coffee	12	sd	6.65	7.27	0.48	0.49	0.40	0.42	0.27
Cerrado	Natural	6	mean	21.66	8.66	0.80	0.66	0.16	0.33	0.20
Cerrado	Natural	6	sd	5.04	8.18	0.40	0.47	0.37	0.47	0.40
Cerrado	Coffee	8	mean	12.71	5.42	0.47	0.32	0.05	0.12	0.07
Cerrado	Coffee	8	sd	8.93	6.48	0.50	0.47	0.22	0.33	0.26

Table S7. The first column presents the comparison of ant composition between land use types: Natural AR (forest in the Atlantic rainforest), Natural Ce (woodland savannah in Cerrado), Coffee AR (coffee plantation in the Atlantic rainforest), and Coffee Ce (coffee plantation in Cerrado); and resource types: AA (amino acids), CHO (carbohydrates), Lipids (vegetable oil), NaCl (sodium) and Larvae (predation experiment). The table includes degrees of freedom (d.f.), sums of squares (SumOfSqs), coefficient of determination (R^2), F value (F), and P value (p-value; significant values are < 0.05).

<i>Question 1: How similar is the species composition across land uses and resources?</i>					
Natural AR vs Natural Ce	d.f.	SumOfSqs	R^2	F	p-value
Land use type	1	0.74	0.29	4.50	0.002
Resource type	4	1.08	0.45	1.64	0.054
Natural AR vs Coffee AR					
Land use type	1	1.49	0.54	12.47	0.002
Resource type	4	0.77	0.28	1.62	0.231
Natural AR vs Coffee Ce					
Land use type	1	1.25	0.38	5.77	0.003
Resource type	4	1.11	0.34	1.27	0.280
Natural Ce vs Coffee AR					
Land use type	1	1.12	0.48	9.02	0.002
Resource type	4	0.71	0.30	1.42	0.235
Natural Ce vs Coffee Ce					
Land use type	1	1.21	0.38	5.34	0.006
Resource type	4	1.03	0.32	1.13	0.374
Coffee AR vs Coffee Ce					
Land use type	1	0.51	0.26	3.62	0.003
Resource type	4	0.88	0.45	1.56	0.132

921 Figure S3



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923 Figure S3. Ant species composition differs between land use types: Natural AR (forest in the

924 Atlantic rainforest; medium pink), Natural Ce (woodland savannah in Cerrado; orange), Coffee

925 AR (coffee plantation in the Atlantic rainforest; grey), and Coffee Ce (coffee plantation in

926 Cerrado; purple). However, it does not differ significantly with respect to resource types: Larvae

927 (predation experiment; full triangle), CHO (carbohydrates; empty triangle), Lipids (vegetable

928 oil; diamond), AA (amino acids; square), and NaCl (salt; circle). The species composition used

929 was measured using the turnover component of Sørensen dissimilarity (β_{sim}).

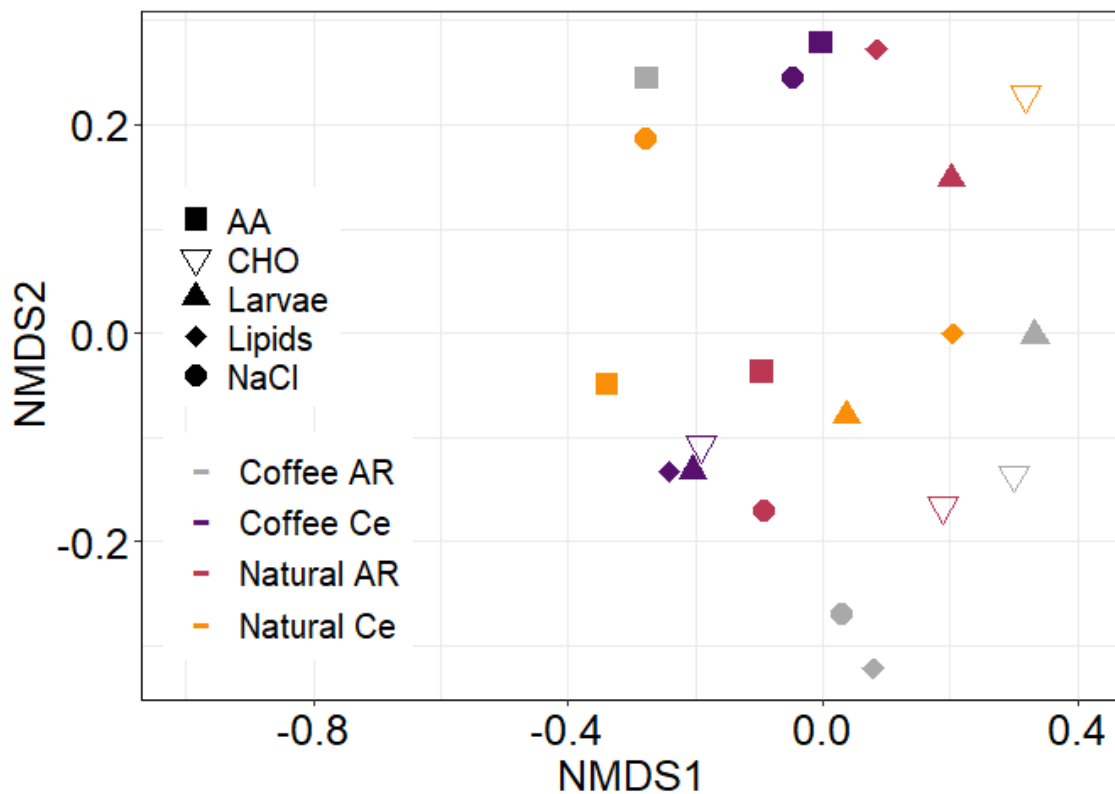
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934 Figure S4



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936 Figure S4. Ant species composition differs between land use types: Natural AR (forest in the
 937 Atlantic rainforest; medium pink), Natural Ce (woodland savannah in Cerrado; orange), Coffee
 938 AR (coffee plantation in the Atlantic rainforest; grey), and Coffee Ce (coffee plantation in
 939 Cerrado; purple). However, it does not differ significantly with respect to resource types: Larvae
 940 (predation experiment; full triangle), CHO (carbohydrates; empty triangle), Lipids (vegetable
 941 oil; diamond), AA (amino acids; square), and NaCl (salt; circle). The species composition used
 942 was measured using nestedness component of Sørensen dissimilarity (β_{sne}).

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ARTIGO 2 - Land use changes have direct and indirect negative effects on ant species richness and predation

Versão preliminar para submissão e nas normas da revista *Biodiversity and Conservation*

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Abstract

Land use change is the primary driver of biodiversity decline in tropical terrestrial ecosystems. However, the direct and indirect effects of land use changes on other environmental variables and biodiversity remain largely unexplored. Here, our aim was to evaluate the direct and indirect effects of land use changes on microclimate, species richness, and ecosystem function. To achieve this, we sampled ants in natural sites and coffee plantations in two Neotropical biomes: the Atlantic rainforest and Cerrado. We assessed microclimate (temperature and humidity) using a thermohygrometer. Species richness was measured using pitfall traps to collect ants. Ecosystem function was evaluated using insect predation, which we assessed through experiments with *Tenebrio molitor* larvae. For these measurements, we conducted 32 replicates (n = 32). Our results showed that land use changes directly increased temperature, likely due to reduced vegetation cover and higher solar radiation. However, we did not find an effect of microclimate on species richness or ecosystem function. Additionally, we found that land use changes directly decreased ant species richness. This is likely because land use changes severely impact most ant species, excluding a greater number of sensitive species and favouring only generalist species. Furthermore, the reduction in ant species richness led to a decline in predatory ants. A highly diverse ant assemblage can support a greater number of species across different guilds and functional groups. Finally, we found an indirect effect of land use change on insect predation, mediated by the reduction in predatory ants, which resulted in a decline in insect predation, likely due to a smaller number of different species performing this function. In conclusion, we found both direct and indirect effects of land use change on microclimate, ant species richness, and predation function in anthropized regions, likely due to alterations in vegetation structure. Therefore, we recommend maintaining vegetation structure in anthropized sites similar to the original vegetation to minimize changes in microclimate, species richness, and, consequently, ecosystem functions.

26 **Keywords:** Microclimate, Neotropical, insect predation, ecosystem function, structural
27 equation model, coffee plantation

28 **Introduction**

29 Tropical habitats host a large portion of global biodiversity, which is threatened by land use
30 changes for supposed economic development (Jayathilake et al. 2021; Raven et al. 2020).
31 Although land use changes primarily impact biodiversity by removing natural habitats, it also
32 generates a series of modifications on ecosystems (Barnes et al. 2017). First, land uses can cause
33 changes in the resources that are available to species (Stein et al. 2014) and in the microclimate
34 that they are exposed to, such as temperature and humidity (Machado et al. 2023). These
35 changes can lead to a decrease in species diversity that can ultimately alter ecosystem
36 functioning (Newbold et al. 2020; Wu et al. 2023), consequently, affecting the stability of
37 natural ecosystems and the provision of ecosystem services in anthropized land uses (Le
38 Provost et al. 2023). Therefore, understanding the direct and indirect effects of how land use
39 changes affect community structure can enhance our knowledge of how ecosystem functions
40 are maintained in human-altered habitats.

41 The conversion of tropical forests to anthropogenic land uses causes a drastic shift in
42 conditions and resources, resulting in negative impacts on species (Manlick and Newsome
43 2021). The loss of plant abundance and diversity tends to decrease resources available for
44 species (Stein et al. 2014), excluding most specialists and favouring just a few generalist and
45 opportunist species (Filgueiras et al. 2021). Moreover, the loss of vegetation cover causes an
46 increases in solar radiation, raising average temperatures and decreasing humidity (Machado et
47 al. 2023; Senior et al. 2017). More specifically, in open anthropogenic habitats, there is an
48 increase in maximum temperature (hot extremes), mean temperature, and minimum
49 temperature (cold extremes) compared to closed natural habitats (Alkama and Cescatti 2016;
50 Medvigy et al. 2012). These drastic alterations in microclimate exclude most tropical species
51 that are sensitive to temperature changes, favouring a few thermally resistant species that are
52 better adapted to extreme conditions (Outhwaite et al. 2022). Thus, drastic changes in

microclimate caused by land use changes can decrease the diversity of most tropical species and favour a few generalist and resistant species.

Changes in microclimate can also affect ecosystem functioning through alternative mechanisms. In general, an increase in temperature can have a positive effect on species activity (Lasmar et al. 2021) and, consequently, on ecosystem functions. This increase in activity may occur due to the rise in metabolic rates at higher temperatures (González-Tokman et al. 2020). However, with higher and more variable temperatures, ecosystem functions may also be negatively affected, due to the reduced activity of organisms during very hot periods, as they avoid thermal and desiccation risks (Parr and Bishop 2022). Thus, although extreme microclimate may favour more resistant species in anthropogenic land uses, higher temperatures can have a negative impact on the activity of these species and their ecosystem functions.

Complementary to the effects of microclimate on ecosystem functions, species richness can also alter ecosystem functions in different ways (Le Provost et al. 2023). First, the maintenance of species diversity can favour ecosystem functions (Le Provost et al. 2023). This can occur through functional redundancy (Biggs et al. 2020), where species perform the same function, and functional complementarity (Loreau and Hector 2001), where species perform different functions. In this way, a loss of species can consequently lead to a loss of functions due to fewer species acting in the ecosystem. However, in some cases, ecosystem functions can still be preserved even when the environment loses species. This can occur due to ecological release, caused by the reduction in competition resulting from the loss of specialist species, leading to increased activity of generalist and opportunistic species in anthropogenic land use (Manlick and Newsome 2021). Therefore, even though land use reduces species richness, ecosystem functions can still be maintained by generalist species. Thus, assessing whether species richness

is directly related to ecosystem functions is important for a better understanding of the role of species diversity in anthropogenic ecosystems.

Land use can affect species richness and their ecosystem functions due to microclimatic changes, however, the indirect effects and the mechanisms through which these impacts occur are still poorly explored (Ceresa et al. 2021). Land use changes directly affect species richness and ecosystem functions; however, these changes can vary depending on microclimatic conditions. Moreover, regarding ecosystem functions, a decrease in species richness can help explain alterations in these functions. However, despite several studies assessing these variables, the direct and indirect effects along with indirect mechanisms, remains underexplored. Therefore, understanding the direct and indirect effects of land use on microclimate, species richness, and, consequently, ecosystem functions is crucial for species conservation and for understanding their interactions and roles in anthropized regions (Barnes et al. 2017).

Here, we aimed to assess the direct and indirect effects of land use change (conversion from forest to agriculture) on microclimate, species richness and ecosystem functions. We used ants and their predation activity as a model to study land use in tropical environments because ants are sensitive to anthropogenic impacts and are among the main arthropod predators in tropical forests and agricultural systems (Anjos et al. 2022; Philpott and Armbrrecht 2006; Philpott et al. 2004; Wilker et al. 2023). More specifically, we constructed a structural equation model (SEM) to test the direct and indirect effects among land use, microclimate and species richness, and ultimately on ecosystem functions following these hierarchical predictions: (i) land use change increases air temperature but decreases air humidity; (ii) land use changes and increase in temperature decreases ant species richness; (iii) the decrease in ant species richness decreases the species richness of predatory ants; and (iv) the decrease in the species richness of predatory ants decreases insect predation.

Methods

Study site

We collected data on ant diversity and insect predation in three regions of the state of Minas Gerais, Brazil, covering two Neotropical biomes: the Atlantic rainforest and the Cerrado (Fig. 1). We sampled four sites in rural areas of the municipality of Lavras (21°14'43"S, 44°59'59"W) and 14 sites in rural areas of the municipality of Santo Antônio do Amparo (SAA; 20°57'19"S, 44°55'0"W), both in the Atlantic rainforest. We also sampled 14 sites in rural areas of the municipality of Patrocínio (18°56'38"S, 46°59'34"W), located in the Cerrado. In total, we sampled 32 sites, comprising 12 natural habitats and 20 anthropogenic land uses. In each site, we created a transect with five sampling points spaced 50 meters apart, totalling 200 meters.

The Atlantic rainforest is a tropical forest, while the Cerrado features various vegetation types, ranging from open habitats to closed forests. In all regions, we collected data in forest vegetation (tropical forest and woodland savanna) within a natural habitat, and coffee plantation with an anthropogenic land use. We sampled between January and March of 2022 and 2023, during the rainy season. In the rainy season, the Atlantic rainforest has an average precipitation of 134.54 mm and an average temperature of 20.41 °C (INMET 2024), while the Cerrado has an average precipitation of 212.87 mm and an average temperature of 22.16 °C.

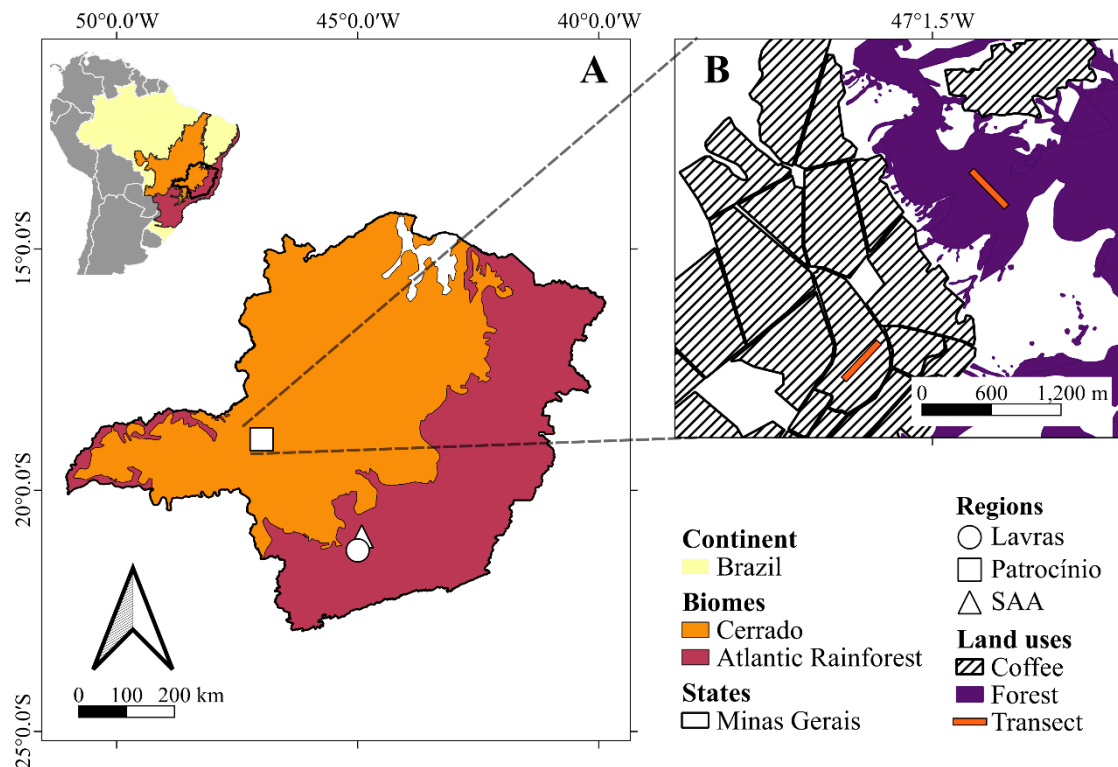


Fig. 1 The panel A indicates the Brazilian state of Minas Gerais, including its position in South America and the location of the biomes and sampled regions. The panel B indicates two transects within the region of Patrocínio. The figure was generated using QGIS version 3.32 (QGIS.org 2023) and adapted biome and state data from Instituto Brasileiro de Geografia e Estatística (IBGE 2019). The panel B was adapted by satellite image from Google Satellite (2024).

Insect predation by ants

We assessed insect predation by ants placing beetle larvae (*Tenebrio molitor* Linnaeus, 1758) along a transect with five sampling points spaced 50 meters apart. At each sampling point, we placed two beetle larvae. The larvae were attached with touch fastener to an ethylene-vinyl acetate (EVA) surface to prevent them from escaping (Figure S1). At each sampling point, between 8 a.m. and 12 p.m. (after the baited tubes), we observed insect predation by ants in four rounds of five minutes each. At the beginning of the experiment, we attached the larvae to the ground at the first sampling point and immediately observed the ants' attack for five minutes. Then, we attached the larvae at the second sampling point and observed them for five minutes. We repeated this process until completing the transect, and then started again for the second, third, and fourth rounds. This totalled 20 minutes per sampling point and 100 minutes

per transect. The ants that engaged in predation were collected and stored in 70% alcohol for later identification. We considered “predatory ants” as the number of ant species collected per transect in this predation experiment and “predation” was measured by the number of larvae attacked per transect. In this way, each of the 32 transects ($n = 32$) has a measure of predatory ants and a measure of insect predation.

Microclimate measurements

Alongside the insect predation experiment, we measured temperature and relative humidity. We measured at each sampling point for each of the four rounds of the predation experiment. We used a digital thermo-hygrometer to measure air temperature ($^{\circ}\text{C}$) and humidity (%) at 5 cm above the ground at each sampling point. We used the mean temperature and humidity per transect.

Ant species richness

After insect predation experiment, in the same transect with five pitfall traps spaced 50 meters apart, we installed pitfall traps. The traps consisted of plastic pots with a diameter of 12 cm and a depth of 11 cm, installed in the ground. We added a solution composed of 200 ml of water mixed with salt and detergent to capture and preserve the collected ants. Each trap operated for a period of 48 hours. After this period, the captured ants were stored in 70% alcohol. We considered “ant species richness” as the number of ant species collected per transect ($n = 32$).

Ant species identification

We identified all ants collected from the pitfall and predation experiments to the genus level based on Baccaro et al. (2015) and morphotyped them according to external morphological characters. Identification and confirmation of species and morphospecies were made by Rodrigo M. Feitosa and Ana Carolina A. Neundorff at the Laboratório de Sistemática e Biologia de Formigas at the Universidade Federal do Paraná (UFPR). Specific published descriptions were used to identify species in the genera *Acromyrmex* (Gonçalves 1961), *Acropyga* (LaPolla

2004), *Apterostigma* (Lattke 1997), *Basiceros* (Probst and Brandão 2022), *Brachymyrmex* (Ortiz-Sepúlveda et al. 2019), *Carebara* (Fernández 2004), *Ectatomma* (Kugler and Brown 1982), *Gnamptogenys* (Camacho et al. 2020), *Labidus* (Watkins 1976), *Linepithema* (Wild 2007), *Neivamyrmex* (Watkins 1976), *Odontomachus* (Brown 1976), *Pheidole* (Wilson 2003), *Strumigenys* (Bolton 2000), and *Wasmannia* (Longino and Fernández 2007). Voucher specimens were deposited in the reference collection of Laboratório de Ecologia de Formigas at UFLA and the Coleção Entomológica Padre Jesus Santiago Moure at UFPR (DZUP).

Data analysis

Before the analyses, we tested for a correlation between the microclimate variables of temperature and humidity. We found that these variables were strongly negatively correlated ($\rho = -0.86$; $p < 0.001$), and we decided to use only temperature as a microclimate variable in subsequent analyses. After these steps, we constructed five generalized linear mixed models (GLMM) to test our predictions. For normalized assumptions, we square root transformed the data for ant species richness and insect predation. In all models, we included the regions as a random variable to control for the effects of different regions and biomes (Bates et al. 2015), as different regions can support distinct regional species pools, and different biomes have intrinsic abiotic and biotic characteristics that can generate partially context-dependent patterns (Lasmar et al. 2023). For detailed data, see Supplementary Material, Table S1.

Our structural equation modelling (SEM) was based in four models. For the first model, (i) testing whether the conversion from natural habitat to coffee plantation (land use change) alters microclimate variables, we used temperature as the response variable and land use change as the predictor. For the second model, (ii) testing whether land use changes and an increase in temperature decrease ant species richness, we used ant species richness as the response variable and land use change and temperature as predictors. For the third model, (iii) testing whether the decrease in ant species richness decreases the number of predatory ants, we used the predatory

ants as the response variable and land use change, temperature, and ant species richness as predictors. For the fourth model, (iv) testing whether the decrease in the predatory ants decreases insect predation, we used the number of insect predations by ants as the response variable and land use change, temperature, ant species richness, and predatory ants as predictors. For models with normalized response variable, we analysed with *lmer* function. For models with count response variable, we analysed with *glmer.nb* function. We used Negative Binomial for count due overdispersion. All GLMMs were made with ‘lme4’ R package version 1.1.35.5 (Bates et al. 2015). For detailed models, see Supplementary Material, Full models.

To avoid overfitting in SEM analyses in our models, we used the *dredge* function (‘MuMIn’ package version 1.47.5; Bartoń 2023) for selected the best predictors in each model, based on the Akaike information criterion corrected for small sample sizes (AICc). We selected the variables in models with $\Delta AICc < 2$ (Burnham and Anderson 2002). When more than one variable was selected, we used the function *model.avg* (package ‘MuMIn’, version 1.47.5; Bartoń 2023) to detect uninformative parameters and avoid Type I errors (Leroux 2019). Uninformative parameters are predictors selected in good models but that do not have a significant effect on the response variable (false positive). For detailed selected models, see Supplementary Material, Tables S2-S6.

For testing the direct and indirect effects of land use and microclimate changes on ecosystem function, we used the best predictors in each model for conducted structural equation modelling analyses (SEM). For this, we used the *psem* function of the ‘piecewiseSEM’ R package version 2.3.0 (Lefcheck 2016). We construct the model connecting the mixed models (i) to (iv), following the hypothetical cascade effect starting from changes in land use and temperature affecting ant species, which, in turn, affects predatory ants, and consequently insect predation (details of model in Supplementary material - *psem model*). For the *psem* function, we assess the Global goodness-of-fit through Fisher’s C, considering it a good fit if $p > 0.05$. We also

assess the independence of the variables through Tests of Directed Separation, considering them independent if $p > 0.05$ and to assure that there were no missing paths in our SEM. In addition, we ensure that all predictors influenced the response variables within the *psem* model, considering significant if $p < 0.05$.

To assess direct, mediator, indirect, and total effects for the response variables, we used the function *bootEff* with 1,000 permutations to compute SEM correlated errors and the *semEff* function. Both functions are in ‘semEff’ R package version 0.7.2 (Murphy 2024). The direct effect is the immediate relationship between a predictor and a response variable, for example, an increase in temperature (direct effect) increases insect predation (response variable). However, the effect of a predictor on a response variable can also be mediated by an intermediate variable known as a mediator. In this context, the effect of the predictor variable through the mediator is referred to as the indirect effect. The mediator clarifies how the predictor indirectly affects the response variable. For example, an increase in temperature (predictor) increases ant species richness (mediator), which consequently leads to increased insect predation by ants (response variable). Finally, the sum of the direct and indirect effects is referred to as the total effect of a predictor on a response variable.

All analyses were completed in R 4.3.3 (R Core Team 2024). All graphs were made with the *ggplot2* R package version 3.5.1 (Wickham 2016).

Results

We sampled 127 ant species, belonging to 124 ant species for pitfall data, and 28 ant species for predation (more details in Tables S7-S10). We sampled seven of 12 ant subfamilies from Brazil. According to Feitosa et al. (2022), we found the following percentage of species within each subfamily for Atlantic Rainforest and Cerrado biomes: Dolichoderinae (10 species; 12% of species for both biomes), Dorylinae (2; 5%), Ectatomminae (5; 7%), Formicinae (24; 17%), Myrmicinae (73; 13%), Ponerinae (11; 9%), and Pseudomyrmecinae (2; 3%).

We found direct and indirect effects initiated by land use change, which altered ant species richness and, ultimately, ecosystem function (Fisher's $C = 12.541$; $AIC = 442.530$; $d.f. = 12$; $p = 0.403$; Fig. 2). First, we found that land use change directly affects temperature and ant species richness, increasing temperature (Table 1; Fig. 3A; Table S2) but decreasing species richness (Table 1; Fig. 3B; Table S3). Temperature, which we hypothesized would impact other variables, had no effect on any response variable (Fig. 2; Tables S4-S6). Ant species richness had a direct and positive effect on predatory ants (Table 1; Fig. 3C; Tables S4-S5). In turn, predatory ants had a direct and positive effect on insect predation (Table 1; Fig. 3D; Table S6). However, land use change had an indirect and negative effect on insect predation (Table 1). This occurs through the mechanism whereby land use change reduces the number of predatory ants, which in turn has a negative effect on insect predation (Table 1).

Table 1 Table of direct, indirect, total, and mediator effects on the response variable in the structural equation model (SEM). "Effect" denotes the effect of the predictor on the response variable. "Std. Err." provides the standard errors. "Lower CI" and "Upper CI" are the lower and upper confidence intervals, respectively. No confidence intervals overlapped with zero, indicating that all effects were significant.

(i) Temperature response					
Relationship	<i>Predictor</i>	<i>Effect</i>	<i>Std. Err.</i>	<i>Lower CI</i>	<i>Upper CI</i>
Direct	Land use	0.304	0.201	0.033	0.665
Total	Land use	0.304	0.201	0.033	0.665
(ii) Ant species response					
Relationship	<i>Predictor</i>	<i>Effect</i>	<i>Std. Err.</i>	<i>Lower CI</i>	<i>Upper CI</i>
Direct	Land use	-0.773	0.017	-0.775	-0.754
Total	Land use	-0.773	0.017	-0.775	-0.754
(iii) Predatory ants response					
Relationship	<i>Predictor</i>	<i>Effect</i>	<i>Std. Err.</i>	<i>Lower CI</i>	<i>Upper CI</i>
Direct	Ant species	0.067	0.017	0.030	0.084
Total	Ant species	0.067	0.017	0.030	0.084
(iv) Insect predation response					
Relationship	<i>Predictor</i>	<i>Effect</i>	<i>Std. Err.</i>	<i>Lower CI</i>	<i>Upper CI</i>
Direct	Predatory ants	0.877	0.047	0.770	0.924
Indirect	Land use	-0.045	0.012	-0.057	-0.020
Total	Land use	-0.045	0.012	-0.057	-0.020
Total	Predatory ants	0.877	0.047	0.770	0.924
Mediator	Predatory ants	-0.045	0.012	-0.057	-0.020

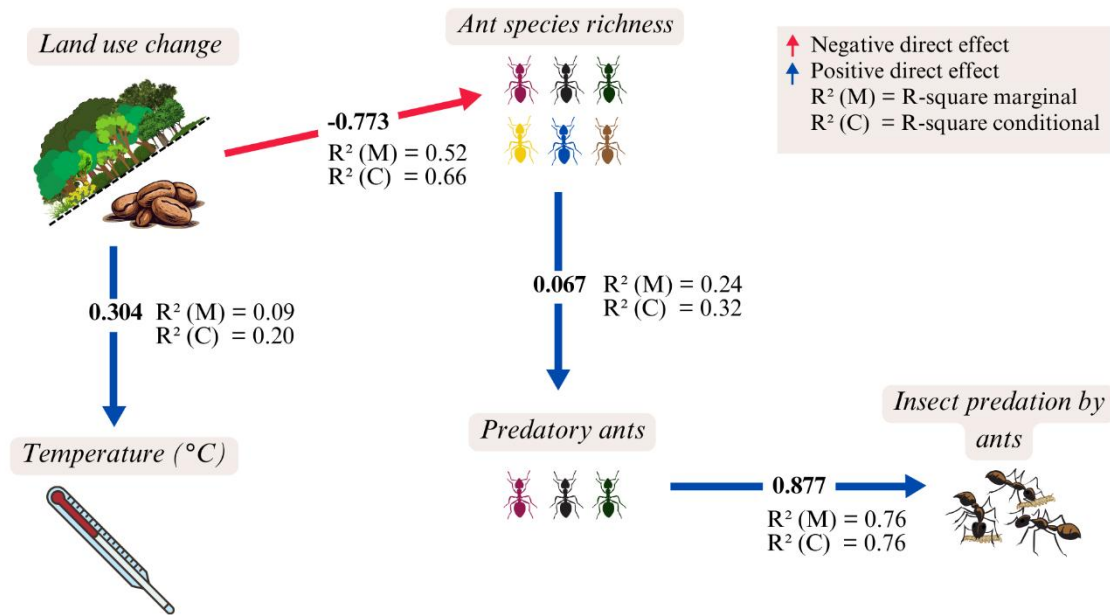


Fig. 2 Direct effects of land use changes on insect predation by ants by Structural Equation Model (SEM). Blue arrows indicate direct positive effects, while red arrows indicate direct negative effects. The effects are represented as overlays on each arrow. R^2 marginal is the coefficient of determination considering only the predictors, while R^2 conditional considers both the predictors and the random variable.

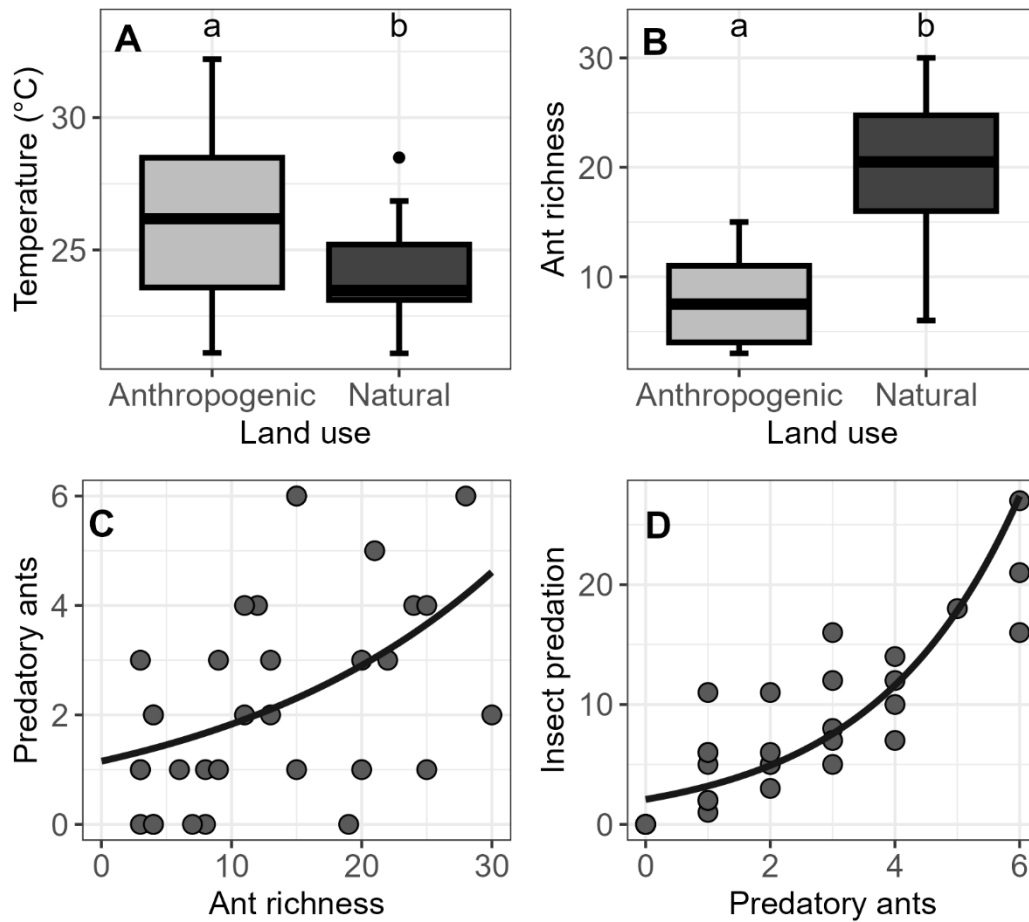


Fig. 3 Panel A shows the increase in temperature (°C) caused by land use changes. Panel B shows the decrease in the number of ant species caused by land use changes. Panel C shows the increase in predatory ants with the increase in ant species richness. Panel D shows the increase in insect predation by ants with the increase in predatory ants.

Discussion

In our study, we identified the hierarchical mechanism through which the land use affects ant species richness and ultimately impact their ecosystem function. First, we found that land use change increases air temperature. However, we did not find support indicating that microclimate affect ant species richness and their predation function. We also identified a negative direct effect of land use change on ant species richness, which, in turn, has a positive direct effect on predatory species. Finally, we identified an indirect effect of land use change on insect predation, mediated by changes in predatory species. This occurs due to the reduction in the number of predatory species caused by land use, leading to a decline in predation activity.

Thus, our findings on the direct and indirect effects of land use change on species and ecosystem function, particularly highlighting the importance of species richness for predation, can contribute to understanding the mechanisms driving alterations in ecosystem functions in anthropized environments.

We found that the conversion of natural habitats to anthropogenic land uses directly increases temperature. However, contrary to our expectations, we did not find an effect of microclimate on species richness and ecosystem function. This is probably related to the low temperature variation observed between natural habitats (mean = 24.16°C; standard deviation = 1.94) and anthropogenic land uses (mean = 26.18°C; standard deviation = 3.10) in our study system. Additionally, the agricultural system studied was a coffee plantation, which is also a tree, acting as an intermediate between closed environments (such as forests or agroforests) and open areas (such as pastures), which may have contributed to the lower variation in the microclimate. Although we detected a significant increase in temperature in anthropogenic land uses, this air temperature variation may have been too small to detect changes in ant species and predatory activity. Moreover, land use changes themselves tend to have a very large negative effect on animals (discussed below), making that small temperature variations almost insignificant in these cases (Englmeier et al. 2023). In addition, ground ants and other ectotherms may find cooler habitats for foraging and nesting, contributing to their thermal plasticity (Parr and Bishop 2022). Thus, although we found an increase in temperature in anthropogenic land uses, microclimatic changes were not a significant predictor of changes in diversity and predation function. This is probably due to the low variability between natural habitats and anthropogenic land uses, as well as the high impact of land use changes themselves.

Land use change decreases species richness, which is consistent with what is widely documented in the literature (e.g., Davison et al. 2021; Newbold et al. 2015). In tropical regions, land use change is the principal driver of biodiversity loss (Jaureguiberry et al. 2022).

Moreover, the conversion of forests to perennial agriculture, such as coffee plantations, tends to decrease ant species richness (Wilker et al. 2024). Although we did not find an effect of microclimate, other important not measured environmental conditions in agricultural land uses, such as increased soil compaction (Zhang et al. 2024) and changes in nutrient deposition (Cappelli et al. 2022), may decrease the sensitive species adapted to the original conditions. In addition, the quantity and diversity of resources decrease, excluding most specialist species (Miao et al. 2022; Ribas et al. 2003). This reduction in species richness tends to increase the presence of generalist and opportunistic species (winners and losers; McKinney and Lockwood 1999; Tabarelli et al. 2012). Thus, land use changes cause drastic alterations in species richness and community structure.

A decrease in species richness leads to a reduction in the number of predatory ants. Predatory ants are a group composed of species that prey on other animals, thus playing an important role in the ecosystem function of predation (Cerdá and Dejean 2011). Several studies have demonstrated a positive relationship between overall species richness and the number of species within a functional group (e.g., Laliberte et al. 2010; Mori et al. 2017), including functional groups such as predatory ants (Wilker et al. 2023). Communities with greater species richness tend to exhibit higher functional redundancy (Biggs et al. 2020), which enhances the stability and resilience of ecosystems (Sadeghinia et al. 2023). This redundancy ensures that if some species are excluded, others can continue performing the same function, maintaining the ecosystem balance (Biggs et al. 2020). Thus, land use changes lead to a decrease in species richness and, consequently, in specific groups such as predators, which can in turn affect ecosystem functions.

Finally, we found a direct and positive effect of predatory ants on insect predation. The positive relationship between ant species richness and insect predation is reported in the literature (Wilker et al. 2023). This occurs due to the greater number of species performing the

same function (Biggs et al. 2020). Furthermore, we found that predatory ants are the mediator through which land use changes reduce insect predation. Thus, as with general species richness, predatory species are also negatively affected by land use changes, leading to a decrease in predation activity (Barnes et al. 2017). Therefore, one way to conserve and promote higher levels of insect predation in anthropogenic land uses is to maintain a higher similarity to natural tropical habitats (e.g., shaded coffee plantations; Manson et al. 2024), which would conserve species richness and, consequently, the functions they perform.

Conclusion

In our study, we identified important direct and indirect effects of land use changes on ecosystem functions, with indirect mediator effects by species richness and predatory species. We found that land use changes increase temperature, but the microclimate did not affect ant species or predation function. This is likely because ground ants can find cooler microhabitats or due to the small temperature differences between natural environments and anthropogenic land uses. For this reason, we suggest further research where microclimate is assessed over longer time scales, such as variations during the day and night (Liu et al. 2020), and even seasonal changes (Queiroz et al. 2022). We found that land use has a direct negative effect on species richness, probably due to ecological filters that exclude most tropical ant species. In turn, overall species richness is directly linked to predator richness, indicating that conserving more species may likely contribute to the preservation of ecosystem functions beyond insect predation. Therefore, we recommend conservation strategies that maintain land uses as similar to natural conditions as possible, as this can enhance species richness and, consequently, the functions and services they provide.

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577 **Supplementary material**



578

579 **Figure S1** For the predation experiment, two beetle larvae were attached with touch fastener to
580 an ethylene-vinyl acetate (EVA) surface to prevent them from escaping.

Table S1 Ecological data for 32 sites across three regions (SAA: Santo Antônio do Amparo; LA: Lavras; PA: Patrocínio) and two biomes (AR: Atlantic rainforest; CE: Cerrado). Temperature was measured in degrees Celsius and humidity in percentage. Richness refers to the number of ant species collected in pitfalls. Predatory ants represent the number of ant species that preyed on insects. Pred. refers to the number of insect predation events.

Site	Region	Biome	Land use	Temperature	Humidity	Richness	Predatory ants	Pred.
A1	SAA	AR	Coffee	26.95	68.30	04	0	00
A2	SAA	AR	Coffee	28.29	69.35	04	2	05
A3	SAA	AR	Coffee	29.64	67.35	03	1	05
A4	SAA	AR	Coffee	27.89	62.70	03	3	08
A5	SAA	AR	Coffee	25.61	68.45	08	0	00
A6	SAA	AR	Coffee	29.85	63.60	08	1	01
A7	SAA	AR	Coffee	23.73	82.72	09	3	12
A8	SAA	AR	Coffee	21.70	81.45	15	6	27
A9	SAA	AR	Coffee	32.21	60.71	12	4	10
A10	SAA	AR	Coffee	26.75	69.15	13	2	05
A11	SAA	AR	Forest	23.24	81.52	24	4	12
A12	SAA	AR	Forest	24.75	87.00	20	3	07
A13	SAA	AR	Forest	25.51	79.35	21	5	18
A14	SAA	AR	Forest	24.83	86.40	15	6	16
A15	LA	AR	Coffee	28.79	69.41	13	3	05
A16	LA	AR	Coffee	28.55	69.43	11	4	14
A17	LA	AR	Forest	23.42	80.78	30	2	11
A18	LA	AR	Forest	22.20	88.91	25	1	06
A19	PA	Ce	Coffee	25.58	70.60	04	2	06
A20	PA	Ce	Coffee	23.53	86.81	03	0	00
A21	PA	Ce	Coffee	22.52	85.77	04	0	00
A22	PA	Ce	Coffee	21.11	88.40	03	1	11
A23	PA	Ce	Coffee	25.37	73.15	07	0	00
A24	PA	Ce	Coffee	23.33	80.20	11	2	03
A25	PA	Ce	Forest	22.81	88.57	22	3	16
A26	PA	Ce	Forest	21.09	95.90	20	1	02
A27	PA	Ce	Forest	23.10	95.31	19	0	00
A28	PA	Ce	Forest	23.51	92.24	15	1	06
A29	PA	Ce	Forest	26.85	69.68	28	6	21
A30	PA	Ce	Forest	25.33	82.61	25	4	07
A31	PA	Ce	Forest	28.49	63.65	06	1	02
A32	PA	Ce	Forest	23.13	96.62	09	1	02

588 **Full models and model selection by AIC**

589 `Model1 <- lmer(Temperature ~ Land_use + (1|Region), data = data)`

590

591 *Model selection by dredge (MuMIn package version 1.47.5)*

592 Table S2. The first column (Int) is the intercept. The columns in blue are the predictors. Df
 593 represents the degrees of freedom. logLik is the log-likelihood. AICc is the Akaike information
 594 criterion corrected for small sample sizes. Delta is the AICc difference between the selected
 595 model and the top model. Weight is the Akaike weight, indicating the relative probability that
 596 the model is the best. The table show only models with AICc < 2.

(Int)	Land	Df	logLik	AICc	Delta	Weight
26.10	+	4	-74.160	157.8	0.00	0.753

597

598 *Model selected*

599 `Model1 <- lmer(Temperature ~ Land_use + (1|Region), data = data)`

600 `Model2 <- lmer(sqrt(Richness) ~ Temperature + Land_use + (1|Region), data = data)`

601

602 *Model selection by dredge (MuMIn package version 1.47.5)*

603 Table S3. The first column (Int) is the intercept. The columns in blue are the predictors. Df
 604 represents the degrees of freedom. logLik is the log-likelihood. AICc is the Akaike information
 605 criterion corrected for small sample sizes. Delta is the AICc difference between the selected
 606 model and the top model. Weight is the Akaike weight, indicating the relative probability that
 607 the model is the best. The table show only models with AICc < 2.

(Int)	Land	Temp	Df	logLik	AICc	Delta	Weight
2.74	+		4	-37.76	85.0	0.00	0.95

608

609 *Model selected*

610 `Model2 <- lmer(sqrt(Richness) ~ Land_use + (1|Region), data = data)`

611 Model3 <- glmer.nb (Predatory_ants ~ + sqrt(Richness) + Temperature + Land_use +
612 (1|Region), data = data)

613

614 *Model selection by dredge (MuMIn package version 1.47.5)*

615 Table S4. The first column (Int) is the intercept. The columns in blue are the predictors. Df
616 represents the degrees of freedom. logLik is the log-likelihood. AICc is the Akaike information
617 criterion corrected for small sample sizes. Delta is the AICc difference between the selected
618 model and the top model. Weight is the Akaike weight, indicating the relative probability that
619 the model is the best. The table show only models with AICc < 2.

(Int)	Land	Temp	Rich	Df	logLik	AICc	Delta	Weight
-2.97		0.083	0.44	5	-55.09	122.5	0.00	0.35
-0.61			0.37	4	-56.58	122.6	0.15	0.32
-1.02	+		0.56	5	-55.73	123.8	1.28	0.18

620

621 *Predictors selection by model.avg (MuMIn package version 1.47.5)*

622 Table S5. The first column indicates the intercept and predictors selected in the *dredge* function.
623 The other columns are the estimate, standard error, adjusted standard error, z-value, and p-value.
624 The best predictors were selected based on $p < 0.05$.

	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)
(Intercept)	-1.664	1.471	1.502	1.108	0.267
Temp	0.083	0.046	0.048	1.717	0.085
Rich	0.444	0.148	0.154	2.878	0.004*
Land	-0.524	0.403	0.422	1.242	0.214

625

626 *Model selected*

627 Model3 <- glmer.nb (Predatory_ants ~ sqrt(Richness) + (1|Region), data = data)

```

628 Model4 <- lmer(sqrt(Predation) ~ Predatory_ants + sqrt(Richness) + Temperature + Land_use
629 + (1|Region), data = data)

```

```

630

```

```

631 Model selection by dread (MuMIn package version 1.47.5)

```

```

632 Table S6. The first column (Int) is the intercept. The columns in blue are the predictors. Df
633 represents the degrees of freedom. logLik is the log-likelihood. AICc is the Akaike information
634 criterion corrected for small sample sizes. Delta is the AICc difference between the selected
635 model and the top model. Weight is the Akaike weight, indicating the relative probability that
636 the model is the best. The table show only models with AICc < 2.

```

(Int)	Land	Temp	Pr.ant	Rich	Df	logLik	AICc	Delta	Weight
0.74			0.69		4	-36.77	83.0	0.00	0.70

```

637

```

```

638 Model selected

```

```

639 Model4 <- lmer(sqrt(Predation) ~ Predatory_ants + (1|Region), data = data)

```

640 **psem model**

```
641 SEMmodel <- psem(  
642   lmer(Temperature ~ Land_use + (1|Region), na.action = na.omit, data = data),  
643   lmer(sqrt(Richness) ~ Land_use + (1|Region), na.action = na.omit, data = data),  
644   glmer.nb(Predatory_ants ~ sqrt(Richness) + (1|Region), na.action = na.omit, data = data),  
645   lmer(sqrt(Predation) ~ Predatory_ants + (1|Region), na.action = na.omit, data = data))
```

646 **Table S7** Presence or absence of ants and ant species richness in natural habitats (forests) in the
 647 Atlantic rainforest. “Pitfall” refers to the ants collected in pitfall traps. “Predation” refers to ants
 648 collected in predation experiments using *Tenebrio molitor* Linnaeus, 1758 larvae.

Atlantic rainforest: Natural habitat		
Species	Pitfall	Predation
Dolichoderinae		
<i>Linepithema gallardoi</i> (Brèthes, 1914)	1	0
<i>Linepithema leucomelas</i> (Emery, 1894)	1	1
<i>Linepithema pulex</i> Wild, 2007	1	1
<i>Linepithema</i> sp. 2	1	0
Dorylinae		
<i>Labidus coecus</i> (Latreille, 1802)	1	0
Ectatomminae		
<i>Ectatomma edentatum</i> Roger, 1863	1	1
<i>Gnamptogenys sulcata</i> (Smith, 1858)	1	0
<i>Holcaponera striatula</i> (Mayr, 1884)	1	1
Formicinae		
<i>Acropyga decedens</i> (Mayr, 1887)	1	0
<i>Brachymyrmex bruchi</i> Forel, 1912	1	0
<i>Brachymyrmex cordemoyi</i> Forel, 1895	1	0
<i>Brachymyrmex minutus</i> Forel, 1893	1	0
<i>Brachymyrmex pictus</i> Mayr, 1887	1	0
<i>Brachymyrmex</i> sp. 1	1	0
<i>Camponotus (Myrmophaenus)</i> sp. 8	1	0
<i>Camponotus cingulatus</i> Mayr, 1862	1	1
<i>Camponotus rufipes</i> (Fabricius, 1775)	1	0
<i>Camponotus lespesii</i> Forel, 1886	1	0
<i>Camponotus melanoticus</i> Emery, 1894	1	0
<i>Camponotus (Tanaemyrmex)</i> sp. 1	1	0
<i>Camponotus (Tanaemyrmex)</i> sp. 4	1	0
Myrmicinae		
<i>Acromyrmex aspersus</i> (Smith, 1858)	1	0
<i>Acromyrmex hispidus</i> Santschi, 1925	1	0
<i>Apterostigma pilosum</i> Mayr, 1865	1	0
<i>Apterostigma</i> sp. 3	1	0
<i>Apterostigma wasmannii</i> Forel, 1892	1	0
<i>Atta sexdens</i> (Linnaeus, 1758)	1	0
<i>Basiceros disciger</i> (Mayr, 1887)	1	0
<i>Crematogaster</i> pr. <i>chodati</i> Forel, 1921	1	0
<i>Crematogaster rochai</i> Forel, 1903	1	0
<i>Cyphomyrmex minutus</i> Mayr, 1862	1	0
<i>Hylomyrma reitteri</i> (Mayr, 1887)	1	0
<i>Mycetomoellerius urichii</i> (Forel, 1893)	1	0

<i>Myrmicocrypta squamosa</i> Smith, 1860	1	0
<i>Pheidole aper</i> Forel, 1912	1	1
<i>Pheidole brevicona</i> Mayr, 1887	1	0
<i>Pheidole fallax</i> Mayr, 1870	1	1
<i>Pheidole sigillata</i> Wilson, 2003	1	0
<i>Pheidole</i> sp. 3	1	0
<i>Pheidole</i> sp. 4	1	0
<i>Pheidole</i> sp. 12	1	1
<i>Pheidole</i> sp. 30	1	0
<i>Pheidole</i> sp. 55	1	0
<i>Pheidole</i> sp. 73	1	1
<i>Pheidole</i> sp. 77	1	0
<i>Pheidole transversostriata</i> Mayr, 1887	1	0
<i>Solenopsis</i> sp. 1	1	0
<i>Solenopsis</i> sp. 3	1	0
<i>Solenopsis</i> sp. 4	1	0
<i>Solenopsis</i> sp. 7	1	0
<i>Solenopsis</i> sp. 8	1	1
<i>Solenopsis</i> sp. 10	1	0
<i>Solenopsis</i> sp. 11	1	0
<i>Strumigenys appretiata</i> (Borgmeier, 1954)	1	0
<i>Strumigenys denticulata</i> Mayr, 1887	1	0
<i>Strumigenys subdentata</i> Mayr, 1887	1	0
<i>Wasmannia affinis</i> Santschi, 1929	1	0
Ponerinae		
<i>Hypoponera</i> sp. 3	1	0
<i>Neoponera marginata</i> (Roger, 1861)	1	0
<i>Odontomachus chelifer</i> (Latreille, 1802)	1	1
<i>Odontomachus meinerti</i> Forel, 1905	1	0
<i>Pachycondyla harpax</i> (Fabricius, 1804)	1	0
<i>Pachycondyla striata</i> Smith, 1858	1	1
Total of ant species	63	12

650 **Table S8** Presence or absence of ants and ant species richness in coffee plantations in the
 651 Atlantic rainforest. “Pitfall” refers to the ants collected in pitfall traps. “Predation” refers to ants
 652 collected in predation experiments using *Tenebrio molitor* Linnaeus, 1758 larvae.

Atlantic rainforest: Coffee plantation		
Species	Pitfall	Predation
Dolichoderinae		
<i>Dorymyrmex brunneus</i> Forel, 1908	1	0
<i>Linepithema cerradense</i> Wild, 2007	1	0
<i>Linepithema neotropicum</i> Wild, 2007	1	1
<i>Linepithema pulex</i> Wild, 2007	1	0
<i>Linepithema</i> sp. 4	0	1
Ectatomminae		
<i>Ectatomma brunneum</i> Smith, 1858	1	0
<i>Ectatomma permagnum</i> Forel, 1908	1	0
<i>Holcaponera striatula</i> (Mayr, 1884)	1	1
Formicinae		
<i>Brachymyrmex cordemoyi</i> Forel, 1895	1	0
<i>Brachymyrmex pictus</i> Mayr, 1887	1	0
<i>Brachymyrmex pilipes</i> Mayr, 1887	1	0
<i>Camponotus melanoticus</i> Emery, 1894	1	0
<i>Nylanderia</i> sp. 7	1	0
Myrmicinae		
<i>Atta sexdens</i> (Linnaeus, 1758)	1	0
<i>Carebara</i> pr. <i>brasiliensis</i> Fernández, 2004	1	0
<i>Mycetomoellerius</i> sp. 1	1	0
<i>Mycocepurus smithii</i> (Forel, 1893)	1	0
<i>Pheidole fallax</i> Mayr, 1870	1	0
<i>Pheidole obscurithorax</i> Naves, 1985	1	1
<i>Pheidole oxyops</i> Forel, 1908	1	1
<i>Pheidole radoszkowskii</i> Mayr, 1884	1	1
<i>Pheidole subarmata</i> Mayr, 1884	1	1
<i>Pheidole</i> sp. 5	1	0
<i>Pheidole</i> sp. 6	0	1
<i>Pheidole</i> sp. 12	1	0
<i>Pheidole</i> sp. 65	1	1
<i>Pheidole</i> sp. 73	1	1
<i>Pheidole</i> sp. 75	1	0
<i>Pheidole</i> sp. 99	1	0
<i>Pogonomyrmex naegelii</i> Emery, 1878	1	0
<i>Solenopsis</i> gr. <i>saevisissima</i> sp. 1	1	1
<i>Solenopsis</i> sp. 2	1	0
<i>Solenopsis</i> sp. 4	1	0
<i>Solenopsis</i> sp. 8	1	0

<i>Strumigenys louisianae</i> Roger, 1863	1	0
Ponerinae		
<i>Hypoponera</i> sp. 1	1	0
<i>Hypoponera</i> sp. 2	1	0
<i>Hypoponera</i> sp. 3	1	0
<i>Hypoponera</i> sp. 4	1	0
<i>Hypoponera</i> sp. 5	1	0
<i>Pachycondyla striata</i> Smith, 1858	1	1
Total of ant species	39	12

654 **Table S9** Presence or absence of ants and ant species richness in natural habitat (woodland
 655 savannah) in the Cerrado. “Pitfall” refers to the ants collected in pitfall traps. “Predation” refers
 656 to ants collected in predation experiments using *Tenebrio molitor* Linnaeus, 1758 larvae.

Cerrado: Natural habitat		
Species	Pitfall	Predation
Dolichoderinae		
<i>Linepithema neotropicum</i> Wild, 2007	1	0
<i>Linepithema pulex</i> Wild, 2007	1	0
<i>Lenepthema</i> sp. 1	1	0
<i>Lenepthema</i> sp. 3	1	0
Dorylinae		
<i>Neivamyrmex</i> sp. 1	1	0
Ectatomminae		
<i>Ectatomma edentatum</i> Roger, 1863	1	1
<i>Gnamptogenys sulcata</i> (Smith, 1858)	1	0
<i>Holcaponera striatula</i> (Mayr, 1884)	1	0
Formicinae		
<i>Brachymyrmex minutus</i> Forel, 1893	1	0
<i>Brachymyrmex pictus</i> Mayr, 1887	1	0
<i>Brachymyrmex</i> sp. 2	1	0
<i>Brachymyrmex</i> sp. 3	1	0
<i>Brachymyrmex</i> sp. 4	1	0
<i>Camponotus crassus</i> Mayr, 1862	1	0
<i>Camponotus fastigatus</i> Roger, 1863	1	1
<i>Camponotus atriceps</i> (Smith, 1858)	1	0
<i>Camponotus cingulatus</i> Mayr, 1862	1	0
<i>Camponotus ager</i> (Smith, 1858)	1	0
<i>Camponotus lespeii</i> Forel, 1886	1	1
<i>Camponotus (Tanaemyrmex)</i> sp. 1	1	0
<i>Nylanderia docilis</i> (Forel, 1908)	1	0
<i>Nylanderia</i> sp. 7	1	0
<i>Nylanderia steinheili</i> (Forel, 1893)	1	0
Myrmicinae		
<i>Acromyrmex aspersus</i> (Smith, 1858)	1	0
<i>Acromyrmex hispidus</i> Santschi, 1925	1	0
<i>Acromyrmex subterraneus</i> (Forel, 1893)	1	0
<i>Atta sexdens</i> (Linnaeus, 1758)	1	0
<i>Carebara brevopilosa</i> Fernández, 2004	1	0
<i>Crematogaster corticicola</i> Mayr, 1887	0	1
<i>Cyphomyrmex minutus</i> Mayr, 1862	1	0
<i>Mycetomoellerius urichii</i> (Forel, 1893)	1	0
<i>Mycetomoellerius</i> sp. 1	1	0
<i>Mycetophylax lectus</i> (Forel, 1911)	1	0

<i>Ochetomyrmex</i> sp. 1	1	0
<i>Pheidole aberrans</i> Mayr, 1868	1	0
<i>Pheidole fallax</i> Mayr, 1870	1	1
<i>Pheidole jelskii</i> Mayr, 1884	1	1
<i>Pheidole oxyops</i> Forel, 1908	1	1
<i>Pheidole</i> pr. <i>deima</i> Wilson, 2003	1	0
<i>Pheidole radoszkowskii</i> Mayr, 1884	1	1
<i>Pheidole sarcina</i> Forel, 1912	1	0
<i>Pheidole</i> sp. 12	1	0
<i>Pheidole</i> sp. 15	1	0
<i>Pheidole</i> sp. 19	1	0
<i>Pheidole</i> sp. 41	1	0
<i>Pheidole</i> sp. 55	1	1
<i>Pheidole</i> sp. 65	1	0
<i>Pheidole</i> sp. 71	1	0
<i>Rogeria lirata</i> Kugler, 1994	1	0
<i>Sericomyrmex saussurei</i> Emery, 1894	1	0
<i>Solenopsis</i> sp. 3	1	0
<i>Solenopsis</i> sp. 4	1	0
<i>Solenopsis</i> sp. 10	1	0
<i>Solenopsis</i> sp. 11	1	0
<i>Wasmannia auropunctata</i> (Roger, 1863)	1	0
Ponerinae		
<i>Hypoponera</i> sp. 2	1	0
<i>Neoponera</i> sp. 1	1	0
<i>Odontomachus chelifer</i> (Latreille, 1802)	1	0
<i>Pachycondyla striata</i> Smith, 1858	1	1
Pseudomyrmecinae		
<i>Pseudomyrmex</i> gr. <i>pallidus</i> sp. 1	1	0
<i>Pseudomyrmex phyllophilus</i> (Smith, 1858)	1	0
Total of ant species	60	10

658 **Table S10** Presence or absence of ants and ant species richness in coffee plantations in the
 659 Cerrado. “Pitfall” refers to the ants collected in pitfall traps. “Predation” refers to ants collected
 660 in predation experiments using *Tenebrio molitor* Linnaeus, 1758 larvae.

Cerrado: Coffee plantation		
Species	Pitfall	Predation
Dolichoderinae		
<i>Dorymyrmex brunneus</i> Forel, 1908	1	1
<i>Linepithema neotropicum</i> Wild, 2007	1	0
Ectatomminae		
<i>Holcaponera striatula</i> (Mayr, 1884)	1	1
Formicinae		
<i>Brachymyrmex cordemoyi</i> Forel, 1895	1	0
<i>Brachymyrmex pilipes</i> Mayr, 1887	1	0
<i>Camponotus cingulatus</i> Mayr, 1862	1	0
<i>Camponotus melanoticus</i> Emery, 1894	1	0
Myrmicinae		
<i>Cardiocondyla minutior</i> Forel, 1899	1	0
<i>Mycocepurus smithii</i> (Forel, 1893)	1	0
<i>Pheidole aberrans</i> Mayr, 1868	1	0
<i>Pheidole fallax</i> Mayr, 1870	1	1
<i>Pheidole gertrudae</i> Forel, 1886	1	0
<i>Pheidole oxyops</i> Forel, 1908	1	0
<i>Pheidole radoszkowskii</i> Mayr, 1884	1	0
<i>Pheidole</i> sp. 5	0	1
<i>Pheidole</i> sp. 6	0	1
<i>Pheidole</i> sp. 75	1	0
<i>Pheidole subarmata</i> Mayr, 1884	1	1
<i>Pheidole vallifica</i> Forel, 1901	1	0
<i>Solenopsis</i> gr. <i>saevissima</i> sp. 1	1	1
<i>Solenopsis</i> sp. 17	1	0
<i>Solenopsis</i> sp. 18	1	0
Total of ant species	20	7

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ARTIGO 3 - A systematic review of the land use change effects on ant diversity in Neotropics

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Abstract

Land use changes represent one of the leading causes of terrestrial biodiversity loss, particularly in tropical ecosystems. In Brazil, a country that encompasses six distinct biomes and one of the world's highest ant diversities, the increasing land use changes are having detrimental effects on biodiversity. Our aim in this study is to summarize the impact of land use changes on ants in Brazil through a systematic review. We adhered to the PRISMA Eco-Evo methodology and conducted a qualitative review of studies, as well as a meta-analysis focusing on ant species richness and abundance. Especially, we observe a more pronounced negative effect in more contrasting conversions, such as from tropical forest to open anthropogenic land uses. We associate the decrease in richness with drastic changes in the vegetation structure. Consequently, this leads to extreme temperature variations, reduced humidity, and a decline in both the variety and quantity of food resources and nesting sites. Our findings provide a foundation for the conservation and management of anthropogenic land uses in human-impacted regions. More specifically, we highlight that future management plans should aim for anthropogenic land uses that more closely resemble the original natural vegetation, to maintain conditions and increase resource availability for biodiversity in the new habitats. Additionally, avoiding intensive management practices, such as the use of fertilizers and pesticides in agricultural systems, can also support the conservation of entomofauna in terms of species richness and abundance, and potentially benefit ecosystem services.

Keywords: Formicidae; Brazil; meta-analysis; biodiversity; Biomes

1. Introduction

Land use changes, like the conversion of natural habitats into anthropogenic land uses, significantly drive the decline in global biodiversity, potentially hampering ecosystem functioning (de Chazal and Rounsevell, 2009; Newbold et al., 2015, 2019). While these changes occur worldwide, they have more pronounced impacts in tropical regions (Magnusson et al., 2018; Nunes et al., 2022; Sala et al., 2000), which is of concern because tropical areas host the highest terrestrial biodiversity (Antonelli et al., 2018; Gardner et al., 2009). In tropical ecosystems, land use changes often create strong contrasts between natural habitats and altered anthropogenic land use, primarily due to the expansion of the agricultural frontier (Gibbs et al., 2010; Song et al., 2018). For example, in the Brazilian Amazon biome, most conversions involve conversion from forest to soy monoculture and extensive pasture, representing open land uses that significantly differ from the original habitat (FAO, 2016; Nunes et al., 2022; Parente et al., 2021). Anthropogenic land uses, such as agricultural crops and pastures, typically exhibit low environmental heterogeneity, leading to reduced resource quantity and diversity, and more severe alterations to local conditions (Priyadarshana et al., 2024; Stein and Kreft, 2015). In addition, the use of synthetic pesticides can increase the negative effects of land use on several species (Sánchez-Bayo and Wyckhuys, 2019). Similarly, agricultural practices such as the use of fertilizers can alter nutrient deposition (*e.g.*, salinization), impacting species richness and ecosystem processes (Hopmans et al., 2021; Lasmar et al., 2021a). Thus, these impacts on habitat structure and quality result in a substantial loss of specialist species and an increase in generalist ones (Filgueiras et al., 2021; Martins et al., 2022; Tabarelli et al., 2012).

The adverse impacts of land use changes on biodiversity have been extensively researched across various terrestrial organisms, encompassing vertebrates (Newbold, 2018), plants (Laliberté et al., 2010), soil microbiomes (Díaz-Vallejo et al., 2021), and arthropods (Attwood et al., 2008). Among arthropods, ants are regarded as excellent model organisms for

investigating the consequences of land use changes in tropical regions (Andersen et al., 2002; Ribas et al., 2012). This recognition is due to their high species richness (Feitosa et al., 2022) and their significant ecological roles, including seed dispersal, bioturbation, and predation (Folgarait, 1998; Lach et al., 2010). Ants exhibit a high sensitivity to anthropogenic land uses (*e.g.*, Queiroz et al., 2020; Rabello et al., 2018; Wilker et al., 2023).

Within the Neotropical Region, Brazil encompasses an extensive spatial expanse that includes six biomes: Amazon (tropical forest), Atlantic Forest (tropical forest), Caatinga (xeric shrubland), Cerrado (savannah), Pampa (grassland), and Pantanal (flooded grasslands). Furthermore, within the same biome, multiple vegetation types can coexist. For example, in the Cerrado biome, comprising forested vegetation (*cerradão* or woodland savannah), savannah, and open vegetation (grasslands). However, despite the high biodiversity found in these biomes, they undergo significant land use changes, with the Cerrado and the Atlantic Forest biomes considered global biodiversity hotspots (Trew and Maclean, 2021). Indeed, currently all Brazilian biomes are under severe threat due to land use changes (Magnusson et al., 2018; Projeto MapBiomias, 2022).

While some general patterns have indicated that anthropogenic impacts can reduce ant assemblage diversity (*e.g.*, fire effects: Vasconcelos et al., 2017) and ecosystem functions, such as the reduced removal of diaspores by ants (Bona et al., 2023), the intensity of these impacts is largely determined by their association with habitat openness (Andersen, 2019). Therefore, ant assemblages from closed-forested vegetation types are more sensitive to the impacts promoted by the establishment of pastures and agricultural land uses (Costa and Schmidt, 2022; Lasmar et al., 2021b; Queiroz et al., 2020) than ant assemblages in open vegetation types (*e.g.*, grasslands; Queiroz et al., 2020). Furthermore, ant assemblages from closed-forested vegetation types require more time to recover from anthropogenic impacts than those from open vegetation types (Casimiro et al., 2019). Considering Brazil's significance in global ant diversity (Feitosa

et al., 2022; Schmidt et al., 2022) and the escalating threats faced by its biodiversity, such as agricultural frontiers and mining projects (Pereira et al., 2020), the country serves as an excellent model for studying the effects of land use changes on biodiversity.

Thus, we conducted a systematic review, including both a qualitative review and a meta-analysis, with the aim of assessing the impact of land use changes on ant assemblages in Brazil. We conducted a qualitative review examining studies that evaluated the effects of land use changes on ants in Brazil, identifying knowledge gaps and proposing new approaches for future studies. We also conducted a meta-analysis to determine if the negative effects on species richness and abundance of ants resulting from land use change are associated with the biome and land use change type. Specifically, we predict that (i) the negative impacts of land use changes in species richness and abundance will be more significant in tropical forest biomes (e.g., Amazon and Atlantic Forest) compared to grassland biomes (e.g., Pampa and Pantanal), and (ii) these negative effects in species richness and abundance will be more pronounced in cases of intense conversion, such as the conversion from forests habitat to pasture or mining anthropogenic land uses.

2. Methods

2.1. Data collection

We followed the PRISMA-EcoEvo methodology (O’Dea et al., 2021). First, we conducted a search for studies on the effects of land use change on ants in Brazil using the Ants of Brazil Project database (Feitosa et al., 2022; Schmidt et al., 2022). We also performed a preliminary search (naïve search) for relevant studies in the “Web of Science databases - Main Collection (Clarivate Analytics)” (www.webofscience.com), “Scopus” (www.scopus.com), and “SciELO.ORG” (www.scielo.org). Initially, we carried out a preliminary search using pertinent keywords related to the topic (Grames et al., 2019). To achieve this, we categorized the keywords into four sections, following the PICO/PECO model (population,

intervention/exposure, comparator, outcome; Haddaway et al., 2016). The “Population” section pertained to the specific population under study (e.g., Ants), the “Intervention/Exposure” section referred to various exposure or environmental factors (e.g., Land use), the “Comparator” section related to what the exposure would be compared to (e.g., Biomes), and the “Outcome” encompassed the measured variables (e.g., Diversity). The naïve search conducted in November 2023. The titles, abstracts, and keywords of these studies were exported, and additional keywords were identified using the “litsearchr” package (Grames et al., 2019), within the R software (R Core Team, 2021). In the analysis of the new keywords, we included the term 'species composition' as an outcome and performed a subsequent search. In addition to the search using English terms, we also conducted searches in Portuguese and Spanish in the same databases (see Appendix A: Keywords). The new search returned 3,488 studies in Web of Science, 1,573 in Scopus, and 16 in SciELO.ORG. We also included an additional 72 studies from the Ants of Brazil Project, bringing the total to 5,149.

2.2. *Exclusion and inclusion criteria*

We removed duplicate studies and conducted a screening of titles, abstracts, and full articles. Our inclusion criteria focused on studies that specifically assessed the impact of land use changes on ant assemblages in Brazil. We applied exclusion criteria, including: (1) studies conducted outside Brazil; (2) studies unrelated to ant communities or assemblages; (3) studies not addressing the effects of land use changes; (4) studies lacking a comparison between natural habitat and anthropogenic land use. We also excluded non-case studies (e.g., reviews) and studies dealing with anthropogenic disturbances not related to land use categorization (e.g., chronic disturbances like logging or non-timber forest product extraction). Furthermore, we omitted studies focusing on ecological succession (e.g., succession or restoration) and those where it was impossible to separate the impact on ant assemblages from other evaluated organisms (e.g., macrofauna). Out of the initial pool of 5,149 studies, 128 remained for the

qualitative review (Fig. 1A), and 42 were eligible for the meta-analysis. Detailed information is available in Appendix B (PRISMA-EcoEvo). A list of data sources used in the study are provided in the Appendix A: Data sources.

Fig. 1

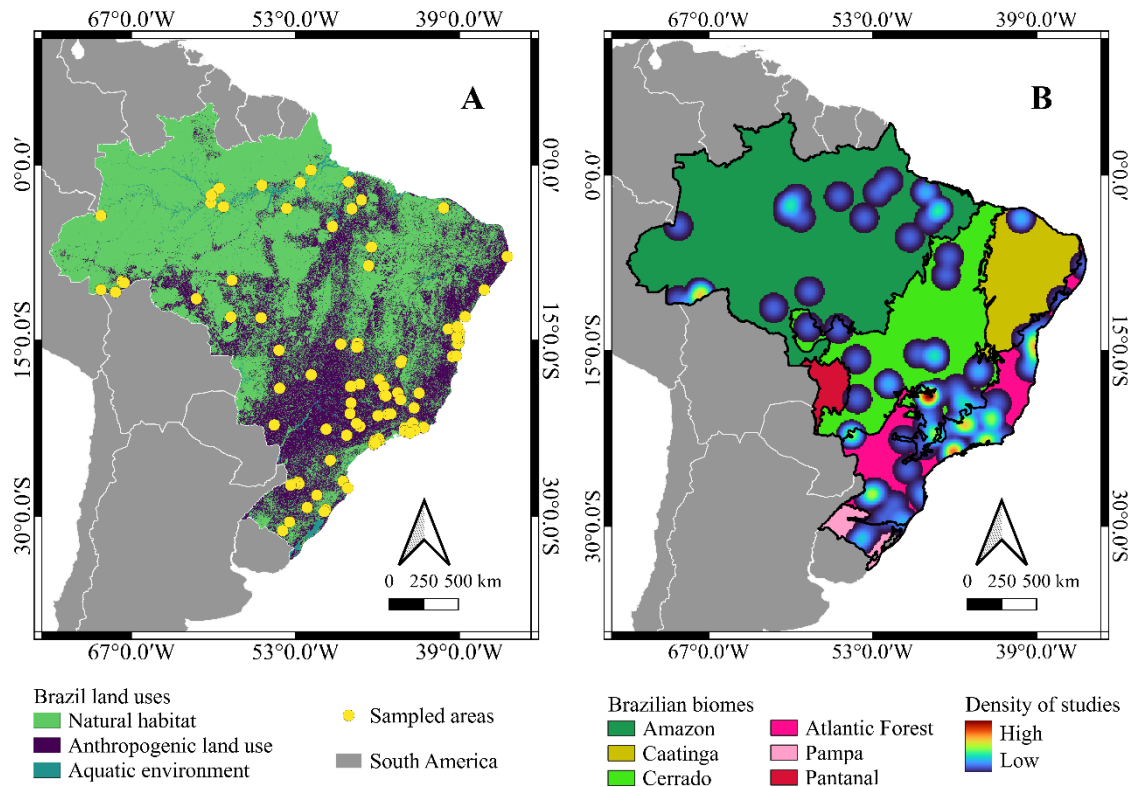


Fig. 1. Study sites extracted from the 128 studies concerning the effects of land use changes on ants in Brazil. The figure 1A indicates the concentration of study sites in regions with a high degree of land use changes, and figure 1B indicates the concentration of studies in the Brazilian biomes Atlantic Forest and Cerrado. The figure was generated using QGIS.org version 3.32 (QGIS.org, 2023) and adapted from the land use and land cover map for the year 2021 provided by MapBiomas (Projeto MapBiomas, 2022) and biome data from Instituto Brasileiro de Geografia e Estatística (IBGE, 2019).

2.3. Qualitative review

From the 128 studies, we extracted qualitative data including the study ID (citation), publication year, language, journal, impact factor, biome, sampling season, vegetation type, anthropogenic land use, sampling methods, sampled strata (epigeic, leaf-litter, subterranean, and arboreal), and response variable, such as species richness and abundance. We are counting votes for qualitative data from the studies and assessed whether land use affects species compositions. Species composition refers to the differences in the identity of ant species between natural habitats and anthropogenic land uses, extracted from analyses such as PERMANOVA (Permutational Multivariate Analysis of Variance) and ANOSIM (Analysis of Similarities) (Anderson, 2001; Clarke, 1993; Warton et al., 2012).

2.4. Extracting and calculating effect sizes

For the meta-analysis, we gathered data on the most frequently assessed response variable, including species richness and abundance. Species richness was reported in studies as either observed species richness or estimators (*e.g.*, Chao1, Chao2, Jackknife1, individual-based rarefaction, and sample-based rarefaction). Abundance was reported in studies as number of ant workers and species frequency. For these response variables, we collected mean values, sample size, and dispersion metrics such as variance, standard deviation, standard error, and 95% confidence intervals. We extracted these data from the text, tables, and figures of the studies. When the data was solely presented in figures, we utilized WebPlotDigitizer version 4.6 to extract the mean and dispersion metrics (www.automeris.io/WebPlotDigitizer/). We standardized all the dispersion metrics into standard deviation. We also obtained data regarding vegetation type and anthropogenic land uses. Vegetation types were classified into various categories, encompassing forest types such as primary and secondary forests, riparian forests, and woodland savannah, as well as grassland, “restinga”, savannah, “vereda”, mangrove, and “canga”. The anthropogenic land use data were classified into agriculture and pasture categories when these two anthropogenic uses were sampled jointly, annual agriculture (*e.g.*,

soybean plantation), perennial agriculture (e.g., coffee plantation), mining, pasture, silviculture (e.g., *Eucalyptus* spp. plantation), and urbanization.

We analyzed a total of 42 studies and 212 comparisons for the meta-analysis, which were categorized according to the response variable: species richness (studies: $n = 36$; comparisons: $n = 171$) and abundance (studies: $n = 14$; comparisons: $n = 41$). For this, we determined an effect size that could be summarized across all studies. The effect size is a metric that quantifies the relationship between two entities, capturing the direction and magnitude of this relationship (Harrer et al., 2021). In our case, the effect size indicated the effects of land use change on the richness and abundance of ants. To calculate the effect size (Hedges' g), we used the standardized mean difference (SMD) metric corrected for small sample sizes (J-corrected form; Goulet-Pelletier and Cousineau, 2018; Hedges, 1981) and utilized the “escalc” function of the “metafor” R package (Viechtbauer, 2010). A negative Hedges' g indicates an adverse effect of a given response variable resulting from the land use change, while a positive value indicates the opposite. The zero value represents the absence of an effect size. We only analyzed comparisons involving three or more elements. For instance, we excluded the conversion from “canga” to mining because we found only one comparison in this case.

2.5. Meta-analysis

We analysed nine multilevel linear (mixed-effects) models using the “rma.mv” function from the “metafor” R package (Viechtbauer, 2010). In all models, we used the study ID as a random variable due to the non-independence of the effect sizes found in the same study. We constructed three general models with no fixed moderators (only with the random variable): one with all effect sizes for the general model ($n = 212$), one for species richness ($n = 171$), and one for abundance ($n = 41$). Additionally, we established six models with moderators to test our two predictions, both for richness and abundance. To test our prediction that (i) the negative impacts of land use changes in species richness and abundance will be more significant in tropical forest

biomes, we created two models with the biome as the moderator. To test our prediction that (ii) the negative impacts of land use changes in species richness and abundance will be more pronounced in cases of intense conversion, we built two models with the land use conversion type as the moderator.

For each model, we assessed Cochran's Q. In these statics, using the chi-square distribution with $n-1$ degrees of freedom, significant results ($p < 0.05$) indicate heterogeneity, suggesting substantial variability among the effect sizes. We evaluated both total heterogeneity (Q_T) and moderator heterogeneity (Q_W). Additionally, we examined publication bias through funnel plots. Publication bias refers to the tendency to publish studies with significant results (Rosenthal, 1979), which can introduce bias into the effect sizes available for meta-analyses. Identifying publication bias is a critical aspect of meta-analyses, as it facilitates the validation of these findings through additional investigations (Nakagawa and Santos, 2012). The figures were generated using the R package "ggplot2" (Wickham, 2016).

3. Results

3.1. Qualitative review

The first study found was published in 1995, and since then, there has been a growth trend over the years, with a peak of 12 studies in 2013 and 2018. Most of the studies evaluated were published in English (101 studies; 79%) and Portuguese (26 studies; 20%). Studies were published in 71 journals, with Sociobiology (13 studies; 10%) and Neotropical Entomology (10 studies; 08%) having the highest publication numbers. Of the journals with impact factors, the values ranged from 0.271 to 13.211, with a mean ($\bar{x}$) and standard deviation ($\pm$ SD) of 4.126 and 2.671, respectively. The most sampled biomes included the Atlantic Forest (53 studies; 41%), Cerrado (29 studies; 23%), and Amazon (28 studies; 22%) (Fig. 1B).

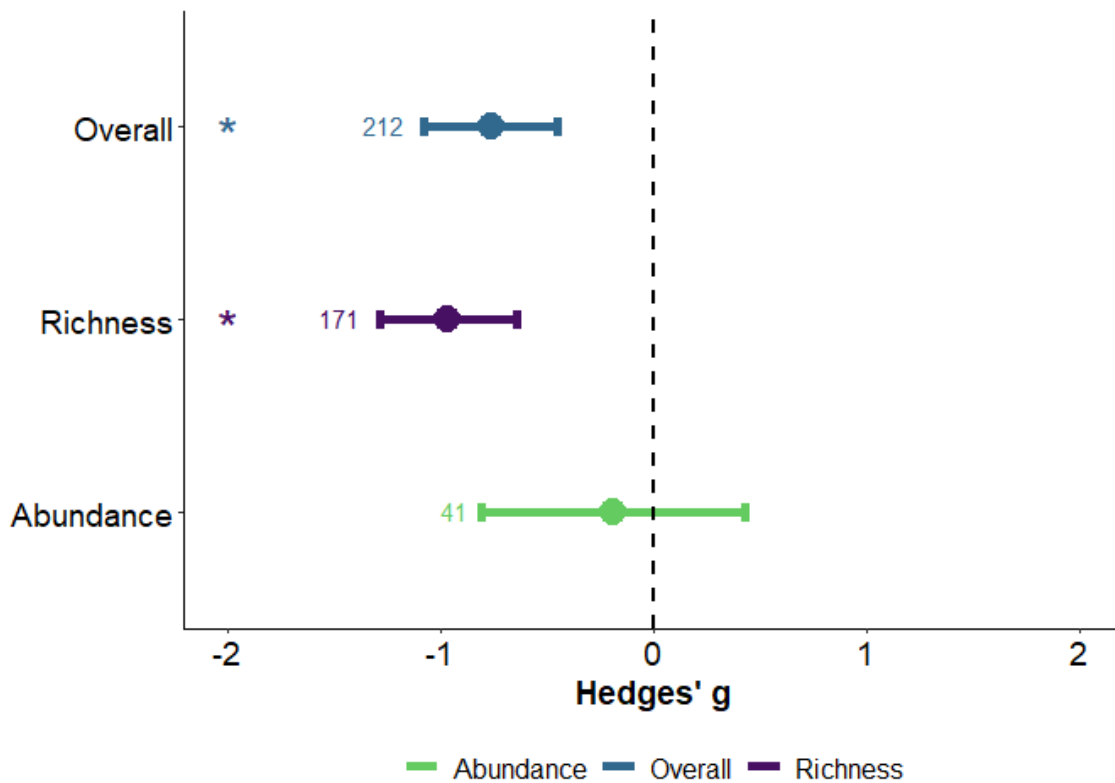
Most studies sampled ants during both the dry and rainy seasons (45 studies; 35%) or solely in the rainy season (45 studies; 35%). In line with the trend of the most frequently sampled biomes,

the vegetation types most studied were forests (106 studies; 83%) and savannahs (25 studies; 19%). The most studied anthropogenic land uses were pasture (51 studies; 40%), silviculture (46 studies; 36%), and annual agriculture (41 studies; 32%). Pitfall traps (68 studies; 53%) were the most used sampling method, and the most studied habitat stratum was the epigeic stratum (82 studies; 64%). Most studies assessed the effects on species richness (114 studies; 89%), diversity indices (65 studies; 51%), species composition (64 studies; 50%), and abundance (62 studies; 48%). Of the 64 studies that evaluated species composition, 56 studies (87%) reported differences in composition between ant assemblages from natural habitats and those from anthropogenic land uses. In addition, few studies have evaluated ecosystem functions and functional groups, making it impossible to find general patterns among them. For qualitative review graphs, see Appendix A, Fig. A.1-A.14.

3.2. *Meta-analysis*

We identified a detrimental impact on ants due to land use change ($E_{++} = -0.763$, $CI = -1.079$ to -0.447 , $df = 211$; where E_{++} represents Hedges' g (effect size), CI represents confidence interval, and df represents degrees of freedom). Furthermore, we observed that the land use change reduces ant species richness ($E_{++} = -0.962$, $CI = -1.286$ to -0.638 , $df = 170$; Fig. 2), but we did not detect any significant impact on ant abundance ($E_{++} = -0.188$, $CI = -0.803$ to 0.427 , $df = 40$; Fig. 2).

237 Fig. 2



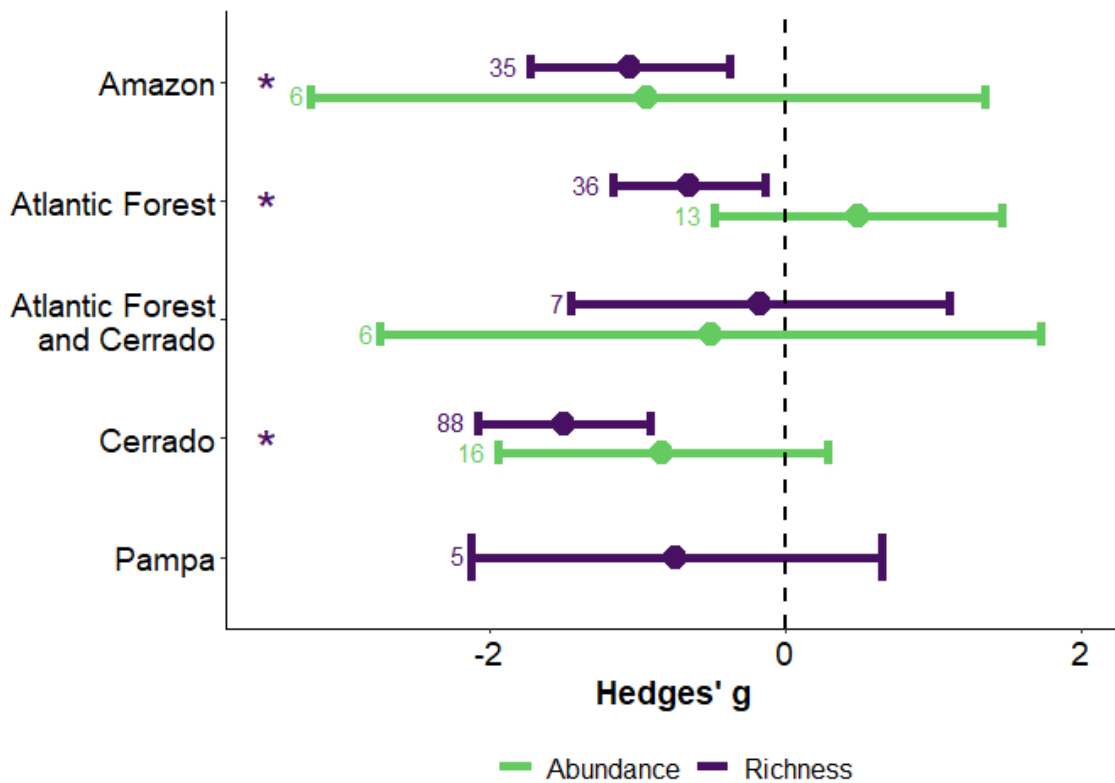
238

239 Fig. 2. Negative impacts were observed on ant species richness due to land use changes, but we
 240 did not find an effect for abundance. The numbers adjacent to the confidence interval denote
 241 the quantity of effect sizes analyzed. The data points represent the estimated mean effect size
 242 (Hedges' g), and the bars indicate the 95% confidence interval. The asterisk indicates a
 243 significant result.

244 For our first prediction, we found that land use changes lead to a more pronounced decrease in
 245 ant species richness in the Amazon, Atlantic Forest, and Cerrado biomes (Fig. 3, Table A.1).
 246 However, no significant impact was observed on ant abundance (Fig. 3, Table A.1). For our
 247 second prediction, we observed that land use changes, mainly from forests and savannahs to
 248 open anthropogenic land uses, resulted in a reduction in ant species richness and ant abundance
 249 (Fig. 4, Table A.2).

250

251 Fig. 3



252

253 Fig. 3. Negative effects of land use changes (biome moderator) on ant species richness, but we
 254 did not find an effect for abundance. The “Atlantic Forest and Cerrado” indicates the presence
 255 of effect sizes for both biomes in the study. Biomes that are not shown in the figures lacked
 256 effect sizes for inclusion in the meta-analysis. The numbers adjacent to the confidence interval
 257 denote the quantity of effect sizes analyzed. The data points represent the estimated mean effect
 258 size (Hedges' g), and the bars indicate the 95% confidence interval. The asterisk indicates a
 259 significant result.

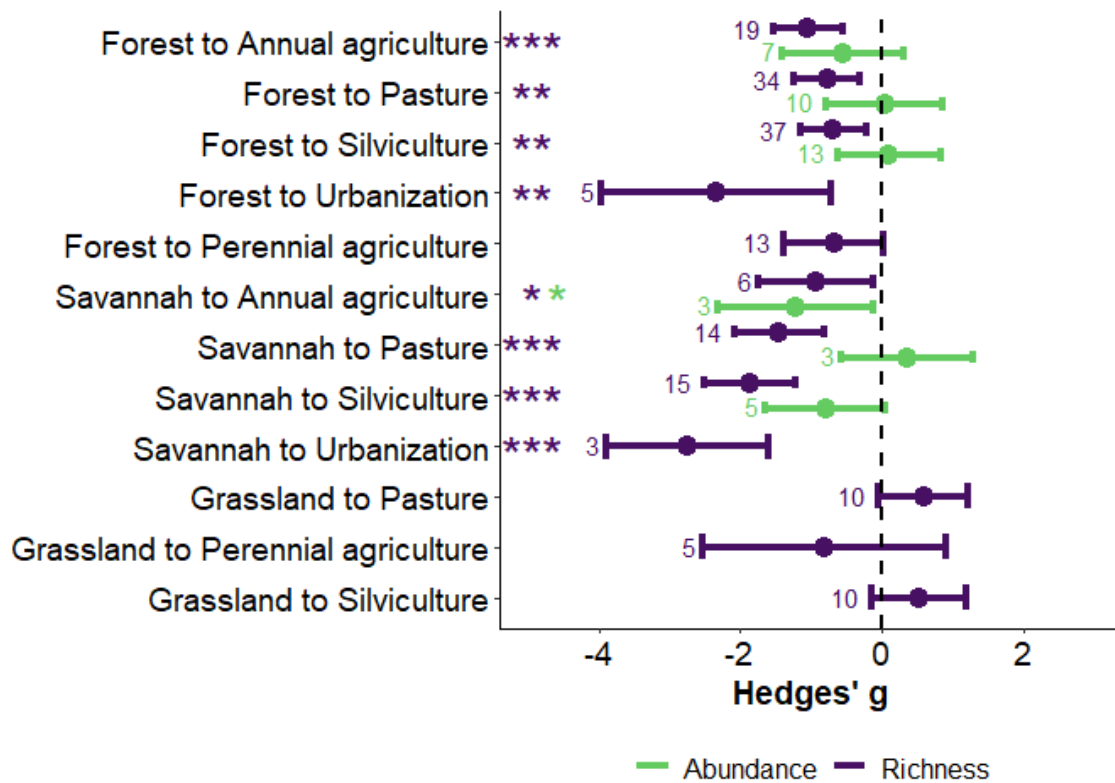
260

261

262

263

264 Fig. 4



265

266 Fig. 4. Negative and null effects of land use (conversion type moderator) changes on ant species
 267 richness and abundance. Points represent the estimated mean effect size (Hedges' g), and the
 268 lines represent the 95% confidence interval. Numbers next to the confidence interval indicate
 269 the number of effect sizes analyzed. The asterisk indicates a significant result.

270 3.3. Heterogeneity and publication bias

271 We found high heterogeneity in the overall model without moderators ($Q_T = 1\,591.202$, $p <$
 272 0.001 , $df = 211$). For species richness, we also observed high heterogeneity ($Q_T = 1\,467.317$, p
 273 < 0.001 , $df = 170$), which was partially explained by biome ($Q_W = 41.915$, $p < 0.001$, $df = 5$)
 274 and conversion type ($Q_W = 117.463$, $p < 0.001$, $df = 12$). For abundance, we similarly found
 275 high heterogeneity ($Q_T = 102.095$, $p < 0.001$, $df = 40$), which was not explained by biome (Q_W
 276 $= 3.971$, $p = 0.409$, $df = 4$), but yes for the conversion type ($Q_W = 17.532$, $p = 0.007$, $df = 6$).

We evaluated publication bias using funnel plots, which revealed asymmetry and the presence of bias in the articles evaluated, indicating that studies with smaller samples (larger standardized error) tend to be published if the result found is negative (Appendix A, Fig. A.15-A.17).

4. Discussion

Here, we synthesized the negative and neutral effects of land use changes on ants in Brazil, a significant part of the Neotropical space. In general, land use changes decrease ant diversity, mainly ant richness. Additionally, this decrease in richness is more pronounced in tropical forests and tropical savannahs. More specifically, the more significant changes in land use, such as the conversion from closed tropical forests to open agricultural systems, excluded a larger proportion of ants, decreasing richness and altering species compositions. These patterns highlight the negative impact of land use changes in tropical ecosystems, where the primary land use changes are often from closed habitats to open anthropogenic habitats, as we found. On the other hand, we only found a negative effect of conversion from savannah to annual agriculture on ant abundance. This may have occurred due to the management of these areas, due use of synthetic fertilizers and pesticides, causing negative effects on the diversity of entomofauna. Moreover, few studies have assessed the effects of land use changes on ecosystem functions and interactions. As a result, despite the decrease in species richness in anthropogenic land uses, the different effects on ecosystem functioning remain unknown. Thus, our results suggest that, to conserve most of the species' diversity, it may be important to implement management plans aimed at maintaining habitat similarity in anthropogenic land uses similar to the original habitats, also avoiding use of pesticides in agriculture systems.

Studies about land use change effects on ants in Brazil have focus on the three major Brazilian biomes and primary land use conversions, aiming to grasp ant diversity responses in these prevalent changes. However, certain biomes, vegetation types, and land uses lack adequate research and documentation, necessitating further exploration, like Caatinga (xeric shrublands),

Pantanal (flooded grasslands), and mining activities. Most of the sampling was carried out within the epigeic strata (epigeic and leaf-litter). This was primarily accomplished using pitfall traps and mini-Winkler extractors, as they provide the highest ant diversity and foraging activity (Lasmar et al. 2021a, 2023). Pitfall traps are cost-effective and simple sampling methods, applicable across diverse vegetation types and human-altered land uses (Schmidt et al., 2022). Furthermore, most samples were collected during both the rainy and dry seasons, or only during the rainy season, when ant diversity is higher (Queiroz et al., 2023). Our results show that although the sampling effort maximize ant diversity and activity, moreover the focus relies on the most common land use changes in Brazil. However, there is still a need for more studies in other biomes, vegetation types, and anthropogenic land uses, as the effects of land use changes may differ in these cases.

We observed marked species richness loss likely attributable to the presence of ecological filters (Diamond et al., 2012; Ribas et al., 2003). When forested and savannah vegetation types are transformed into open anthropogenic land uses, there is a change in conditions, such as greater temperature variation and decreased humidity, as well as a decrease in the quantity and diversity of food and nesting resources (da Silva et al., 2022; Mathieu et al., 2005; Pacheco and Vasconcelos, 2007). This change tends to favour only a few more resilient and generalist ant species, allowing them to increase their numbers if they were already present in natural habitats or invade these anthropogenic land uses (Andersen, 2019; McKinney and Lockwood, 1999). When the vegetation structure is still maintained, as in the case of converting forest to silviculture, there can still be ecological filters. Even though the conditions remain similar (*e.g.*, high forest cover), a significant portion of the resources is lost with the conversion to monoculture (Simberloff et al., 2010). For ant abundance, we only found a negative effect of the conversion from savannah to annual agriculture. This could be due to land use management, such as the use of fertilizers and insecticides, which are usual procedures in conventional

agriculture in Brazil (Dalle Laste et al., 2019). Insecticides are the second-largest driver of entomofauna loss, behind land use change (Sánchez-Bayo and Wyckhuys, 2019). Therefore, maintaining the similarity of the original habitat in anthropogenic land uses can promote the conservation of diversity. However, in some cases where the higher vegetation structure is maintained, diversity can still decrease, highlighting the importance of plant diversity for resource availability in these new habitats. Additionally, avoiding intensive management practices, such as the use of fertilizers and pesticides in agricultural systems, can also promote the conservation of diversity.

We observed no effects on species richness and abundance across various biomes and land use change types. In many instances, these outcomes might be attributed to the limited number of comparisons. Furthermore, certain anthropogenic land uses maintain conditions and resource diversity like those of biomes and vegetation types, potentially bolstering ant richness and abundance, such as conversion from grassland to pasture and from forest to perennial agriculture (Bos et al., 2007; Delabie et al., 2021; Lassau and Hochuli, 2004; Queiroz et al., 2020; Solar et al., 2015; Vasconcelos et al., 2017). Additionally, in some anthropogenic land uses, the survival of generalist ants may lead to increased abundance, resulting in a no effect of land use change on overall ant abundance (Wilker et al., 2023). Moreover, these areas often exhibit a higher presence of invasive ant species (Baidya and Bagchi, 2022; Holway et al., 2002), which tend to have higher abundances (Lester and Gruber, 2016) and may also contribute to the null effect we observed in ant abundance.

Regarding the assessment of ant abundance, it is important to consider that the term “ant abundance” may not directly reflect the actual number of individuals, but rather the foraging activity. In ants, where the colony is regarded as the individual (Wilson, 1987), the present ants are part of this collective organism. Therefore, when using methods such as “ant trapping or area-based ant counting”, it is crucial to understand that this might indicate more about foraging

activity than the true abundance of ants. Despite observing a decrease in species diversity, the quantity of ants engaged in foraging activities remained no effect in most of the comparisons, suggesting the necessity for further studies to comprehend the ecosystem functions and interactions of these ants in anthropogenic land uses. Moreover, colony counting as a method to evaluate ant abundance still poses a challenge in diversity studies, particularly due to difficulties in nest counting, especially in polydomous species. Only six studies opted to use species occurrence frequency per trap as a viable alternative to circumvent issues related to ant foraging and colony size (Brandão et al., 2011; Rizzotto et al., 2019). Moreover, it is important to acknowledge that our data might have certain biases, as there is a tendency to publish articles that report negative effects on ant assemblages, while smaller articles with null or positive results might go unpublished. This pattern of bias toward publishing articles that support our hypotheses is also found in other scientific fields, and the publication and citation of studies with neutral effects are encouraged (Mlinarić et al., 2017).

Contrary to responses related to taxonomic metrics, the impacts of land use changes on functional ecology and interactions remain uncertain. Outcomes for ecosystem functions are contingent upon the function type, vegetation type, and land use type. They may reveal a negative effect (*e.g.*, reduced seed removal when changes from grassland to silviculture; Rabello et al., 2018), a positive effect (*e.g.*, increased seed removal and insect predation when shifting from forest to pasture; Fontenele and Schmidt, 2021; Wilker et al., 2023), or null effect (*e.g.*, unchanged seed removal when changing from savannah to pasture, Rabello et al., 2018). Thus, ecosystem functions may exhibit effects different from those found for species richness (Queiroz et al., 2021; Wilker et al., 2023). Moreover, the frequent increase in invasive ants in anthropogenic land uses (Baidya and Bagchi, 2022) has a high impact on interactions with other species, increasing competition with other ants (Neumann and Pinter-Wollman, 2022) and decreasing pollinators' activity (Unni et al., 2021). Along with the decrease in pollination and

seed dispersal (Bona et al., 2023), other ant-plant interactions may also decline due to land use changes. For instance, a few ants are involved with several plant species and multiple ecosystem functions (Costa et al., 2016), which can decrease due to reduced stability caused by anthropogenic disturbance (Câmara et al., 2019) or the loss of plant resource availability (Fagundes et al., 2016). Thus, this knowledge gap regarding ecosystem functions and interactions must be addressed, given the vital role played by ants in various biomes, vegetation types, and anthropogenic land uses.

5. Conclusions

Here, we identified the negative effects of land use changes on ant diversity in Brazil, a vast Neotropical country. Although we found a greater number of studies in biomes, vegetation types, and anthropogenic land uses with a higher frequency of land use changes, we recommend more efforts in less-explored areas, such as the xeric shrublands of the Caatinga and land uses associated with mining. However, despite some biomes being underexplored, like the Pampa and Pantanal, their vegetation types can be found in more studied biomes, like the Cerrado, and can therefore serve as references for possible effects. Our meta-analysis revealed that land uses that significantly alter vegetation structure lead to a reduction in species richness, but largely maintain abundance, with a decrease in abundance occurring only in certain conversions to agriculture. From this, we emphasize the importance of management plans in areas of anthropogenic land use, maintaining habitat-specific environmental similarity (Arroyo-Rodríguez et al., 2020), supporting higher vegetation diversity to ensure resource availability and avoiding intensive use of pesticides in agricultural systems. Additionally, we suggest that future research on land use effects also focus on ecosystem functions, traits, guilds, and interactions to assess possible changes in the functioning of these new ecosystems, as well as the ecosystem services provided by species that remain in anthropogenic land uses.

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Appendix A

Keywords

English

population (Ants OR Formicidae AND Brazil OR Brazilian); **intervention/exposure** (Land use OR Farming OR Pasture OR Agriculture OR Forest plantation OR Silviculture OR Urban area OR Urbanization OR Mining); **comparator** (Biomes OR Amazon OR Atlantic Forest OR Pampa OR Caatinga OR Cerrado OR Forest OR Savanna OR Mangrove OR Wetland OR Grassland); **outcome** (Diversity OR Richness OR Abundance OR α -diversity OR β -diversity OR Community OR Assemblage OR Ecosystem function OR Ecosystem services OR Ecological role OR Functional groups OR Harvester OR Seed dispersal OR Seed removal OR Myrmecochory OR Diaspore dispersal OR Diaspore removal OR Bioturbation OR Predation OR Scaveng* OR Predator*)

Portuguese

population (Formiga* OR Formicidae AND Brasil OR Brasileir*); **intervention/exposure** (Uso do solo OR Cultivo* OR Pastage* OR Pasto* OR Agricultura OR Plantaç* florestal OR Silvicultura OR Área* urbana* OR Urbanizaç* OR Mineraç*); **comparator** (Bioma* OR Amazônia OR Mata Atlântica OR Pampa OR Caatinga OR Cerrado OR Floresta* OR Savanna* OR Manguê* OR Várzea* OR Campo*); **outcome** (Diversidade OR Riqueza OR Abundância OR α -diversidade OR β -diversidade OR Comunidade* OR Assembleia* OR Funç* ecossistêmica* OR Serviço* ecossistêmica* OR Pape* ecológico* OR Grupo* funciona* OR Granívora* OR Dispersão de semente* OR Remoção de semente* OR Mirmecocoria OR Dispersão de diásporo* OR Remoção de diásporo* OR Bioturbação OR Predação OR Detritívora* OR Predador* OR Composição de espécie*)

Spanish

population (Hormiga* OR Formicidae AND Brasil OR Brasileñ*); **intervention/exposure** (Uso del suelo OR Cultivo* OR Pasto* OR Agricultura OR Plantaci* forestal* OR Silvicultura OR Zona* urbana* OR Urbanizacion* OR Minería*); **comparator** (Biomass OR Amazonía OR Bosque Atlántico OR Pampa OR Caatinga OR Cerrado OR Bosque OR Savanna OR Manglar OR Humedal OR Campo*); **outcome** (Diversidad OR Riqueza OR Abundancia OR α -diversidad OR β -diversidad OR Comunidad OR Ensamblaje OR Función ecosistémica OR Servicio ecosistémico OR Rol ecológico OR Grupo* funcional* OR Cosechador* OR Dispersión de semilla* OR Transporte de semilla* OR Mirmecocoria OR Dispersión de diáspora* OR Transporte de diáspora* OR Bioturbaci* OR Depredación OR Carroñer* OR Depredador* OR Composición)

714 **Data sources**

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Figures of qualitative review

Fig. A.1

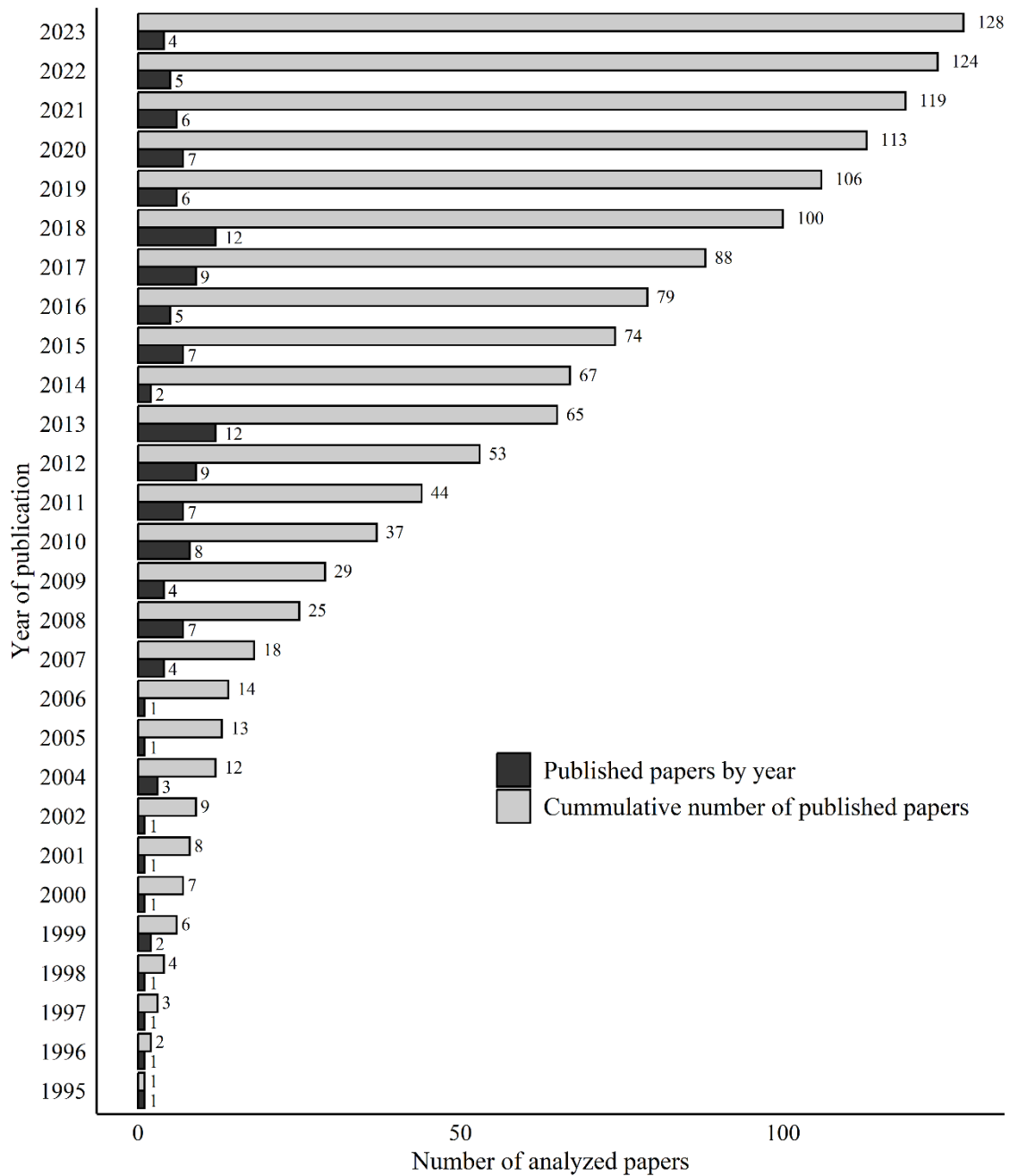


Fig. A.1. Number of analyzed studies related to ants and land use changes in Brazil.

Fig. A.2

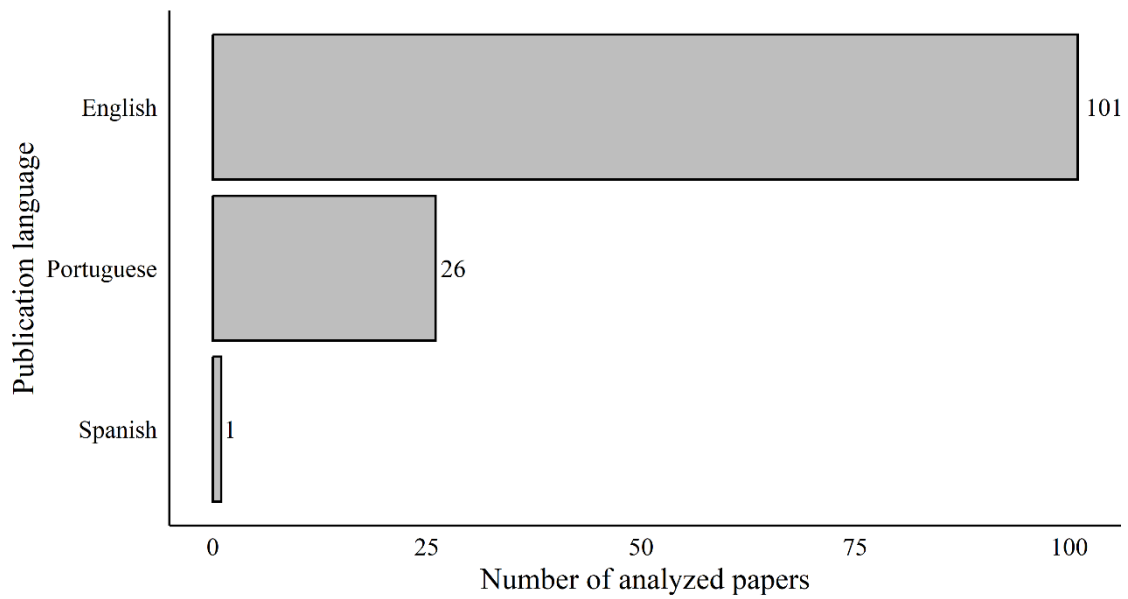
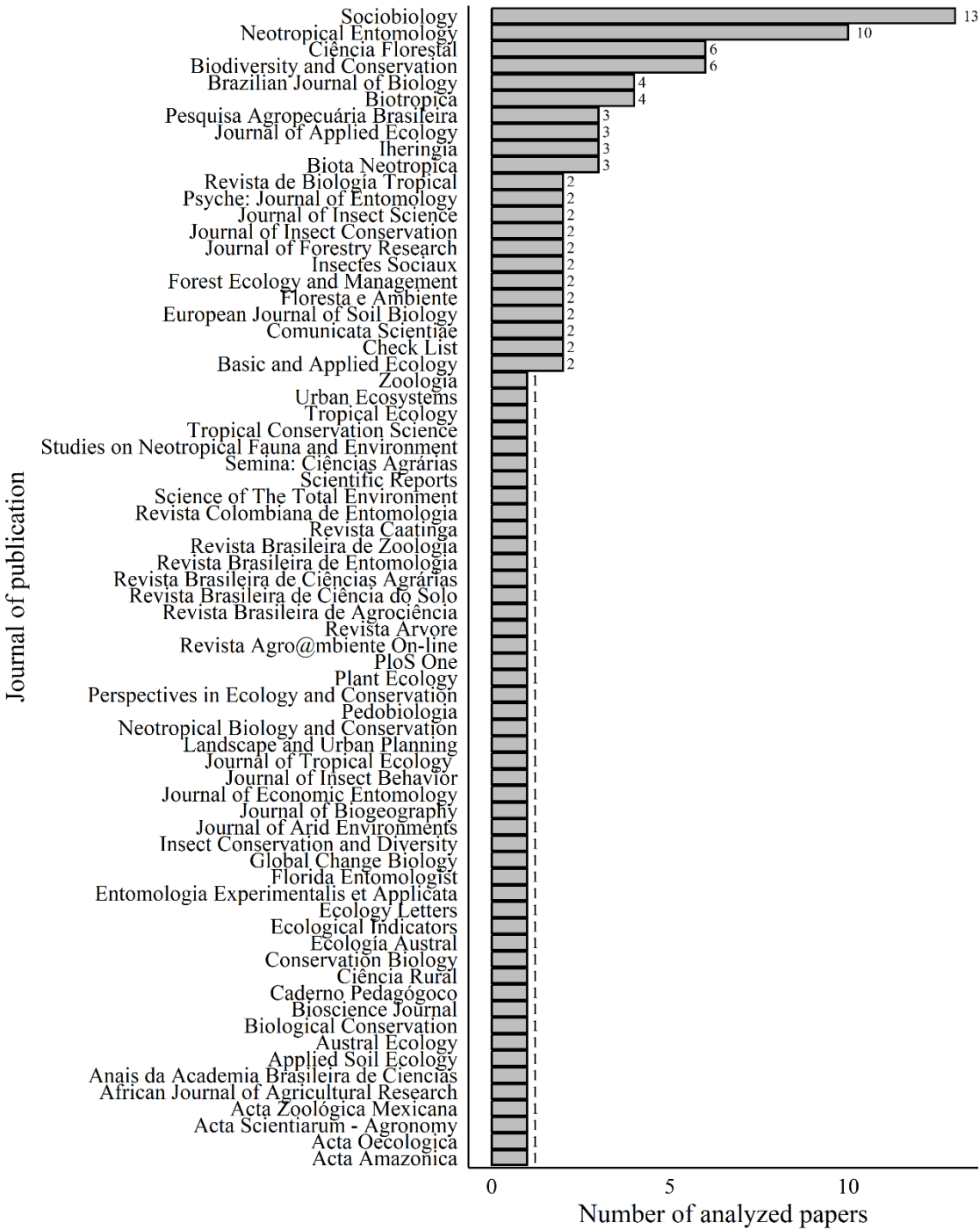


Fig. A.2. Number of analyzed studies related to ants and land use changes in Brazil.

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1204 Fig. A.3. Number of analyzed studies related to ants and land use changes in Brazil.

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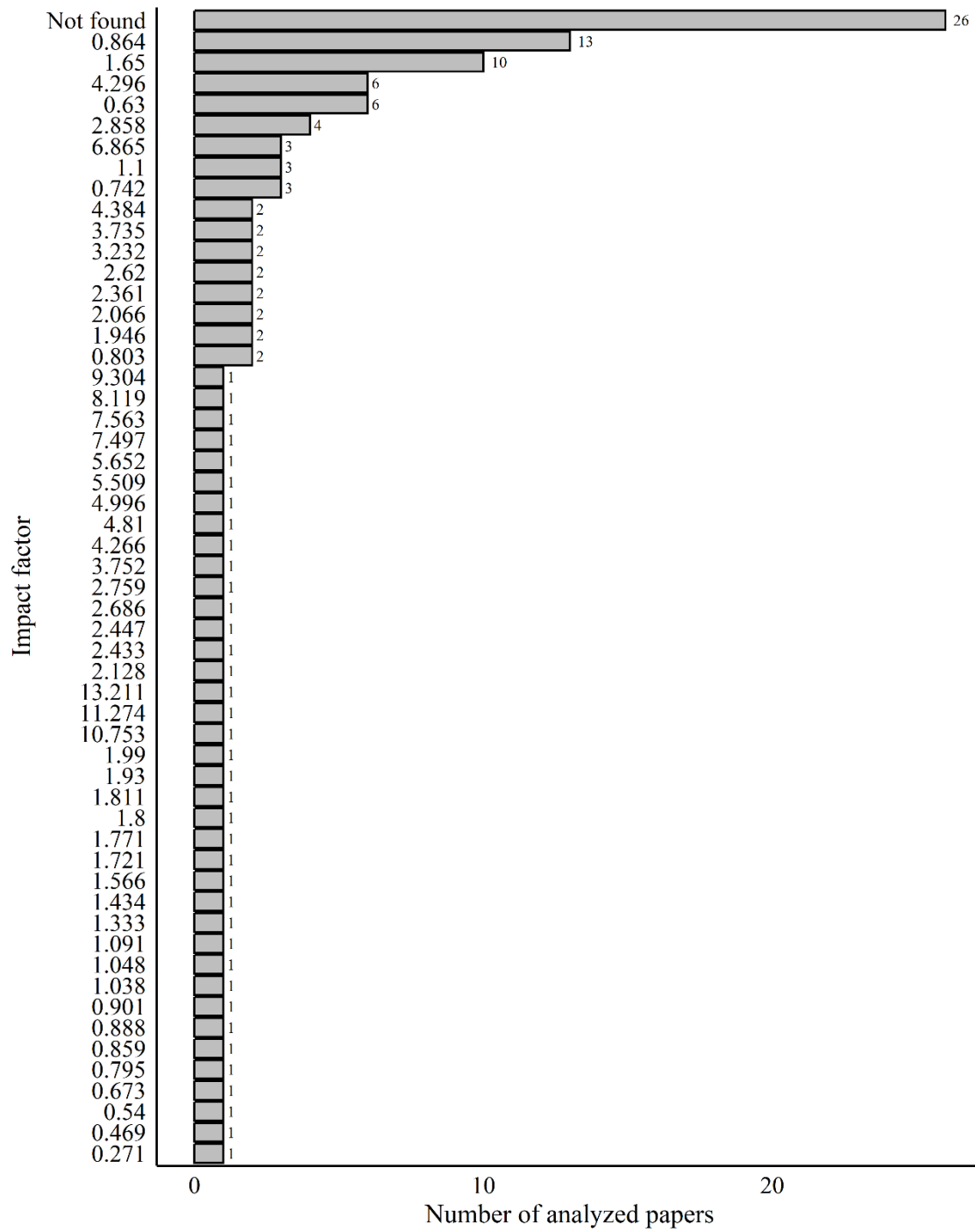
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1210 Fig. A.4



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1212 Fig. A.4. Number of analyzed studies related to ants and land use changes in Brazil. “Not found”
 1213 means that the impact factor is not found for the journal.

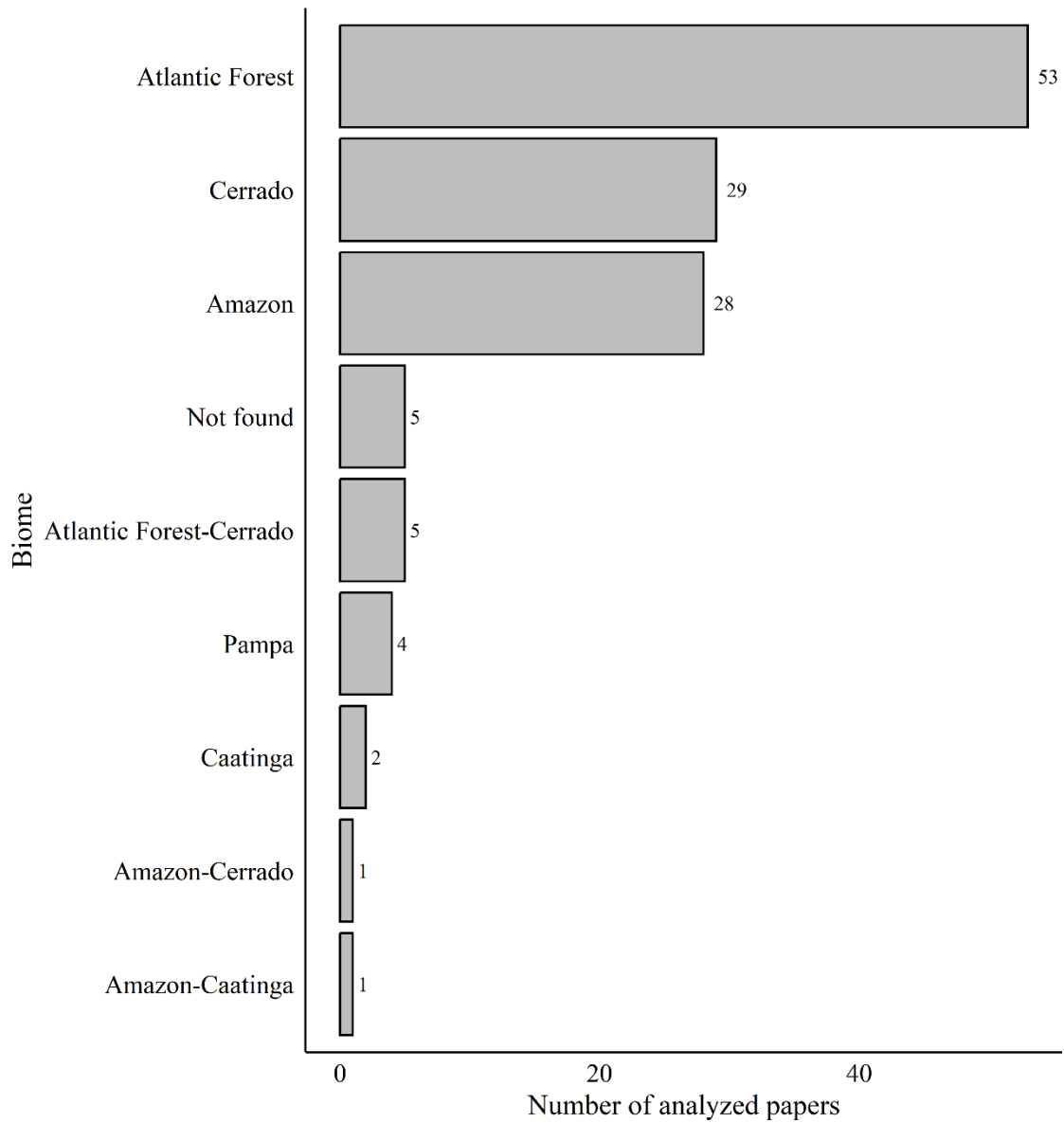
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1218 Fig. A.5



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1220 Fig. A.5. Number of analyzed studies related to ants and land use changes in Brazil. “Atlantic
 1221 Forest-Cerrado”, “Amazon-Cerrado”, and “Amazon-Caatinga” means collection in two
 1222 biomes. “Not found” means that the biome is not found in the article.

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Fig. A.6

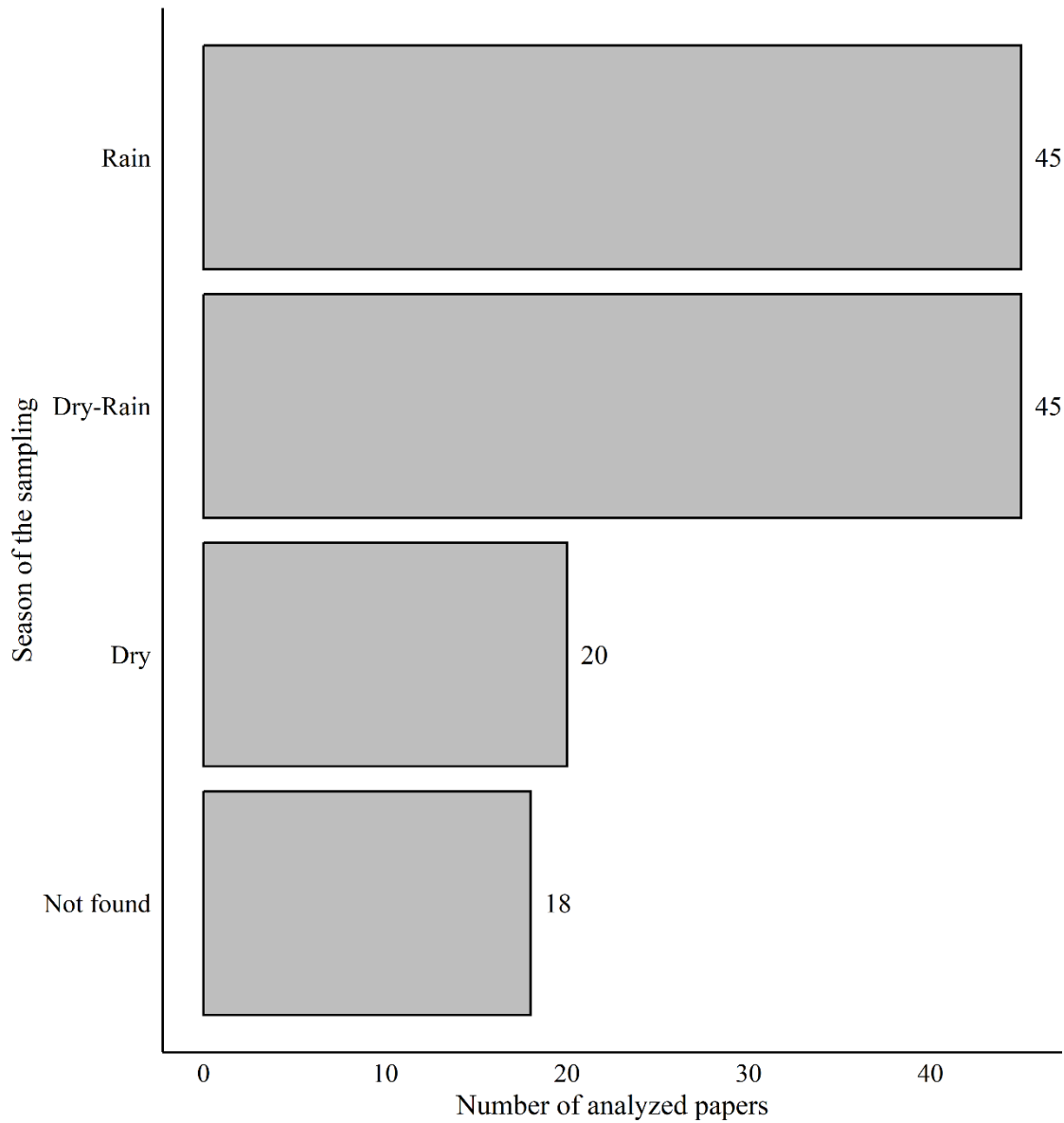
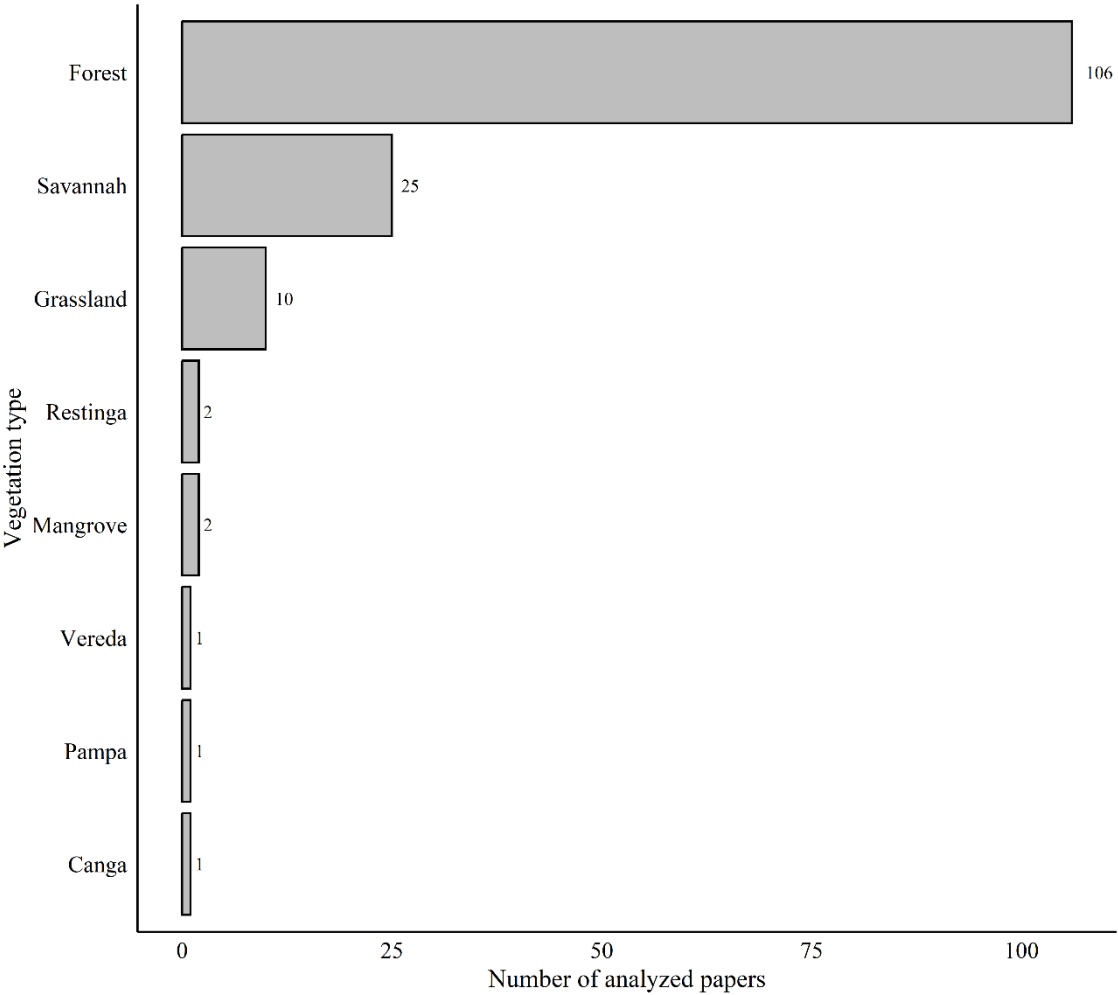


Fig. A.6. Number of analyzed studies related to ants and land use changes in Brazil. “Dry-Rain” means collection in two periods (rain and dry). “Not found” means that the climate seasonality is not found in the article.

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1244 Fig. A.7. Number of analyzed studies related to ants and land use changes in Brazil.

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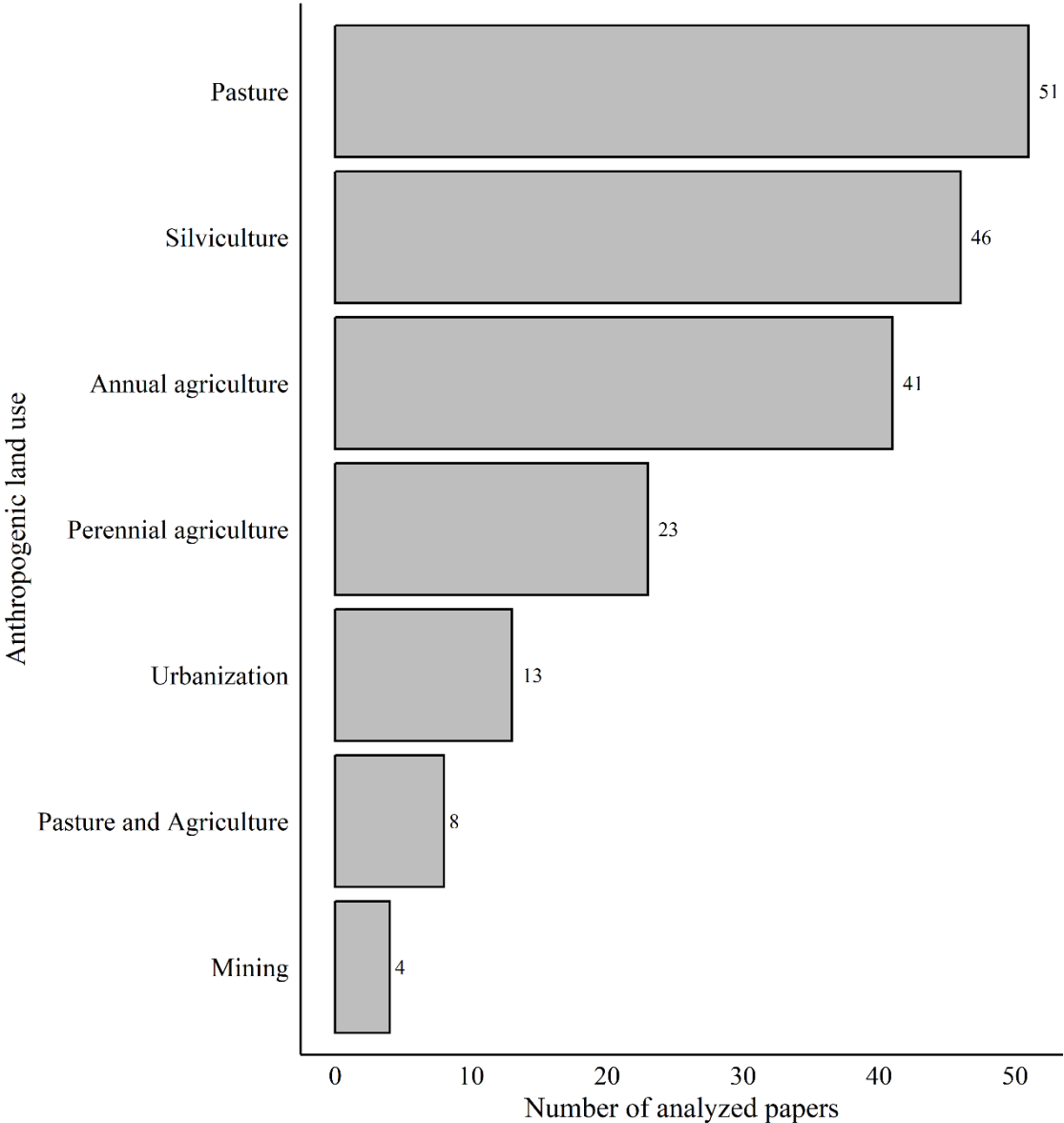
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1256 Fig. A.8



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1258 Fig. A.8. Number of analyzed studies related to ants and land use changes in Brazil.

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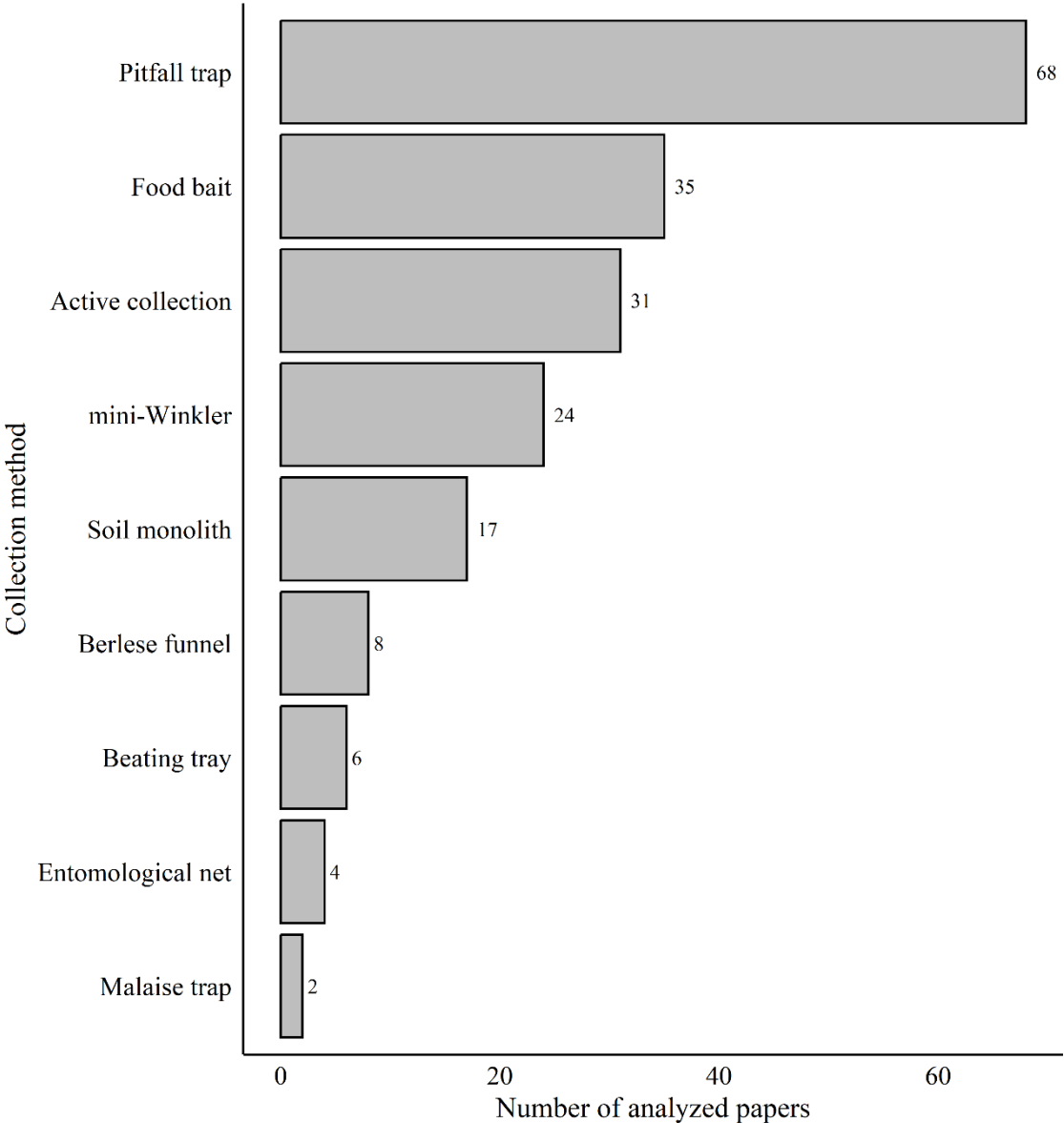
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1267 Fig. A.9



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1269 Fig. A.9. Number of analyzed studies related to ants and land use changes in Brazil.

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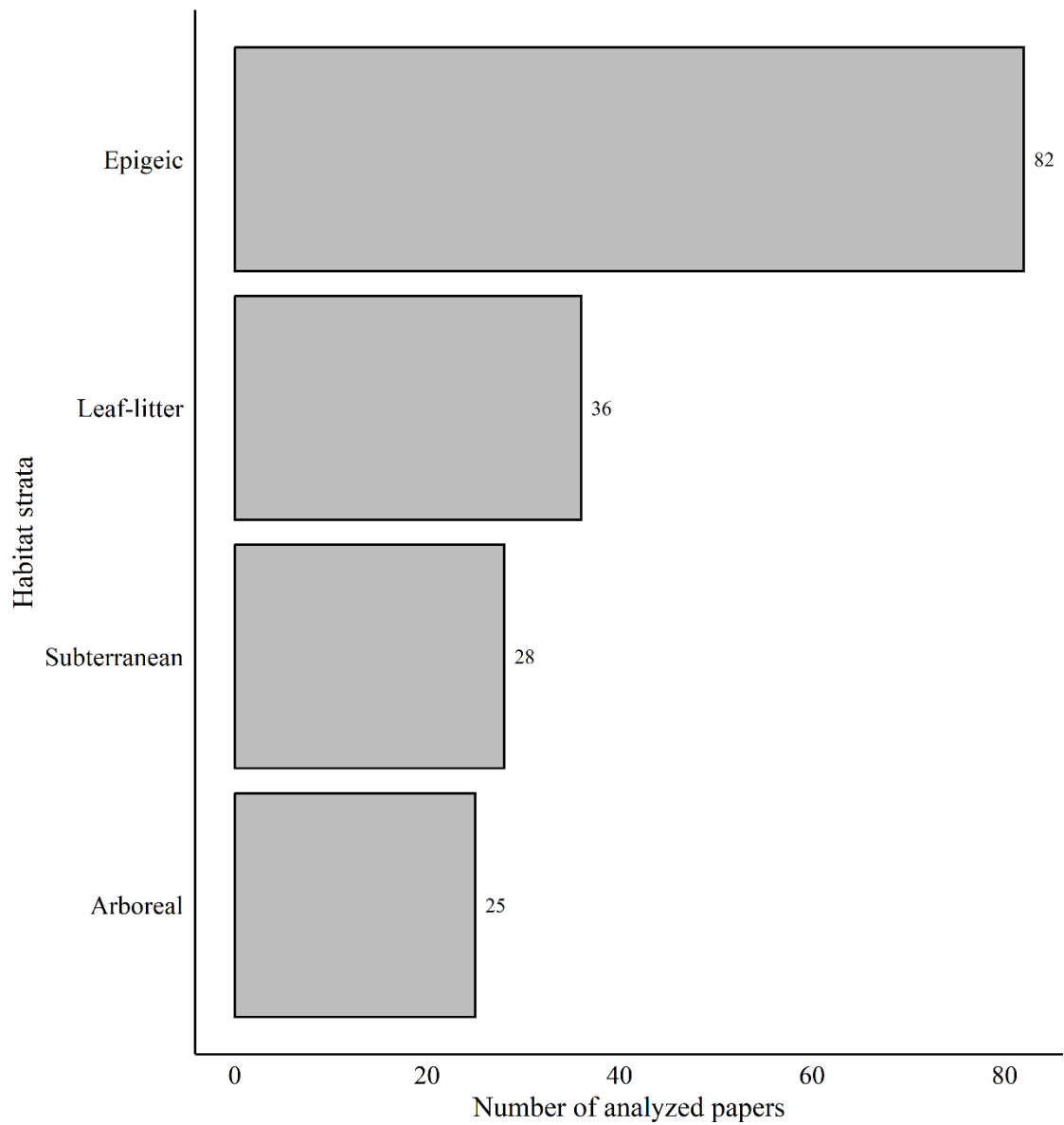
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1278 Fig. A.10



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1280 Fig. A.10. Number of analyzed studies related to ants and land use changes in Brazil.

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Fig. A.11

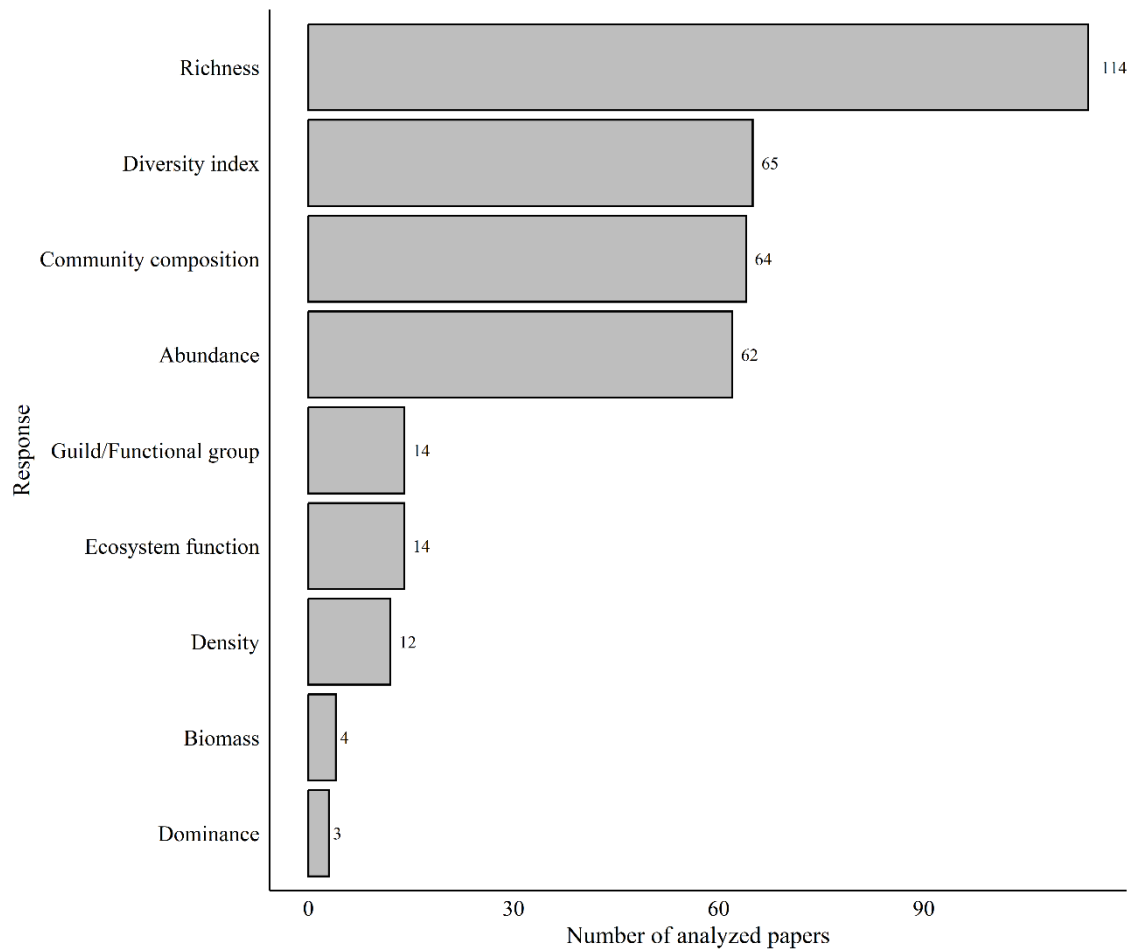
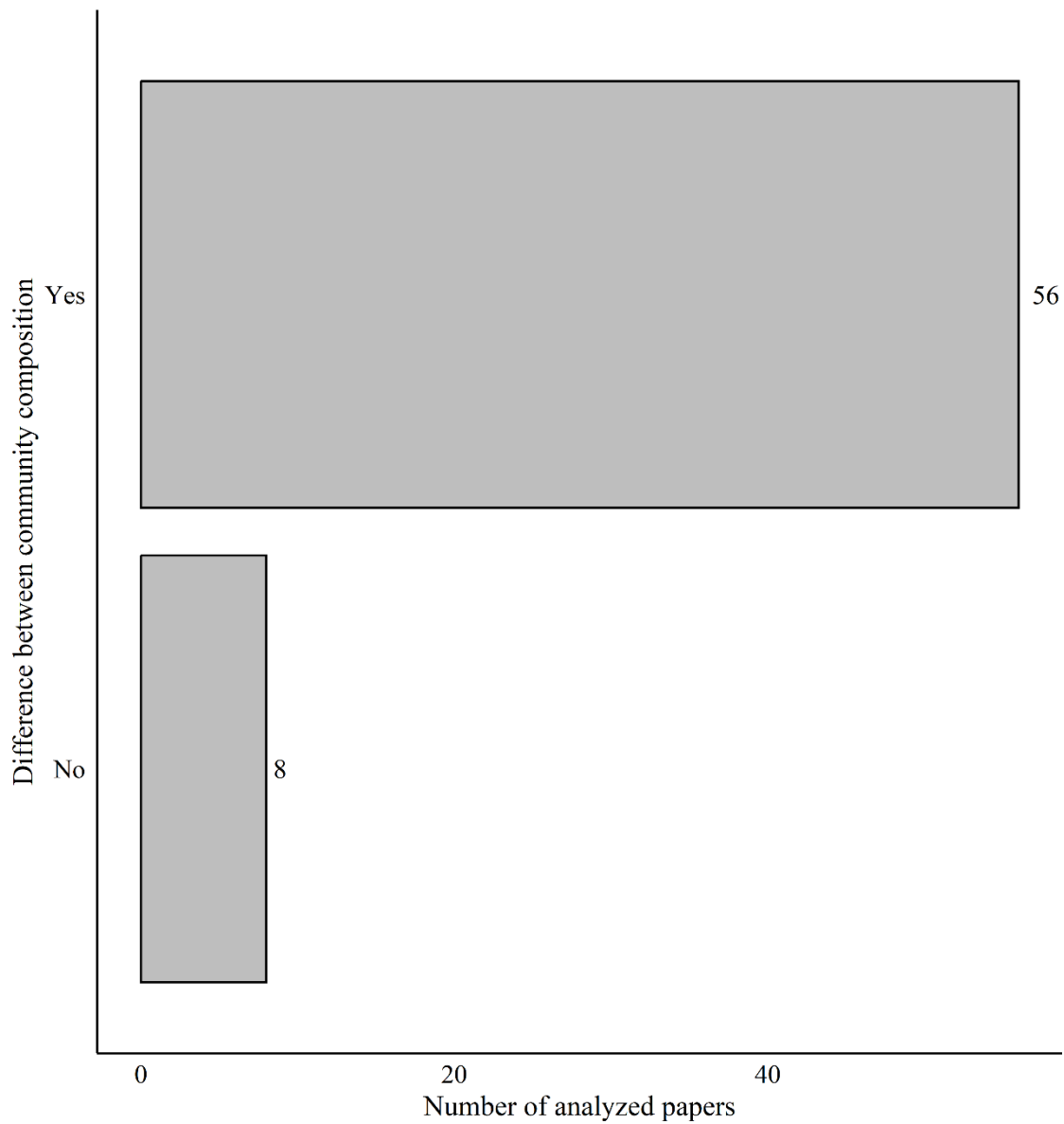


Fig. A.11. Number of analyzed studies related to ants and land use changes in Brazil.

1304 Fig. A.12



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1306 Fig. A.12. Number of analyzed studies related to ants and land use changes in Brazil. The bars
1307 indicate the difference of community composition between natural habitat and anthropogenic
1308 land use.

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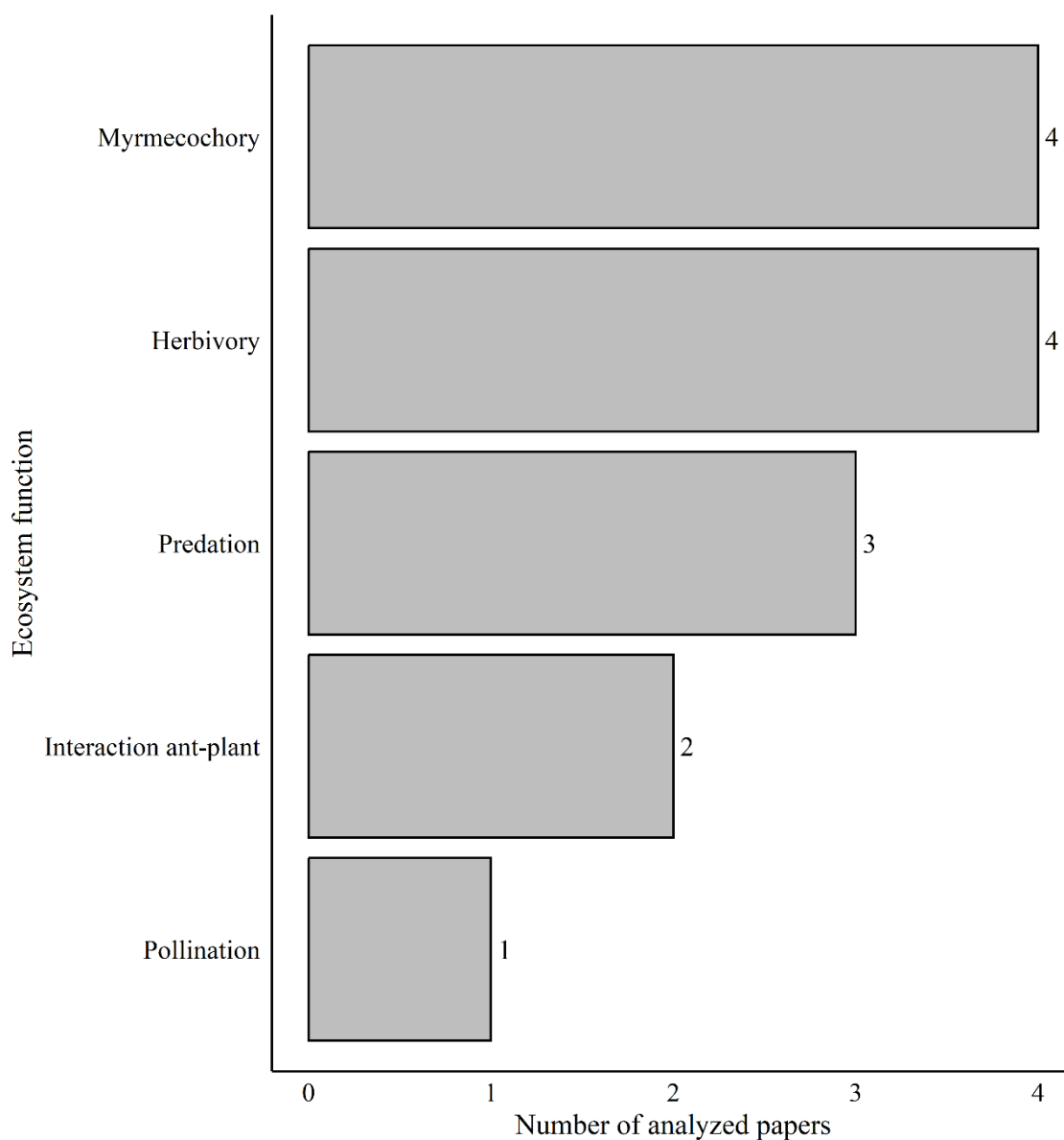
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1318 Fig. A.13. Number of analyzed studies related to ants and land use changes in Brazil.

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Fig. A.14

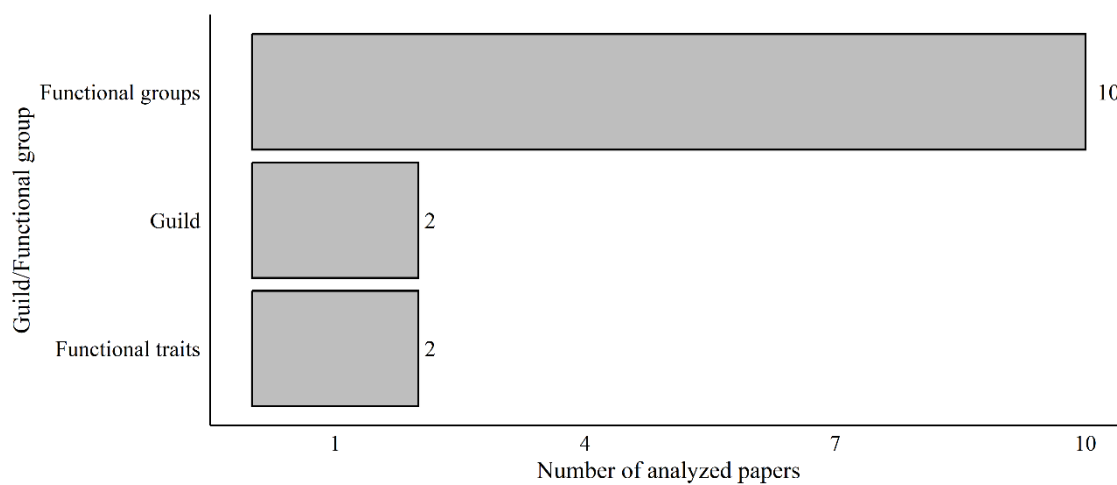
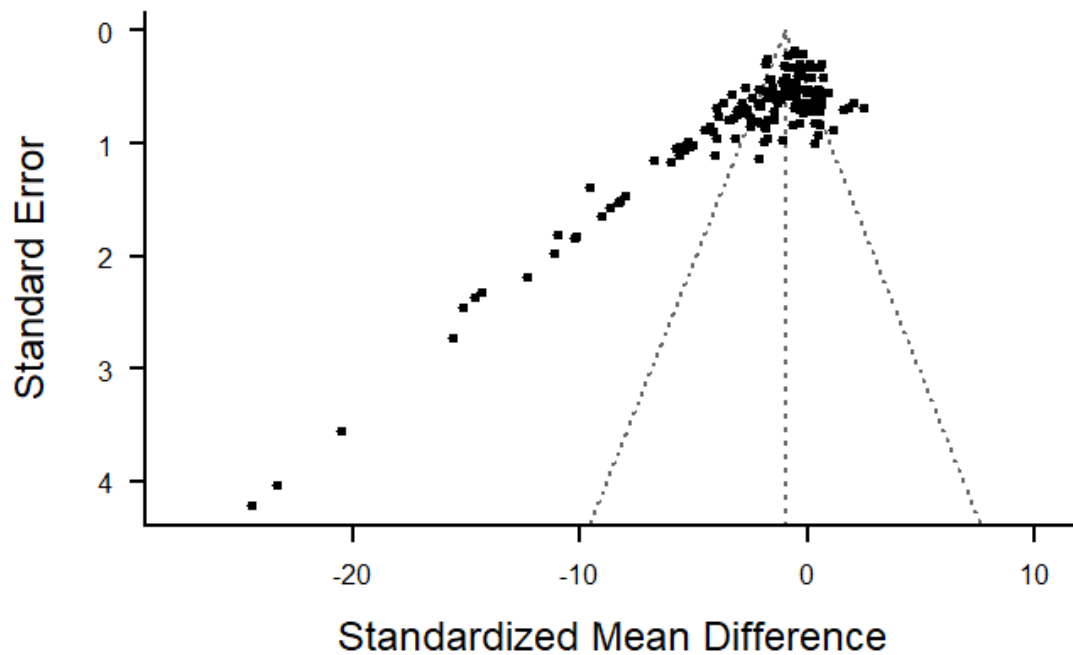


Fig. A.14. Number of analyzed studies related to ants and land use changes in Brazil.

1349 **Funnel plots**

1350 Fig. A.15



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1352 Fig. A.15. Funnel plot for richness of the meta-analysis of published studies on the conversion
1353 of natural land use to anthropogenic land use in ant richness. The x-axis indicates de Observed
1354 outcome (standardized mean difference), and the y-axis indicates standard error. The white
1355 triangle represents the region where 95% of the data points would lie in the absence of a
1356 publication bias.

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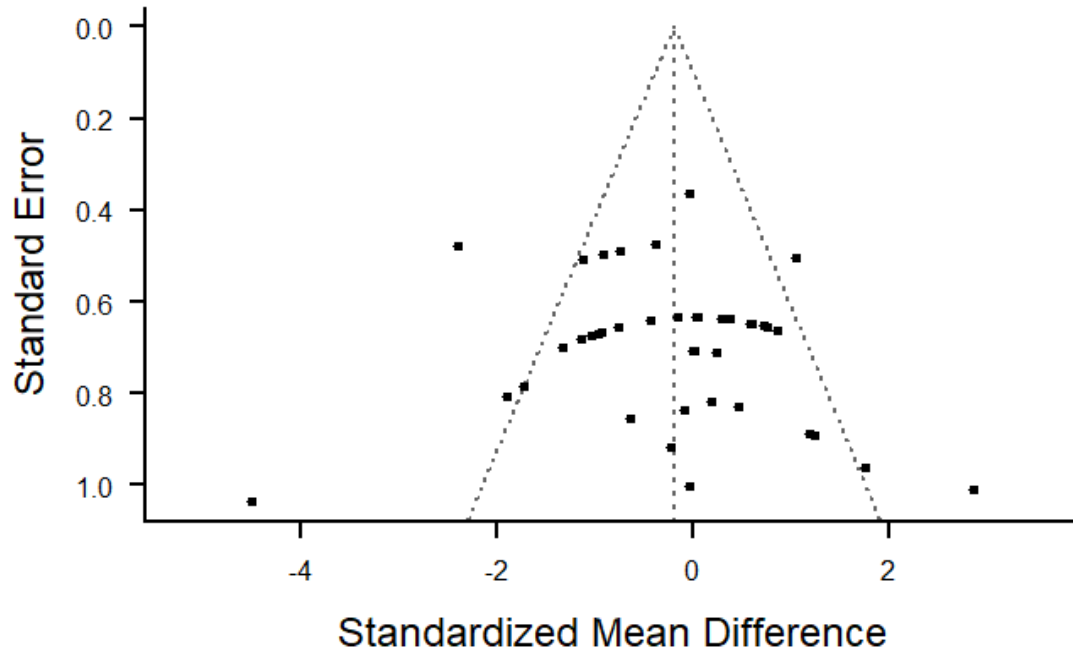
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1367 Fig. A.16



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1369 Fig. A.16. Funnel plot for abundance of the meta-analysis of published studies on the
 1370 conversion of natural land use to anthropogenic land use in ant abundance. The x-axis indicates
 1371 de Observed outcome (standardized mean difference), and the y-axis indicates standard error.
 1372 The white triangle represents the region where 95% of the data points would lie in the absence
 1373 of a publication bias.

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Fig. A.17

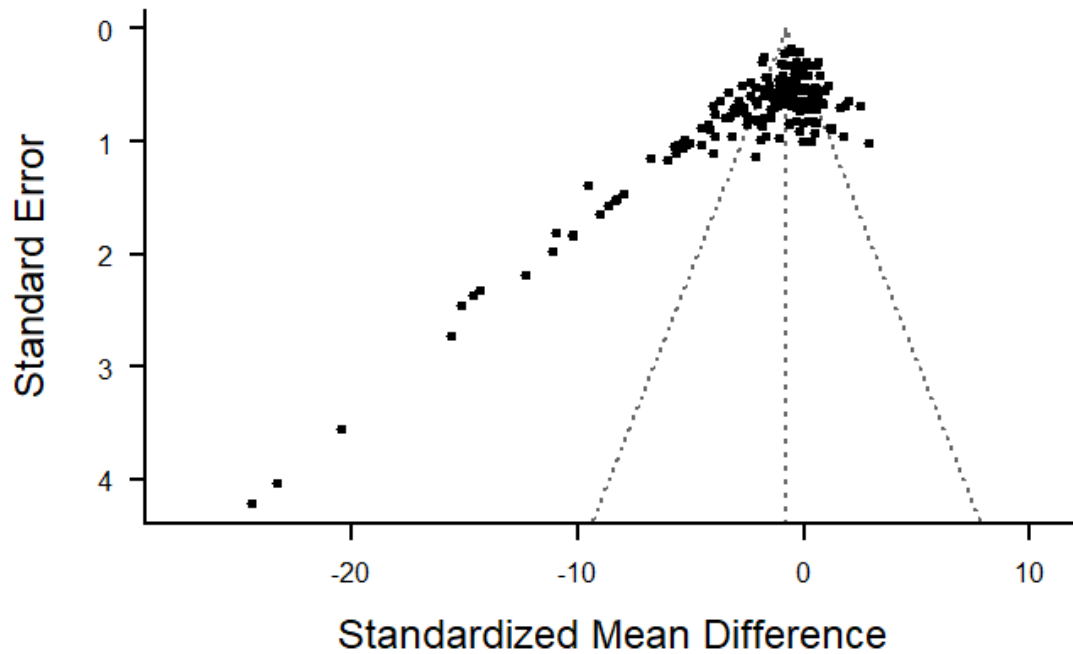


Fig. A.17. Overall funnel plot of the meta-analysis of published studies on the land use changes on ants in Brazil indicating publication bias. The x-axis indicates the Observed outcome (standardized mean difference), and the y-axis indicates standard error. The white triangle represents the region where 95% of the data points would lie in the absence of a publication bias. The funnel indicates that studies with smaller sample sizes (larger standardized error) tend to be published if the result found is negative.

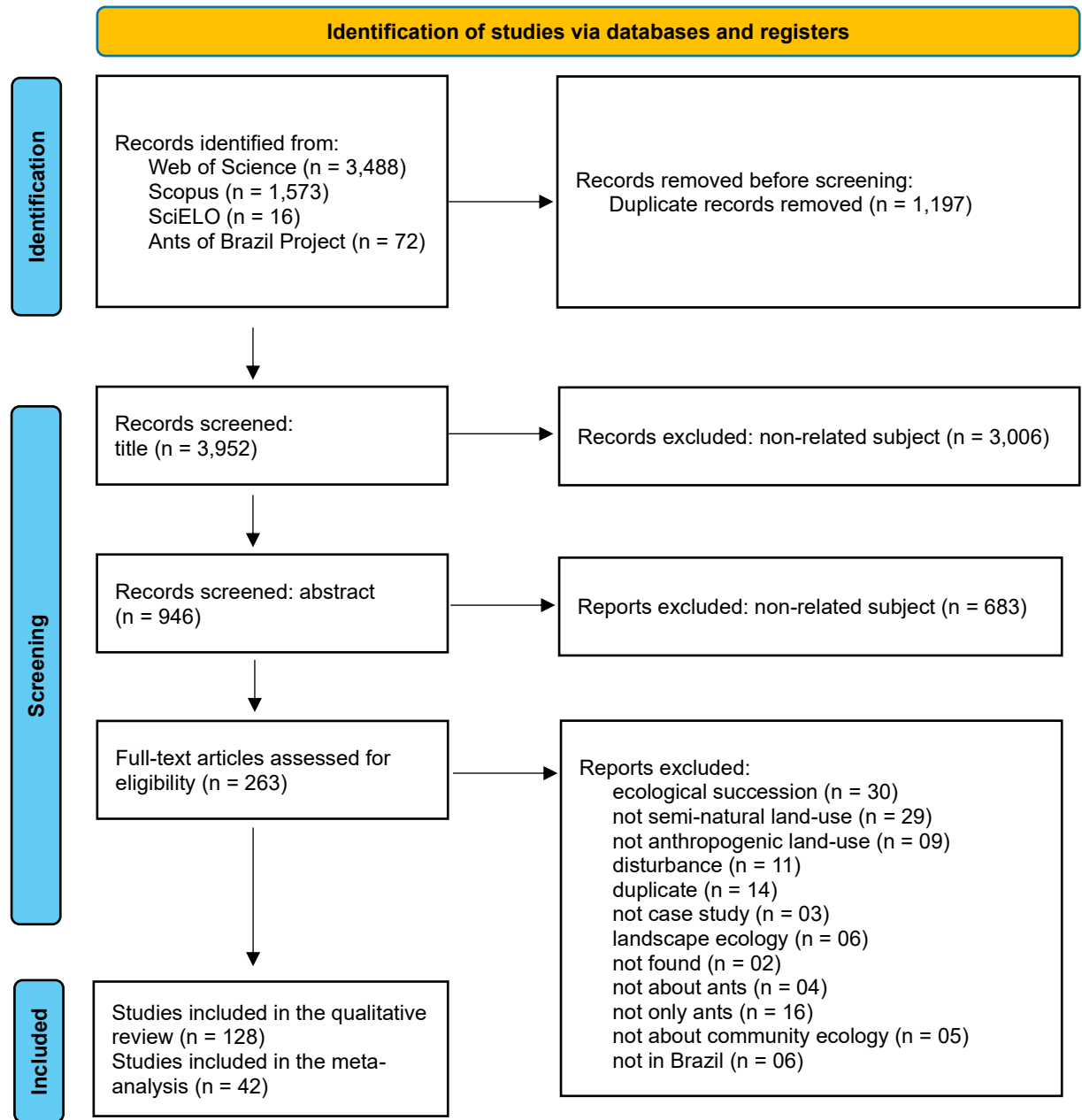
Table A.1. Effect size (E++; Hedges' g, J-corrected form) and confidence intervals (ci.lb: lower bound of the confidence intervals; ci.ub: upper bound of the confidence intervals) for meta-analysis on effects of land use changes with vegetation type moderator. "pval" indicate p value and "p<0.050" indicate significance code "****" to p value < 0.001, "***" to p value = 0.001 and "**" to p value < 0.050. "ns" indicate statistically non-significant.

Biome	E++	ci.lb	ci.ub	pval	p<0.05
Richness					
Amazon	-1.0549	-1.7286	-0.3812	0.0021	**
Atlantic Forest	-0.6516	-1.1643	-0.1390	0.0127	*
Atlantic Forest-Cerrado	-0.1702	-1.4510	1.1106	0.7945	ns
Cerrado	-1.4942	-2.0783	-0.9101	<.0001	***
Pampa	-0.7382	-2.1260	0.6496	0.2971	ns
Abundance					
Amazon	-0.9350	-3.2131	1.3432	0.4212	ns
Atlantic Forest	0.4941	-0.4737	1.4619	0.3170	ns
Atlantic Forest-Cerrado	-0.5038	-2.7366	1.7289	0.6583	ns
Cerrado	-0.8305	-1.9464	0.2854	0.1446	ns

Table A.2. Effect size (E++; Hedges' g, J-corrected form) and confidence intervals (ci.lb: lower bound of the confidence intervals; ci.ub: upper bound of the confidence intervals) for meta-analysis on effects of land use changes with natural ecosystem moderator. "pval" indicate p value and "p<0.050" indicate significance code "****" to p value < 0.001, "***" to p value = 0.001 and "*" to p value < 0.050. "ns" indicate statistically non-significant.

Land-use change type	E++	ci.lb	ci.ub	pval	p<0.05
Richness					
Forest to Annual agriculture	-1.0470	-1.5399	-0.5540	<.0001	***
Forest to Pasture	-0.7776	-1.2409	-0.3143	0.0010	**
Forest to Perennial agriculture	-0.6824	-1.3793	0.0146	0.0550	ns
Forest to Silviculture	-0.6847	-1.1522	-0.2172	0.0041	**
Forest to Urbanization	-2.3533	-3.9813	-0.7253	0.0046	**
Savannah to Annual agriculture	-0.9282	-1.7453	-0.1111	0.0260	*
Savannah to Pasture	-1.4501	-2.0835	-0.8167	<.0001	***
Savannah to Silviculture	-1.8633	-2.5047	-1.2220	<.0001	***
Savannah to Urbanization	-2.7566	-3.8982	-1.6150	<.0001	***
Grassland to Pasture	0.5893	-0.0439	1.2226	0.0681	ns
Grassland to Perennial agriculture	-0.8206	-2.5454	0.9042	0.3511	ns
Grassland to Silviculture	0.5165	-0.1575	1.1904	0.1331	ns
Abundance					
Forest to Annual agriculture	-0.5558	-1.4137	0.3022	0.2042	ns
Forest to Pasture	0.0367	-0.7962	0.8695	0.9312	ns
Forest to Silviculture	0.1016	-0.6232	0.8264	0.7835	ns
Savannah to Annual agriculture	-1.2261	-2.3209	-0.1312	0.0282	*
Savannah to Pasture	0.3573	-0.5819	1.2966	0.4559	ns
Savannah to Silviculture	-0.7927	-1.6420	0.0567	0.0674	ns

Appendix B



*Consider, if feasible to do so, reporting the number of records identified from each database or register searched (rather than the total number across all databases/registers).

**If automation tools were used, indicate how many records were excluded by a human and how many were excluded by automation tools.

From: Page MJ, McKenzie JE, Bossuyt PM, Boutron I, Hoffmann TC, Mulrow CD, et al. The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. BMJ 2021;372:n71. doi: 10.1136/bmj.n71

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TERCEIRA PARTE

CONSIDERAÇÕES FINAIS

Nesta tese, encontrei importantes resultados para a ecologia de comunidades e ecossistemas, abordando os impactos dos usos do solo em ambientes tropicais. Avancei na compreensão da ecologia trófica e funcional ao identificar que as formigas modificam suas preferências por recursos alimentares dependendo do bioma e do tipo de uso do solo. Por exemplo, observamos maior forrageamento por aminoácidos na Mata Atlântica em comparação ao Cerrado, sugerindo que formigas da Mata Atlântica são mais limitadas por aminoácidos. Também encontrei uma relação positiva entre o consumo de recursos energéticos e a predação de insetos, sugerindo que formigas predadoras apresentam limitações energéticas. Adicionalmente, verifiquei que os usos do solo afetam direta e indiretamente a função de predação de insetos, sendo esse efeito mediado pela riqueza geral de espécies e pela riqueza de formigas predadoras.

Adicionalmente, fiz uma revisão sistemática com meta-análise e constatei que, no Brasil, usos do solo mais contrastantes (por exemplo, a conversão de florestas para pastagens) reduzem drasticamente a riqueza de formigas e alteram a composição das espécies. Esse tipo de impacto é especialmente evidente nos biomas Amazônia, Cerrado e Mata Atlântica, sendo os dois últimos considerados *hotspots* globais de biodiversidade. No entanto, identifiquei lacunas no conhecimento sobre os efeitos dos usos do solo no Brasil, como a escassez de estudos sobre interações tróficas e funções ecossistêmicas, além do baixo número de estudos em biomas como Caatinga, Pantanal e Pampa.

De maneira geral, identifiquei que as alterações no uso do solo causam impactos negativos significativos nas comunidades terrestres, especialmente em conversões entre habitats com estruturas contrastantes. Diante disso, considero fundamental que as avaliações desses impactos levem em conta o contexto espacial das comunidades, abrangendo tipos de habitat, vegetação e biomas. Além disso, os efeitos do uso do solo podem se manifestar de forma direta e indireta, influenciando as atividades de forrageio e funções ecossistêmicas, onde o mecanismo principal pode ser a perda de riqueza de espécies e alteração na composição de espécies. Assim, como estratégia prática de conservação, evitar conversões extremas no uso do solo pode minimizar impactos negativos sobre a biodiversidade, tanto na conservação de espécies quanto no funcionamento dos ecossistemas. Isso não apenas contribui para a preservação da riqueza e composição das espécies, mas também ajuda a mitigar efeitos adversos sobre funções e serviços ecossistêmicos em habitats antropizados, promovendo a conservação da biodiversidade em ambientes naturais.

Por fim, as mídias de divulgação científica da tese buscam aproximar o conhecimento acadêmico do público em geral, despertando a curiosidade de pessoas fora da universidade sobre a ecologia. A notícia veiculada no Portal da Ciência da UFLA apresentou, de forma acessível, como os usos do solo no Brasil impactam a fauna de formigas, destacando a relevância da manutenção de áreas antropizadas próximas ao habitat nativo original. A notícia foi publicada em 09 janeiro de 2025, e até então, possui 673 acessos. Além disso, como popularização da ciência, desenvolvi um jogo de cartas com livro de regras ilustrado sobre interações tróficas e efeitos de impactos antrópicos no Cerrado, voltados principalmente para crianças a partir de oito anos e professores do ensino básico. Esses materiais têm o objetivo de auxiliar no ensino de cadeias alimentares de maneira lúdica e dinâmica.

APÊNDICE A – Mídias de divulgação

Pesquisa da UFLA analisa como as mudanças nos usos do solo afetam a diversidade de formigas no Brasil

Notícia escrita por Mayara Mesquita Silva

A primeira mídia de divulgação desta tese é uma notícia publicada no Portal da Ciência da UFLA, voltada principalmente para o público adulto. Nela, apresentamos de forma acessível a revisão sistemática com meta-análise publicada na revista *Biological Conservation*. Explicamos de maneira clara como o estudo foi conduzido e destacamos seus principais resultados.

Link da notícia: <https://ciencia.ufla.br/reportagens/meio-ambiente/1046-pesquisa-da-ufla-analisa-como-as-mudancas-nos-usos-do-solo-afetam-a-diversidade-de-formigas-no-brasil>

Figura 1 – Postagem da notícia no Instagram



Legenda: Primeira imagem da postagem do perfil @cienciaufla no Instagram sobre a notícia da revisão sistemática do Formigas do Brasil.

Fonte: Universidade Federal de Lavras (2024).

Guardiões do Cerrado: Entre Predadores e Presas

Icaro Wilker, Dara V. Alves, Guilherme P. Alves, Chaim J. Lasmar, Antônio C. M. Queiroz, Marília M. S. Costa, Carla R. Ribas

A segunda mídia de divulgação desta tese é um jogo de cartas de duelo ambientado no bioma Cerrado. O jogo explora relações tróficas, onde herbívoros atacam plantas, predadores atacam herbívoros e assim por diante, tornando o aprendizado sobre ecologia dinâmico e acessível ao público fora da academia. Além das relações tróficas, incluímos cartas de mutualismo, competição e decomposição, ampliando a compreensão das interações ecológicas. Cartas de habitat natural fortalecem as espécies, enquanto impactos antrópicos as enfraquecem, abordando a conservação da biodiversidade. O jogo e o livro de regras serão disponibilizados gratuitamente *online*, com foco especial em professores e alunos do 4º ano do ensino fundamental, alinhando-se a três das cinco habilidades da BNCC¹.

Figura 1 – Exemplo de carta



Legenda: Exemplo de uma carta de Planta do jogo de baralho sobre interações tróficas.

Fonte: Wilker (2025)

(EF04CI04): Analisar e construir cadeias alimentares simples, reconhecendo a posição ocupada pelos seres vivos nessas cadeias e o papel do Sol como fonte primária de energia na produção de alimentos;

(EF04CI05): Descrever e destacar semelhanças e diferenças entre o ciclo da matéria e o fluxo de energia entre os componentes vivos e não vivos de um ecossistema;

(EF04CI06): Relacionar a participação de fungos e bactérias no processo de decomposição, reconhecendo a importância ambiental desse processo.

¹BRASIL. Ministério da Educação. **Base Nacional Comum Curricular**. Brasília, DF: MEC, 2018.