UNIVERSIDADE FEDERAL DE LAVRAS

CHAIM JOSÉ LASMAR

BRAZILIAN ANTS: THE ROLE OF ECOLOGICAL FACTORS ON THEIR DIVERSITY AND FORAGING ACTIVITY PATTERNS

LAVRAS – MG
2020

CHAIM JOSÉ LASMAR

BRAZILIAN ANTS: THE ROLE OF ECOLOGICAL FACTORS ON THEIR DIVERSITY AND FORAGING ACTIVITY PATTERNS

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

Dra. Carla Rodrigues Ribas
Orientadora

Dra. Catherine Lucy Parr
Co-orientadora

Dr. Fernando Augusto Schmidt
Co-orientador

LAVRAS – MG
2020

Ficha catalográfica elaborada pelo Sistema de Geração de Ficha Catalográfica da Biblioteca Universitária da UFLA, com dados informados pelo(a) próprio(a) autor(a).

Lasmar, Chaim José.
Brazilian ants: the role of ecological factors on their diversity and foraging activity patterns / Chaim José Lasmar. - 2020.
98 p.

Orientador(a): Carla Rodrigues Ribas.
Coorientador(a): Catherine Lucy Parr, Fernando Augusto Schmidt.
Tese (doutorado) - Universidade Federal de Lavras, 2020.
Bibliografia.

1. Ecologia Teórica. 2. Macroecologia. 3. Ecologia Nutricional. I. Ribas, Carla Rodrigues. II. Parr, Catherine Lucy. III. Schmidt, Fernando Augusto. IV. Título.

CHAIM JOSÉ LASMAR

BRAZILIAN ANTS: THE ROLE OF ECOLOGICAL FACTORS ON THEIR DIVERSITY AND FORAGING ACTIVITY PATTERNS

FORMIGAS BRASILEIRAS: O PAPEL DOS FATORES ECOLÓGICOS NOS SEUS PADRÕES DE DIVERSIDADE E ATIVIDADE DE FORRAGEIO

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

APROVADA em 15 de janeiro de 2020

Dra. Fernanda Vieira da Costa	UFOP
Dr. José Henrique Schoereder	UFV
Dr. Renato Gregorin	UFLA
Dra. Tatiana Garabini Cornelissen	UFMG

Dra. Carla Rodrigues Ribas
Orientadora

Dra. Catherine Lucy Parr
Co-orientadora

Dr. Fernando Augusto Schmidt
Co-orientador

LAVRAS – MG
2020

À minha família e ao Boni.

Dedico

AGRADECIMENTOS

A todas as instituições públicas de ensino, gratuitas e de qualidade onde tive minha formação; Creche do Posto de Puericultura (pré-escola); Escola Estadual Conego Ulisses e Escola Estadual Professor José Monteiro (Ensino Fundamental); Escola Estadual Padre Alberto Fuger (Ensino médio); Universidade Federal de Lavras (graduação, mestrado e doutorado). A todas(os) as(os) educadoras(es) e funcionárias(os) de todas as instituições acima citadas(os). Em especial às professoras Cristina (pré-escola), Marcia Vilela e Regina Vilela (ensino fundamental) que me despertaram o interesse pela ciência, ao professor Aladir dos Santos (ensino médio), às(os) professoras(es) Júlio Louzada, Mariana Mansanares, Lucas del Bianco, Renato Gregorin, Marcelo Passamani e Eduardo van den Berg (graduação, mestrado e doutorado).

À Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) pelas bolsas durante o doutorado no país e no exterior (PDSE). À Fundação de Amparo e Pesquisa de Minas Gerais (FAPEMIG) e à *Rufford Foundation's Small Grants* pelo financiamento do meu projeto de doutorado.

Ao Julio Louzada, Luke Parry e Rodrigo Feitosa, por tirarem um tempo para escrever uma carta de referência que foi providencial para conseguir financiamento para o projeto de doutorado.

Às muitas pessoas que se dispuseram a me ajudar durante minhas campanhas de campo, Agnis Souza, Ariel Reis, Clarissa da Rosa, Cynthia Oliveira, Elisa Silva, Icaro Carvalho, Jonas Aguiar, Marcos Mendes, Mariana Rabelo, Marina Angotti, Mayara Imata, Rafael Souza, Rafael Cuissi e Sabrina Farsura. Muito muito obrigado por tudo e, principalmente, pelos bons momentos vividos.

A todas as pessoas que conheci e ajudaram de alguma forma com o trabalho dentro e fora das unidades de conservação, em especial Dalva Junior Alves, Lucas Ruffi, Maurício Scherer, Martin Acosta, Alejandro Cuevas, Seu Adolfo e Genivaldo.

Às(os) amigas(os) e colegas do Laboratório de Sistemática de Formigas da UFPR pela confirmação da identificação das formigas. Em especial ao Rodrigo Feitosa e Alexandre Ferreira, meu muito obrigado por toda ajuda durante minha formação e principalmente por me receber tão bem em Curitiba.

Aos membros da banca, Fernanda Costa, José Schoereder, Lucas Paolucci, Renata Campos, Renato Gregorin, Tatiana Cornellissen, pela disponibilidade e contribuição para com o trabalho.

Ao Programa de Pós-Graduação em Ecologia Aplicada e todas(os) as(os) funcionárias(os), em especial a Ellen Carvalho, Marlene e DomFênica Cristiane.

Ao Ismael Siqueira por me lembrar como é brincar de ser cientista.

Às(os) amigas(os) e colegas que fiz na Ecologia, em especial Cássio Nunes, Filipe França, Yojana Irina, Laís Maia, Mardiany Ribeiro, André Tavares e Wallace Beiroz.

I am very thankful for being part of Funky Ant Lab and for meeting wonderful people during my internship in the University of Liverpool. Thanks specially to Tom Bishop, Steph Law and Alice Walker.

I am grateful for two families that I have got when living in Liverpool. To my British family, Rebecca, Finbar and Fred Russell, thanks for all good moments that I will always remember. And to my British/Irish family, Hannah Griffiths, Dualta Ren, Shay Shay and Pepe for the walks, for the dinners and for all the help.

Às(os) amigas(os) e colegas do Laboratório de Ecologia de Formigas do qual fiz parte por 10 anos. À Luane, Cynthia, Ariel, Mariana, Marina, Jonas, Gaybe, Japonesa, Gui, Icaro, Rafael Casarino e à velha guarda, Vinícius Yoshino, Tamara Moretti, Fefo, Graziele Santiago, Rafael Cuissi e também a duas criaturas estranhas, engraçadíssimas, mas muito amáveis, Ernesto Canedo e Ananza Rabello. Obrigado por ter tido e ter vocês na minha vida. Eu amo vocês.

I am grateful to my co-advisor Kate Parr, for being very kind to me before, during and after I lived in Liverpool. Ao meu co-orientador e amigo Fernando Schmidt, obrigado por todo apoio desde minha graduação.

Ao meu grande amigo e companheiro de trabalho de muitos anos Antônio Queiroz. Obrigado por todos os ensinamentos na academia e fora dela. Obrigado por sempre me botar para cima e sempre acreditar em mim. Obrigado também por ter essa força que me inspira a lutar por um país melhor e mais justo.

À minha orientadora e amiga Carla Ribas, obrigado por todos os ensinamentos que fizeram parte de uma grande construção do que sou hoje, tanto como cientista como ser humano. Obrigado pelas aulas, pelas reuniões, pelas discussões de ecologia, pelas festas, pelas brigas, pelas conversas, pelas desculpas, pelo cuidado, pelo perdão e tudo isso que faz parte do crescimento e amadurecimento humano. Obrigado à sorte por estar no lugar certo na hora certa.

Às(os) amigas(os) que me abraçavam e também fizeram meus dias mais divertidos na Inglaterra, especialmente Danny Tregidgo, Natalie Swan, Cássio Nunes, Pedro Batista, Marcelo Paes e Cybelle Longhini, que além dos abraços, foi minha parceira nas noites de Liverpool.

Às(os) moradoras(es) e irmãs(os) que dividiram o mesmo lar comigo na Chá de Boldo. Meu muito obrigado à Tisa, Lili, Maria, Lela, Lenin, Betinho, Francis, Eri, Sassá, Polly e Chica. Obrigado pelos dias felizes e por aguentarem meu estresse calado nos momentos tensos do doutorado. E, claro, meu muito obrigado à nossa mãe que sempre cuidou de todos nós com muito carinho, Andreia Abreu.

Às(os) amigas(os) de Campo Belo, Melina Vilela, Yandra Campos, Lívia Melo, Maurílio Rodrigues, Hermellis Campos. Obrigado pela amizade e confiança por tanto tempo.

Às(os) amigas(os) de Lavras Marina Lindenbah, Falsie, Clah Clah, Agnis, Tobias, M, Lelê, Patrica, Mansa, Rafa Mahiane, Naries, Mamute, Bruno Abrantes, Esther, Lica, Pedro Bastos, Pedrinho, Julinha, Rubens, Mel e Dora. Muito obrigado por serem parte de mim.

Às(os) amigas(os) que estão num lugar melhor que a Terra, Amanda Azy e Reinaldo Telles, meu muito obrigado por acreditarem em mim e por ter tipo a chance de conhecer dois seres maravilhosos.

À minha segunda família, Regina Souza, José Paulo, Weber, Rinoa e Akira por me receberem em casa e por toda torcida.

À minha família, tias(os) e primas(os), em especial Tias Shirley, Cida e Sirlene, Tio Pedro e primas(os) Rose, Ilson e Marcos Douglas. Aos meus sobrinhos, meus pedaços, Cabeção, Pen Pen, Lenzo e Monicão. Ao Hamtaro e Thor. Eu amo vocês.

Ao Boni, meu companheiro, obrigado por todos os momentos felizes que tivemos. Obrigado por ser meu alívio nos finais de semana e por ser meu motivo feliz para acordar (depois de uma xícara de café, claro). Obrigado por me entender a pressão da pós-graduação e ter tido paciência nos meus momentos difíceis. Obrigado por ter comemorado todas as minhas conquistas. Obrigado pelos vinhos, pelas viagens, por me querer bem, por aprender comigo e principalmente por eu aprender contigo.

Ao meu pai Francisco Vitor que sempre me apoiou nos estudos e em todas as minhas decisões. Obrigado por todo carinho, por ser exemplo de luta e por todas as vezes que não pôde estar em casa, mesmo contra sua vontade, para poder nos dar a chance de estudar.

Às cinco mulheres que me criaram e à época mais saudosa da minha vida. À minha tia Elizena Santos por todo carinho e apoio. À minha irmã Cleide Felix por sempre dar corda à minha imaginação. Às minhas irmãs Erika e Amanda por sempre estarem ao lado, por não medirem esforços em me ajudar e me fazerem feliz. À minha mãe Aparecida Terezinha, por ter sido a pessoa que mais acreditou em mim durante minha vida, que quis me dar a vida que não pôde ter, que sempre me apoiou, que me fez forte quando estava fraco, que sempre falou pouco, mas sempre falou na hora certa. Obrigado mãe.

Por fim, a todas(os) que lutaram e lutam por uma educação gratuita e de qualidade para todas(os) e por um mundo mais justo.

“As pessoas não escolhem os sonhos que têm, São, pois, os sonhos que escolhem as pessoas, Nunca o ouvi dizer a ninguém, mas assim deve ser.” (José Saramago)

RESUMO GERAL

Entender o porquê da variação geográfica da biodiversidade é um dos temas centrais da Ecologia. Apesar de pouco consenso, muitas hipóteses foram postuladas para explicar os mecanismos da variação da riqueza e do nicho ecológico das espécies. Além disso, a variação da atividade de forrageio dos animais, que é a base dos processos ecossistêmicos, sempre foi pouco estudada em comparação aos padrões acima citados. Nesta tese, avalio os efeitos de fatores ecológicos (temperatura, precipitação, estabilidade climática e produtividade primária líquida) sobre a biodiversidade de formigas nos seis biomas brasileiros. Especificamente, avaliei os efeitos dos fatores ecológicos: i) na riqueza e sobreposição de nicho das formigas; ii) sobre a atividade de forrageamento e sobre o uso de diferentes tipos de recursos pelas formigas. Para o objetivo i), no geral, observei que todos os fatores ecológicos influenciam positivamente a riqueza de espécies. Porém, a maior parte da variância é explicada pela precipitação, seguida pela estabilidade climática. Esses fatores ecológicos também influenciaram positivamente a riqueza local de espécies. Porém, não encontramos efeitos indiretos dos fatores ecológicos na riqueza local que fossem mediados pela sobreposição de nicho das formigas. No entanto, a precipitação influenciou negativamente e diretamente a sobreposição de nicho. Provavelmente, num ambiente que apresenta altas temperaturas e é produtivo, que é o caso dos biomas brasileiros, a maior riqueza de espécies e diversidade de nichos podem estar ligadas ao maior tempo de especiação e à redução da taxa de extinção em ambientes úmidos e climaticamente estáveis. Dessa forma, sugiro que provavelmente a diversidade de formigas reflete hoje a história evolutiva da biodiversidade no continente sul americano. Para o objetivo ii), também encontrei que todos os fatores ecológicos influenciam positivamente a atividade de forrageio das formigas. Porém, esses padrões de atividade de forrageio estão ligados à riqueza de espécies. Além disso, os fatores ecológicos também influenciam o uso de diferentes recursos de uma maneira mais complexa. A temperatura e a precipitação podem estar ligadas à melhora da performance da atividade de forrageio enquanto a estabilidade climática e a produtividade podem estar ligadas à maior abundância de formigas nessas regiões, o que aumenta a probabilidade de se encontrar um recurso. Os fatores ecológicos também influenciaram a decisão por determinados recursos, o que pode ter sido devido à atuação deles em tornar um tipo de recurso escasso no ambiente ou agindo na atuação da demanda fisiológica dos organismos. Nesse sentido, a tese avança no conhecimento ecológico teórico que, além de demostrar as causas da variação geográfica da diversidade de formigas, poderá servir de embasamento para a conservação da biodiversidade brasileira. De acordo com os resultados da tese, sugiro também que, possivelmente, aspectos do nicho ecológico conservados no tempo evolutivo, como, por exemplo, a demanda por umidade, podem estar refletindo atualmente na riqueza de espécies, atividade de forrageamento e uso do recurso. Consequentemente, rápidas mudanças ambientais, como climáticas e por desmatamento, podem afetar drasticamente as formigas, que, por sua vez, poderão não ter tempo hábil a se adaptar a tais eventos.

Palavras chave: Ecologia Teórica. Ecologia de Comunidades. Macroecologia. Ecologia Nutricional. Formicidae.

ABSTRACT

One of the main goals of ecology is to understand the geographical variation in biodiversity. Despite little consensus, many hypotheses have been formulated in order to explain the mechanisms of species richness and ecological niche variation. Moreover, the geographical variation of foraging activity, which is the basis of ecological processes, has been neglected in comparison to other macroecological patterns. Here, I evaluated the role of ecological factors (temperature, precipitation, climatic stability and net primary productivity) on ant biodiversity in six Brazilian biomes. Specifically, I evaluated the effects of ecological factors: (1) on ant species richness and niche overlap, and (2) on ant foraging activity and resource use. (1) For the first aim, in general, I observed that all the evaluated ecological factors positively influenced ant species richness. However, the majority of the explained variance was due to precipitation, followed by climatic stability. These ecological factors also positively influenced local species richness; however I found no indirect effects of them on local species richness mediated by niche overlap. Nevertheless, precipitation negatively and directly influenced ant niche overlap. I suggest that in warm and productive regions, such as Brazilian biomes, high species richness and ecological niche diversity could be explained by greater time for speciation and to lower extinctions rates that occur in wet and more climatically stable regions. Thus, I suggest that ant diversity could reflect the evolutionary history of the biodiversity in Neotropics. (2) For the second aim, I also found a positive influence of all ecological factors on ant foraging activity. However, these patterns seem to be confounded with species richness. Ecological factors also influenced ant resource use in a complex way. Temperature and precipitation can be linked to an improved performance in ant foraging activity, and climatic stability and productivity can be linked to an increase in ant abundance in these regions, which increases the probability of finding resources. Ecological factors also influenced the selection for particular resources, which could be due to their role in resource shortfall in the environment and to their action on resource demand by organisms. In this sense, this thesis advances the understanding of ecological theory because, besides demonstrating the possible mechanisms of the geographical variation in ant diversity, these findings may be useful for guiding the conservation of Brazilian biodiversity. According to my results, I also suggest that some niche aspects could be conserved in evolutionary time, for example, humidity demand could reflect current ant species richness and how much and how ants forage. Consequently, rapid environmental changes, such as by climate change and deforestation, could drastically affect ants, that in their turn, may not be able to adapt to such fast changes.

Keywords: Ecological theory. Community Ecology. Macroecology. Nutritional Ecology. Formicidae.

SUMÁRIO

PRIMEIRA PARTE

1 INTRODUÇÃO GERAL

É notável que exista um maior número de espécies de plantas e animais e um maior número de animais forrageando em uma floresta tropical do que em um deserto, assim como que esses números sejam maiores na floresta Amazônica do que nos campos sulinos do Pampa. Por que existe essa variação geográfica na riqueza de espécies? Por que existe essa variação geográfica na atividade de forrageamento dos animais? Estes são exemplos de perguntas que motivam biogeógrafos e ecólogos há mais de três séculos a proporem mecanismos para essa variação no globo terrestre.

Dessa forma, entender os padrões da distribuição da diversidade e seus principais direcionadores pode nos ajudar a fazer previsões sobre os efeitos da perturbação humana nos habitats naturais, tais como mudanças climáticas, desmatamento e expansão descontrolada e insustentável de áreas de agropecuária. Além disso, entender a influência de fatores ecológicos na atividade de forrageamento e no uso dos recursos nos ajuda a entender como esses fatores ecológicos mediam a atuação desses organismos nos processos ecossistêmicos.

Nos últimos 60 anos muitos avanços foram alcançados ao tentar explicar esses possíveis mecanismos da variação geográfica da vida na Terra (PIANKA, 1966; HILLEBRAND, 2004; FINE, 2015). Embora existam mais de 40 hipóteses, há ainda pouco consenso sobre os principais mecanismos que influenciam a variação geográfica da riqueza de espécies (BROWN, 2013). Em geral, essas hipóteses são divididas em duas vertentes: histórica e ecológica (BROWN et al., 2013). Na abordagem histórica, os padrões de diversidade de espécies foram moldados há milhões de anos por eventos geológicos, climáticos e evolutivos (BROWN, 2013). Já a abordagem ecológica consiste em assumir que, independente da origem das espécies, a variação geográfica foi causada e ainda é mantida por fatores ecológicos através de suas influências nas taxas de especiação e extinção (HILLEBRAND, 2004; BROWN, 2013; FINE, 2015). Dentre os fatores ecológicos, quatro deles receberam grande destaque nas últimas décadas. São eles: a produtividade primária líquida (PPL), a precipitação, a temperatura e a estabilidade climática (EVANS et al., 2005; BROWN, 2013; FINE, 2015).

Quatro principais hipóteses foram postuladas em relação à influência da temperatura, PPL, precipitação e estabilidade climática sobre a riqueza de espécies. De acordo com a hipótese *species-energy* (WRIGHT, 1983; EVANS et al., 2005), em regiões onde a PPL é maior encontramos um maior número de espécies, pois se tem mais energia para manter os tamanhos das populações viáveis. Consequentemente, há uma redução da taxa de extinção. Além disso, se temos mais indivíduos em uma região, temos maior probabilidade de um deles sofrer mutação e por fim, chegar a um processo de diversificação (aumento da taxa de especiação). A hipótese *water*, que advém de outra hipótese chamada *water-energy* (HAWKINGS, 2003), postula que a precipitação, através da umidade, influencia positivamente a biodiversidade, diretamente reduzindo o estresse fisiológico dos organismos e indiretamente pelos seus efeitos positivos na PPL. De acordo com a *Metabolic theory of ecology*, a temperatura influencia positivamente as taxas metabólicas e assim, aumenta as taxas de especiação, aumentando o número de espécies em regiões mais quentes. Por último, a hipótese da *estabilidade climática* nos diz que, em regiões com o clima mais estável, as espécies estão ativas na maior parte do ano, o que influencia no número de eventos reprodutivos e no tamanho da prole. Isso pode aumentar os eventos de especiação e diminuir as taxas de extinção, já que os organismos experimentam uma menor oscilação do clima, pois uma grande variação pode ser fatal (FINE, 2015).

Apesar dos mecanismos serem distintos, as quatro hipóteses sempre retomam as taxas de especiação e extinção como explicação dos padrões de riqueza de espécies comparando diferentes regiões geográficas. Além disso, devemos levar em conta que as interações bióticas também possuem um papel importante na comunidade local (WIENS, 2011). E para isso as quatro hipóteses também possuem explicações de como esses fatores ecológicos afetaram as interações das espécies até o ponto de configurar padrões de sobreposição de nicho entre as espécies em uma escala local (BROWN, 2014; WIENS, 2011; FINE, 2015). Por exemplo, aumentando a disponibilidade de recursos (MACARTHUR, 1972; WRIGHT, 1983; EVANS et al., 2005), ou acelerando e mantendo por mais tempo as interações ecológicas (BROWN, 2013; FINE, 2015), aumenta-se a probabilidade das espécies se diferenciarem. Dessa forma, elas são capazes de sobrepor menos seus nichos em relação ao uso de recurso, resultando em um número maior de espécies coexistindo em uma escala local.

A respeito da variação geográfica da atividade de forrageamento, apesar de já ter sido relatada, ela ainda é subestimada e pouco estudada em comparação à variação da riqueza de espécies. Através da atividade de forrageio, os animais se integram no ecossistema exercendo diversas funções ecológicas. Os quatro fatores ecológicos de estudo da tese (temperatura, precipitação, PPL e estabilidade climática) também são conhecidos por afetarem positivamente essa atividade (GILLOOLY et al., 2001; KASPARI; WEISER, 2000; BAUDIER et al., 2018, PRATHER et al., 2018; KASPARI; BEURS, 2019). Além disso, os animais podem fazer esforços distintos (forrageando com maior ou menor intensidade) para determinado tipo de recurso (RAUBENHEIMER et al., 2009). Essa diferenciação da escolha do tipo de recurso pode ocorrer devido à escassez do mesmo no ambiente (e.g.: animais limitados por sódio em ambientes distantes do mar, KASPARI et al., 2008) ou até mesmo a um aumento da demanda causado por um fator ecológico (e.g.: maior consumo de sódio e açúcar em temperaturas mais altas em resposta a maior perda dos mesmos devido à aceleração do metabolismo, PRATHER et al., 2018).

Um dos grandes problemas da influência dos fatores ecológicos na riqueza de espécies é que, comumente, os mesmos são fortemente correlacionados (BROWN, 2013). Além disso, sobre a atividade de forrageio e o uso do recurso, a maioria dos estudos foi feita em laboratórios (e.g. RAUBENHEIMER et al., 2009) ou em uma escala espacial pequena (e.g. PRATHER et al., 2018) ou até mesmo medindo indiretamente a atividade de forrageio (e.g. KASPARI; BEURS, 2019). Nesse sentido, o Brasil é um laboratório ideal para se testar hipóteses ecológicas a respeito da variação da riqueza de espécies e atividade de forrageamento. Isso é devido a grande extensão geográfica do país e por possuir seis biomas continentais que se diferem em magnitude em relação a fatores ecológicos de interesse da tese, e em relação ao número de espécies e atividade de forrageamento dos animais. “Se a gente for subindo no Brasil, vai aumentando o número de bichos. O Rio Grande do Sul não tem quase nada porque é muito frio (...) Eu sempre vi mais bicho no Pantanal e na Amazônia do que no Pampa” (LASMAR, F. P. V [1], informação pessoal).

As formigas são um excelente grupo para se estudar esses padrões biogeográficos por serem muito diversas e abundantes, principalmente nas áreas tropicais (HÖLLDOBLER; WILSON 1990, FOLGARAIT 1998, MOREU; BELL[1] 2013). Além disso, através de sua atividade de forrageio, elas participam de diversos processos ecossistêmicos, tais como dispersão de sementes, predação, ciclagem de nutrientes, além de interagirem com diversos animais e plantas e, por isso, apresentam uma variedade de nichos ecológicos em relação ao uso de recursos (HÖLLDOBLER; WILSON 1990; FOLGARAIT, 1998; BLÜTHGEN; FELDHAAR, 2010; TIEDE ET AL., 2017; CSATA; DUSSUTOUR, 2019).

O objetivo geral dessa tese foi avaliar o papel de fatores ecológicos (temperatura, PPL, precipitação e estabilidade climática) nos padrões geográficos da riqueza de espécies e atividade de forrageamento das formigas. Para isso, a tese possui dois artigos. No primeiro

---

[1] Francisco de Paula Vitor Lasmar, caminhoneiro autônomo por 45 anos, já viajou por todos os estados do Brasil, inclusive por outros países da América Latina.

avaliamos a influência dos fatores ecológicos nos padrões geográficos da riqueza de espécies e se seus efeitos na riqueza de espécies em uma escala local são mediados pela sobreposição de nicho em relação ao uso de recursos. No segundo, avaliamos a influência dos fatores ecológicos na variação geográfica da atividade de forrageio e no uso de recursos das formigas. Além disso, a tese possui um apêndice referente a um trabalho de divulgação científica realizado durante as campanhas de campo. Nesse trabalho de divulgação, tive como objetivo disseminar o conhecimento científico das formigas e dos biomas brasileiros nas escolas rurais e urbanas no entorno das unidades de conservação em que fiz as coletas do material biológico.

REFERÊNCIAS

BLÜTHGEN, N.; FELDHAAR, H. Food and Shelter: How Resources Influence Ant Ecology: In LACH, L., PARR, C. L., & ABBOT, K. L. Ant Ecology. Oxford, Oxford University Press. 2010.

BROWN, J. H. Why are there so many species in the tropics? Journal of Biogeography, v. 41, p. 8–22, 2014.

CSATA E.; DUSSUTOUR, A. Nutrient regulation in ants (Hymenoptera: Formicidae): a review. Mymecological News, v. 29, p. 111–124, 2019.

EVANS, K. L. et al. Species–energy relationships at the macroecological scale: A review of the mechanisms. Biological Reviews, v. 80, n 1,p. 1–25, 2005.

FOLGARAIT, P. J. Ant biodiversity and its relationship to ecosystem functioning: a review. Biodiversity and Conservation, v. 7, p. 1221–1244, 1998.

FINE, P. Ecological and evolutionary drivers of geographic variation in species diversity. Annual Review of Ecology, Evolution, and Systematics, v. 46, p. 369–392, 2015.

GILLOOLY, J. F. et al. Effects of Size and Temperature on Metabolic Rate. Science, v. 293, p. 2248-2251, 2001.

HAWKINS, B. A. et al. Energy, water, and broadscale geographic patterns of species richness. Ecology. V. 84, n 12, p. 3105– 3117, 2003.

HILLEBRAND, H. On the Generality of the Latitudinal Diversity Gradient. The American Naturalist, v. 163, n 2, p. 192–211, 2004.

HÖLLDOBLER, B.; WILSON, E. O. The Ants. Harvard University Press, Cambridge, MA. 1990.

KASPARI, M.; WEISER, M. D. Ant Activity along Moisture Gradients in a Neotropical Forest. Biotropica, v. 32, p. 703-711, 2000.

KASPARI, M. et al. On the biogeography of salt limitation: a study of ant communities. Proceedings of the National Academy of Sciences, v. 105, p. 17848–17851, 2008.

KASPARI, M.; BEURS, K. On the geography of activity: productivity but not temperature constrains discovery rates by ectotherm consumers. Ecosphere, v. 10 p. 2, e02536, 2019.

MACARTHUR, R. H. Geographical ecology: patterns in the distribution of species. Harper & Row Press, 1972.

PIANKA, E. R. Latitudinal gradients in species diversity: a review of concepts. The American Naturalist, v. 100, p. 33–46, 1996.

MOREAU, C. S.; BELL, C. D. Testing the museum versus cradle tropical biological diversity hypothesis: phylogeny, diversification, and ancestral biogeographic range evolution of the ants. Evolution, v. 67, p. 2240-2257, 2012.

PRATHER, R. M. et al. Using metabolic and thermal ecology to predict temperature dependent ecosystem activity: a test with prairie ants. Ecology, v. 99, p. 2113-2121, 2018.

RAUBENHEIMER, D. et al. Nutrition, ecology and nutritional ecology: toward an integrated framework. Functional Ecology, v. 23, p. 4-16, 2009.

TIEDE, Y. et al., Ants as indicators of environmental change and ecosystem processes. Ecological Indicators, v. 83, p. 527-537, 2017.

WIENS, J. J. The niche, biogeography and species interactions. Philosophical Transactions of the Royal Society B, 366: 2336–2350, 2011.

WRIGHT, D. H. Species-energy theory: an extension of species-area theory. Oikos, v. 41, p. 496–506, 1983.

SEGUNDA PARTE

ARTIGOS

ARTIGO 1

PRECIPITATION AND CLIMATIC STABILITY ARE THE MAIN DRIVERS OF ANT SPECIES RICHNESS AND NICHE OVERLAP VARIATION IN THE NEOTROPICS

Versão preliminar para submissão na revista Ecography

Title: Precipitation and climatic stability are the main drivers of ant species richness and niche overlap variation in the neotropics

Chaim J. Lasmar[1], Tom R. Bishop[2,3], Catherine L. Parr[2,3,4], Antônio C.M. Queiroz[1], Rodrigo M. Feitosa[5], Mayara M.G. Imata[6], Ícaro W.G. Carvalho[1], Cynthia V. Oliveira[1], Fernando A. Schmidt[7] and Carla R. Ribas[6]

1- Programa de Pós–Graduação em Ecologia Aplicada, Setor de Ecologia e Conservação, Laboratório de Ecologia de Formigas, Departamento de Biologia, Universidade Federal de Lavras, PO Box 3037, Lavras, MG, 37200-000, Brazil.

2- Department of Earth, Ocean and Ecological Sciences, University of Liverpool, Liverpool, U.K..

3- Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa

4- School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Wits, South Africa

5- Departamento de Zoologia, Universidade Federal do Paraná, CP 19020, Curitiba, PR, 81531-980, Brazil

6- Laboratório de Ecologia de Formigas, Setor de Ecologia e Conservação, Departamento de Biologia, Universidade Federal de Lavras, PO Box 3037, Lavras, MG, 37200-000, Brazil

7- Centro de Ciências Biológicas e da Natureza, Universidade Federal do Acre, Rio Branco, AC, Brazil

Corresponding author: chaimlasmar@gmail.com

Abstract

Geographical variation of species richness has drawn the attention from many ecologists and biogeographers in the last three centuries. Many ecological factors have been reported to shape geographical patterns, as well as to drive species interactions with further consequences for niche overlapping of local assemblages. However, there is a lack of consensus mainly due to the high correlation between the ecological drivers of geographical variation. Here, we disentangled the role four ecological factors (temperature, climatic stability, net primary productivity and precipitation) on ant species richness and tested wether their effects on local species richness are mediated by niche overlapping. To test this, we used pitfall traps to sample ant assemblages across six Brazilian biomes at three habitat strata. For niche overlap, we assessed the niche of ants related to their diet and habitat strata foraged. Despite all ecological factors positively influencing ant species richness, the highest explained variance was due to precipitation, followed by climatic stability. We also found no niche overlap mediation of these ecological drivers on local ant assemblages. Yet, less overlapping in ant species niches occurred in wetter regions. To explain the higher species richness on wet and more climatically stable regions, we suggest that climatic stability could reduce the extinction rates, while precipitation – through physiological constraints – could be related to older speciation events occurring in the past; previous speciation events could also reflect in more specialized species in wet regions. We suggest that more time for speciation resulted in the currently patterns of ant diversity in Brazilian biomes, which could possibly reflect the evolutionary history of Neotropical biodiversity that was originated and have been evolving in wet and climatically stable regions.

Key words: Biodiversity, Macroecology, Niche Conservatism, Community Ecology, Formicidae

Introduction

For three centuries, biologists have aimed to explain the variation of biodiversity across the world. The last 60 years have been marked by great advances in assessing the likely mechanisms underlying such geographical variation (Pianka 1966; Hillebrand 2004; Fine 2015). Tropical areas, specifically in South America, exhibit the highest biodiversity on Earth (Pianka 1966; Hillebrand 2004; Kinlock et al. 2018). However, in some hyperdiverse countries, such as Brazil, the huge biodiversity is threatened by habitat loss and degradation, as well as by government negligence (Urban 2015, Ferrante and Fearnside, 2019; Barlow et al. 2018). Thus, understanding the ecological drivers of species richness variation in the Neotropics is critical to predict the future consequences of ongoing climate changes and anthropogenic disturbance activities at a global scale (Newbold et al. 2015).

Despite little consensus, there are four main hypotheses in macroecology to explain the species richness geographical variation. These are based on the net primary productivity, precipitation, temperature and climatic stability (Table 1). Although these hypotheses are distinct in their key drivers, they are similar at invoking both speciation and extinction rates as underlying mechanisms for variation in species richness (Mittelbach et al. 2007, Brown 2014, Fine 2015). Biotic interactions also play an important role for the variation and maintenance of species richness at local scales (Wiens 2011). For instance, biotic interactions can influence specialization over evolutionary time through co-evolutionary arms races and extinction rates that allow species' coexistence (Schemske et al. 2009, Wiens 2011, Fine, 2015). Hence, tropical areas have many rare and specialized species, higher species niche partitioning (Chase and Leibold 2003, Brown 2014, Chu et al. 2019) and, consequently, higher local species richness. These four ecological hypotheses also aim to explain how distinct drivers may influence the evolutionary and co-evolutionary rates, which reflect on species niche overlap through species specialization, and then reflecting on local assemblages (i.e. ecological drivers influencing alpha diversity mediated by species niche overlap) (Table 1).

Although each of these four hypotheses are focused on one ecological driver, they are not mutually exclusive in the real world (Brown 2014, Fine 2015). For example, Brown (2013) argued that although net primary productivity (NPP) accounts for the explanation of species variation, NPP is a product of temperature gradients, and the influence of temperature and its variability is higher than NPP on biodiversity. Moreover, although two mechanisms are proposed to explain the influence of precipitation (i.e. through reducing physiological stress and NPP effects), many studies invoke NPP effects on species diversity (e.g. Hawkins et al. 2003, Vasconcelos et al. 2018). These confounding effects occur because climatic factors are usually strongly correlated between themselves and with NPP, which makes it hard to disentangle the independent effects of each ecological driver of species variation.

To assess the drivers of geographical variation and diversification of species, studies should adopt large-scale approaches and occur across distinct biomes where biological boundaries may impose geographical range limits for regional species pool (Fine 2015). Brazil is an excellent hyperdiverse country to perform large-scale and multi-biome research, given it has six continental biomes and presents different degrees of NPP resulted from variation of climatic factors and soil types (Cleveland et al. 2011, 2013).

Here we disentangled the effects of distinct ecological drivers (temperature, precipitation, climatic stability and net primary productivity) on ant species richness and their effects mediated by niche overlap in local assemblages using a standard sampling adopted across six Brazilian biomes. We used ants as a biodiversity proxy, as ants are an abundant and high diverse group in Brazil, participating in several ecological interactions and processes; and, consequently, presenting a high diversity of ecological niches (Hölldobler and Wilson 1990, Folgarait 1998, Moreu and Bell 2013). In addition, ants are macroecologically affected by the four ecological drivers of geographical variation we are examining in this research (Dunn et al. 2009, Gibb et al. 2015, Kaspari et al, 2019). Specifically, we asked (1) which ecological drivers (NPP, precipitation, temperature and climatic stability) are the main drivers of ant species richness variation? and (2) does the ant niche overlap mediate their influence on local ant communities? We predicted that (1) the main drivers of species richness would be temperature and climatic stability, (2) which would lead ant species to be more specialized, and result in an ecological community with less niche overlap and, consequently, increasing ant species richness at local scale.

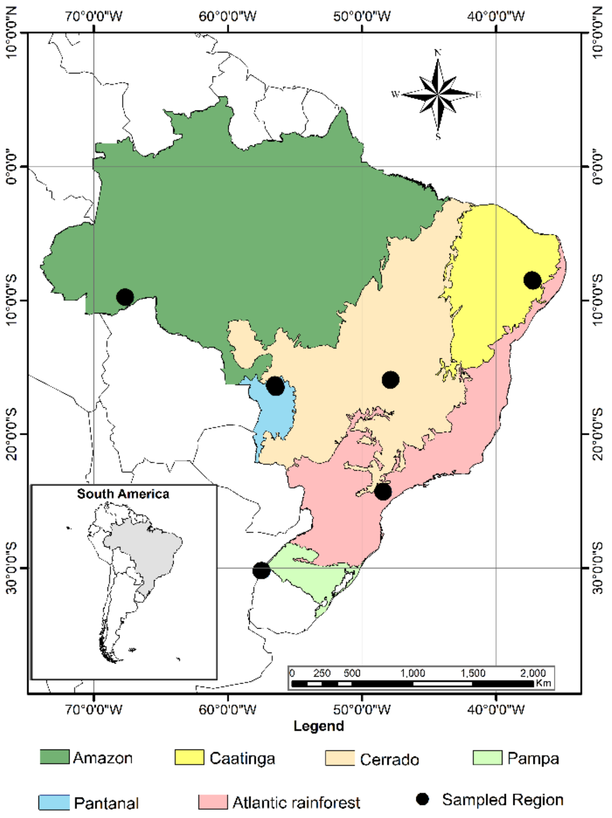
Table 1. Hypotheses of drivers of geographical variation of species richness and maintenance of local communities.

Hypothesis	Mechanism	Maintenance of local species richness through biotic interactions based on niche overlap
Species-energy (MacArthur 1972, Wright 1983, Evans et al. 2005)	**Net primary productivity (NPP)** increases biodiversity. Productive regions can supply more species because there is more energy to maintain viable populations. It also reduces extinction rates and increases speciation rates.	Abundant resources could be sufficiently enough for species to specialize in a portion of resource niche space and then generate species with narrow niches. Thus, it decreases species' niche overlap.
Water (Hawkins et al. 2003)	Water (**precipitation**) positively influences biodiversity directly via physiological constraint (e.g. decreasing desiccation risk) and indirectly via NPP in the tropics.	See above.
*Metabolic theory of ecology (*Allen et al, 2006, Brown 2014)	Biological rates increase exponentially with enhanced **temperatures**, including speciation rates. Hence, warmer regions present more species due to the short generation time and high speciation rates.	Temperature exponentially increases ecological interaction rates, which could fit species being more specialized, that decreases species' niche overlap.
Climatic stability (Sandel et al. 2011, Fine 2015)	In more **climatically stable** regions, speciation events are higher since there has been more time to specialization, and extinction rates are reduced due to less oscillation in climate, that can be fatal to many organisms.	High number of species in more climatically stable regions had more time to interact through time. Thus, higher evolutionary speed of coevolution could lead species to higher specialization and, thus, decreased species' niche overlap.

Material and Methods

Study site

We conducted our study in six Brazilian biomes always at the rainy season of each biome, between November/2016 and March/2018. These biomes present distinct climate and vegetation types (Fig. 1).



Amazon
Reserva Florestal de Humaitá (9°46'13"S, 67°37'7"W)
Open rainforest with palm trees and bamboo.
Mean annual temperature = 25.2°C, Annual precipitation = 1,720 mm.
Elevation = 185 m.a.s.l.

Caatinga
Parque Nacional do Catimbau (8°30'19"S, 37°18'37.86"W)
Shrublands.
Mean annual temperature = 20.5°C; Annual precipitation = 721 mm.
Elevation = 970 m.a.s.l.

Cerrado
Reserva Ecológica do IBGE and Jardim Botânico de Brasília
(15°55'33"S, 47°52'59"W).
Brazilian savannah; Cerrado *stricto sensu*.
Mean annual temperature = 20.1°C; Annual precipitation = 1,519 mm.
Elevation = 1100 m.a.s.l.

Pantanal
RPPN Sesc Pantanal (16°31'19"S, 56°24'90"W)
Different vegetation types varying from grasslands to natural
forest remnants, also presenting natural floods.
Mean annual temperature = 25.2°C; Annual precipitation = 1,317 mm
Elevation = 123 m.a.s.l.

Atlantic rainforest
Parque Estadual Intervales (24°17'13"S, 48°26'41"W)
Montane dense rainforest.
Mean annual temperature = 17.7°C; Annual precipitation = 1,419 mm
Elevation = 800 m.a.s.l.

Pampa
Parque Estadual do Espinilho (30°11'25"S, 57°29'51"W)
Humid stepic savannah
Mean annual temperature = 19.8°C; Annual precipitation = 1,474 mm
Elevation = 51 m.a.s.l.

Figure 1. Six Brazilian biomes and the specific location where samples were carried out.

Ant sampling

In each biome, we used 10 transects separated by at least 800 m, totalizing 60 transects across the study (Fig. 1). To the effects of ecological factors on ant species diversity, transects were 200 m long and had five sampling points separated by 50 m. At each sampling point, we collected ants at three habitat strata using arboreal, epigaeic and hypogaeic pitfall traps. Arboreal traps were installed at 1.5 m above the ground, tied in the middle of a tree trunk

(Ribas et al. 2003). Epigaeic traps were installed at the ground level (Bestelmeyer et al. 2000) and hypogaeic traps were buried at 20 cm under the ground (Schmidt and Solar 2010). Pitfall traps were 8 cm in diameter and 12 cm in depth, and contained a 200 ml solution of water, salt (0.4%) and liquid soap (0.6%) (Canedo-Júnior et al. 2016), presented a lid to cover and protect them against rain, sunlight and soil (only hypogaeic traps) and remained in the field for 48 h.

Niche overlap

To test the influence of ecological drivers on ant species niche overlap and richness, we also had 10 transects per biome, separated by at least 800 m, totalizing 60 transects across the study. These transects were in parallel to the first sampling design (> 20 m apart of the pitfall transects). Transects were 740 m long and presented 75 sampling points, separated by 10 m from each other. We placed 50 ml fisher tubes containing one of five liquids resources soaked in 5 cm cotton balls. Liquid resources were made by a solution of (distilled water/volume): 1% sodium (NaCl), 20% sugar (made with sucrose), 20% amino acids (made with unflavored whey protein isolate) and lipids (extra virgin olive oil) and distilled water, as a control (Fowler et al. 2014). We placed alternatively combinations of five liquid baits (distilled water as control, carbohydrates, amino acids, lipids and sodium) at three habitat strata (arboreal, epigaeic and hypogaeic) that remained operating for 3 h. We, therefore, have a combination of 12 niche aspects related to the use of resource and habitat strata (3 habitat strata × 4 bait types, not including the distilled water bait) and five replications of each niche aspect per transect. Since sampling with pitfall traps may cause depletion of ants' populations (Lasmar et al. 2017), we always performed the bait sampling before pitfall trap sampling.

We identified all collected ant workers into genera following Baccaro et al. (2015), and whenever possible to species or morphospecies using the relevant literature and/or matching individuals with the ant reference collection at the 'Laboratório de Ecologia de Formigas' of the Universidade Federal de Lavras (UFLA) and Entomological Collection Padre Jesus Santiago Moure of Universidade Federal do Paraná (UFPR). Voucher specimens are deposited in the reference collection of both collections at UFLA and UFPR.

Ecological drivers

We obtained current and past climate data for each of our sampling sites. For current climate, we used the annual mean temperature (°C), annual precipitation (mm) and climatic stability (temperature seasonality - standard deviation in °C of annual mean temperature, as a representation of temperature variability) per transect based on Worldclim2 dataset with a resolution of 1 km² and measures between 1970 to 2000 (Fick and Hijmans 2017). For past climate data, we obtained current correspondent ecological drivers (annual mean temperature, annual precipitation and climatic stability) for the last glacial maximum using the Chelsa database, estimated by NCAR-CCSM4 method (Karger et al. 2017). Net primary productivity (NPP) was obtained from MODIS NPP data, which represents the annual average of 2000 – 2015 years (MOD17, from NASA Earth Observation System). This is available in the repository at the University of Montana (www.ntsg.umt.edu/) at 1 km spatial resolution. The data obtained was an improved version of MOD17, which presents a cleaning of cloud-contaminated pixels and considers the difference between gross primary productivity and autotrophic respiration (Zhao and Running 2010).

Statistical analyses

Species richness X Ecological drivers

First, we looked for correlations between our ecological drivers. Since all factors follow a non-normal distribution, we performed a Spearman correlation. We considered as a high correlation when R-values were ≥ 0.70. In this sense, we found no strong correlation between current climate and NPP, neither between past climate and NPP (Appendix, table 1A).

However, when comparing past and current correspondent climate factors (i.e. current annual mean temperature and past annual mean temperature), all current representations were correlated with their past correspondents (Appendix, table 1A). This indicate that at least in a range of 21,000 years, geographical variation in temperature, precipitation and climatic stability of our sampled regions remained almost the same. Thus, we only consider current climate data and NPP in our analyses.

To test which ecological drivers are the main driver of species richness, we constructed four generalized linear models (GLMs). For the first one, we had as response variable the total species richness extracted by the sum of ant species richness per transect (n = 60). For the other GLMs, we extracted the response variable (species richness) for each habitat strata separately – arboreal, epigaeic and hypogaeic. Temperature, climatic stability, NPP and precipitation were the explanatory variables in all four GLMs. For all GLMs, we simplified the models performing a backward approach, which consists in removing non-significant explanatory variables from the models until only the significant ones are present in the model. We used models with a *Poisson* distribution and adjusted to a *quasi-Poisson* when necessary (Crawley 2013). After that, to check the contribution of each explanatory variable in explaining the variation of ant species richness, we submitted only the explanatory variables in the final model to a variance partitioning using the '*hier.part*' function in *hier.part* package in software R (Walsh and Nally 2015).

Niche overlap mediation of the effects of ecological drivers on local species richness

We conducted a confirmatory path analysis to assess if ecological drivers are underlying ant species niche overlap, which could result in a higher local species richness through, for example, lower niche overlapping. Using the the bait experiment, we calculated the niche overlap per transect, using Pianka's index by constructing matrices where each column was one of 12 niche combinations (4 bait types x 3 habitat strata, ignoring distilled water) while rows were the species, using *EcoSimR* package in R software (Gotelli et al., 2015). We ignored distilled water because there were way less visitations to this treatment when compared to the other resources – indicating that ants were mostly attract by the resources rather than by water (see second chapter, for details). In the matrix, the entry was the number of times each species visited one of the 12 niche combinations. Pianka's index quantifies the symmetrical niche overlap among a group of distinct categories (e.g. 12 niche combinations) for each pair of species. Values can range from 1 – indicating complete overlap in the use of resources – to 0 (e.g. no overlap in the resource use). Even though measures of species' niches are complicated to categorize, some authors (e.g. Schoener 1974, Fowler et al. 2014) suggested that habitat strata, diet and temporal activity are the most important niche axes, while a great part of the species' niche variation occur in habitat strata and diet niche axes. To calculate local species richness, we summed the ant species richness from pitfall traps of the three habitat strata in the same sampling point and then we extracted the mean number of ant species of sampling points per transect (n = 60).

We conducted the confirmatory path analysis using *cfa* function from *lavaan* package in R (Rosseel at al. 2018). For this, we assumed direct and indirect effects of each ecological driver on ant niche overlap and species richness and direct effects of niche overlap on local species richness. Direct effects are the standardized partial regression coefficient of a given predictor variable on the response variable. Indirect effects are the sum of the product between standardized partial regression coefficients of a given ecological driver and the mediator factor (niche overlap) on local species richness. To confirm our prediction, we must find an indirect effect of temperature and climatic stability on local species richness. We used two GLMs to perform the path model. The first model was composed by the influence of explanatories variables temperature, precipitation, climatic stability and NPP on ant niche overlap. Our second model was constructed with the influence of the explanatory variables temperature, precipitation, climatic stability, NPP and ant niche overlap on ant species richness. In order to facilitate the comparison of effect size coefficients, we z-transformed all ecological drivers in two models and the response variable in the model one (niche overlap). Since our predictor variables are non-normal distributed, we also computed the Bollen-stine bootstrap using 1000 randomizations (Bollen and Stine 1992), which is more appropriated for this kind of data. The fitness of the path models was evaluated by maximum likelihood $\chi 2$ and by comparative fit index (CFI). Non-significant values of χ^2 and CFI > 0.9 represent a good fit of the paths in the model.

Results

In total, we collected 512 ant species (412 through pitfall traps and 255 from bait sampling) from 12 subfamilies and 64 genera. The richest genera were *Pheidole* (154 species), followed by *Camponotus* (51 species), *Solenopsis* (41 species), *Crematogaster* (34 species), *Brachymyrmex* (16 species), *Pseudomyrmex* (14 species), *Hypoponera* (12 species) and *Cephalotes* (11 species).

Total ant species richness increased with temperature (Chi = 67.42; d.f. = 58; $p < 0.001$), NPP (Chi = 25.39; d.f. = 56; $p < 0.001$), precipitation (Chi = 67.19; d.f. = 55; $p < 0.001$) and climatic stability (Chi = 46.77; d.f. = 57; $p < 0.001$) (Fig. 2). Epigaeic species richness followed the same pattern of total species richness, increasing with temperature (F = 24.31; d.f. = 58; $p < 0.001$), NPP (F = 22.89; d.f. = 56 ; $p < 0.001$), precipitation (F = 41.10; d.f. = 55 ; $p < 0.001$) and climatic stability (F = 23.02; d.f. = 57; $p < 0.001$) (Fig. 3). Arboreal species richness also increased with temperature (F = 40.35; d.f. = 58; $p < 0.001$), precipitation (F = 30.85; d.f. = 56; $p < 0.001$) and climatic stability (F = 39.57; d.f. = 57; $p < 0.001$) (Fig. 3). We found no effect of NPP on arboreal ants (F = 0.00; d.f. = 56; $p = 0.997$). Hypogaeic species richness increased with temperature (F = 15.65; d.f. = 58; $p < 0.001$) and precipitation (F =

05.89; d.f. = 57; $p = 0.018$) (Fig. 2 a, d). No effect of climatic stability (F = 01.86; d.f. = 57; $p = 0.177$) and NPP (F = 00.37; d.f. = 56; $p = 0.618$) was found for hypogaeic ants.

The explained variance for total ant species ($R^2 = 0.78$) was mainly related to precipitation, followed by climatic stability, temperature and NPP (Fig. 4). For the epigaeic stratum ($R^2 = 0.65$) we obtained the same pattern (Fig. 4). For the arboreal stratum, the explained variance ($R^2 = 0.71$) was mainly due to climatic stability and precipitation, followed by temperature (Fig. 4). For the hypogaeic stratum, the explained variance was much lower ($R^2 = 0.26$) and was mainly due to temperature followed by precipitation (Fig. 4).

In this sense, even though our results support all hypotheses tested here, the main drivers follow the *water* and *climatic stability* hypotheses for overall, epigaeic and arboreal species richness. Only the hypogaeic strata supported *Metabolic Theory of Ecology* hypotheses, besides *water* hypotheses.

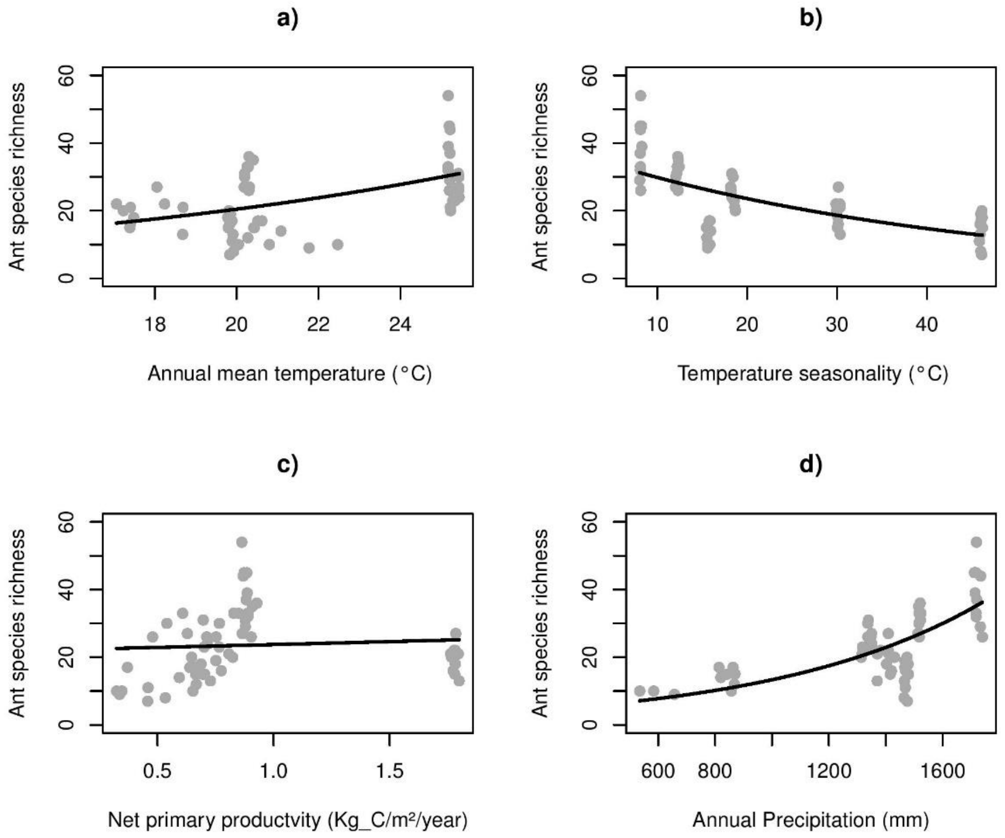


Figure 2. Generalized linear models (GLMs) for distinct ecological drivers (x-axes) of total ant species richness (y-axes). Points represent the sum of ant species richness per transect (N = 60) and the black line are the effects of: a) temperature (annual mean temperature); b) climatic stability (temperature seasonality); c) NPP (net primary productivity) and d) precipitation (annual precipitation). High temperature seasonality means high climatic instability.

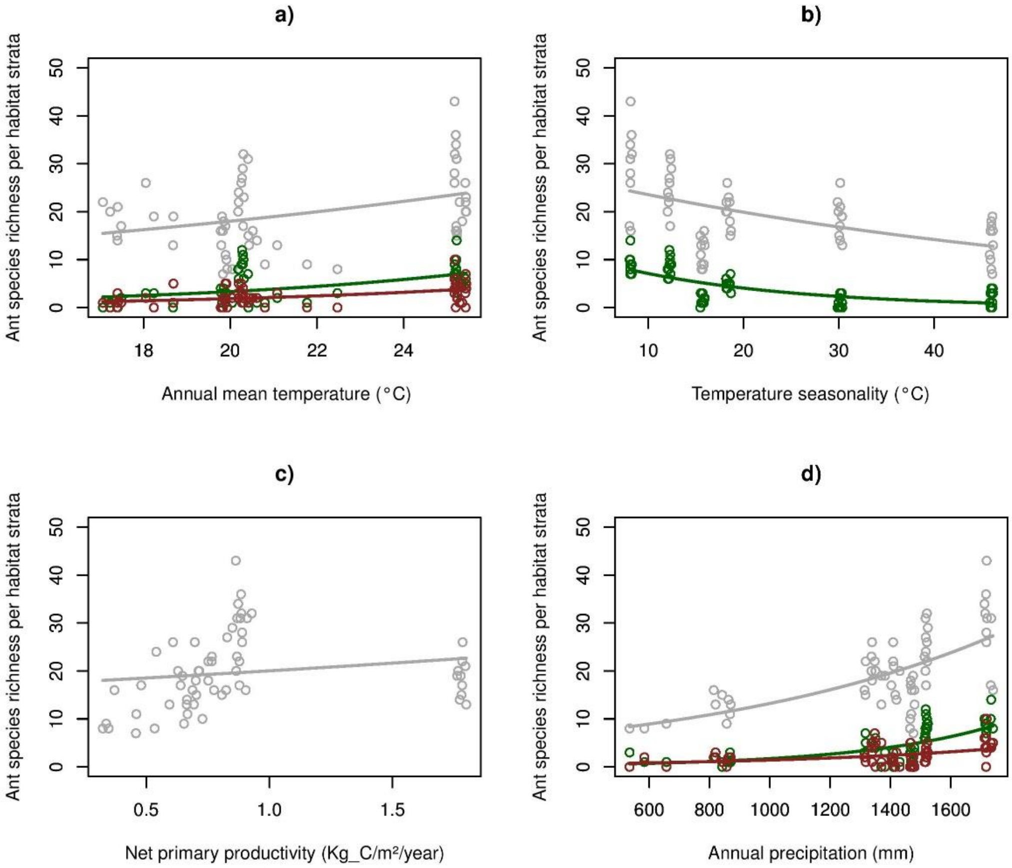


Figure 3. Generalized linear models (GLMs) for distinct ecological drivers (x-axes) of epigaeic (Grey), arboreal (Green) and hypogaeic (Brown) ant species richness (y-axes). Different coloured circles in the graphs are the sum of ant species richness per transect (N = 60) and the different coloured lines are the effects of a) temperature (annual mean temperature); b) climatic stability (Temperature seasonality); c) NPP (net primary productivity) and d) precipitation (annual precipitation) on arboreal (green), epigaeic (grey) and hypogaeic (brown) stratum. High temperature seasonality means high climatic instability.

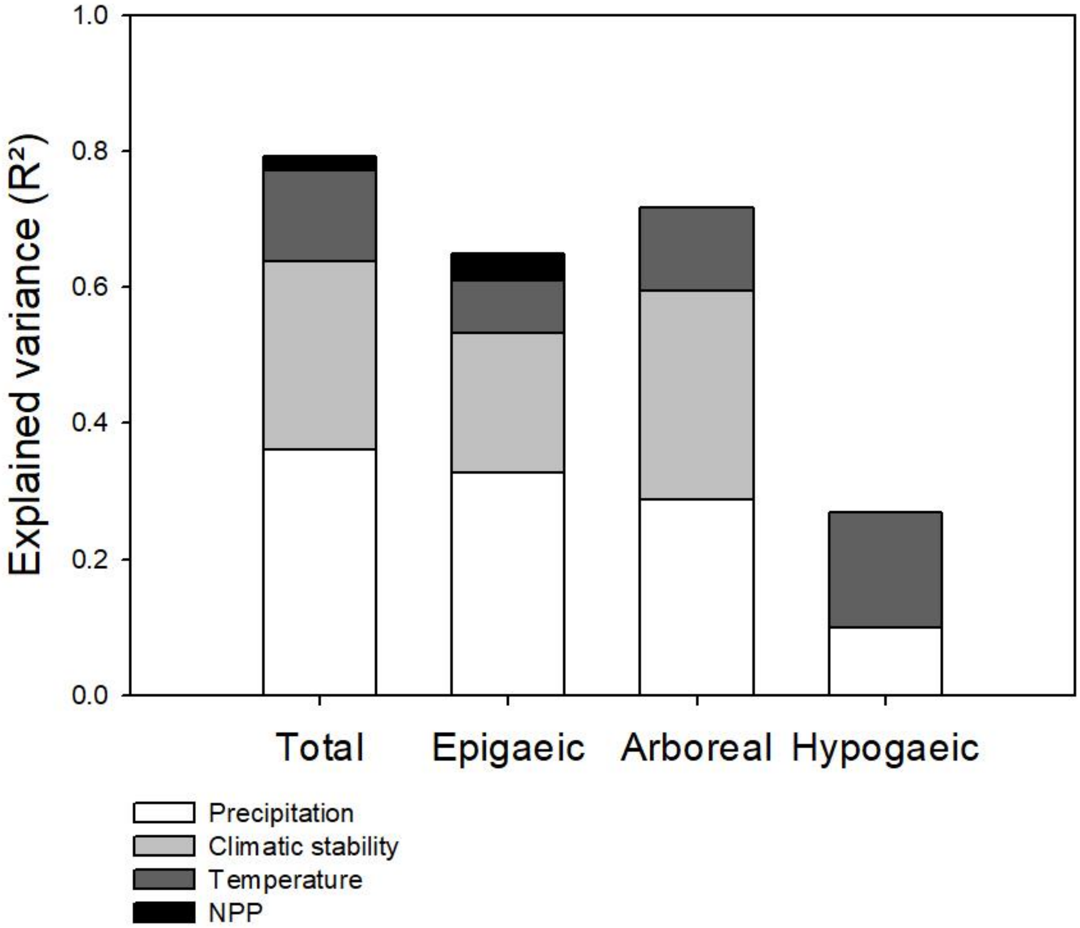


Figure 4. Independent contribution of ecological drivers on the explanation variance of total, epigaeic, arboreal and hypogaeic ant species richness per transect (N = 60). Temperature (annual mean temperature); climatic stability (temperature seasonality); NPP (net primary productivity) and precipitation (annual precipitation).

We obtained a good fit for our path model ($\chi 2 = 1.634$, d.f = 2, $p = 0.44$; CFI = 1). Even though we observed some direct effects of ecological drivers on niche overlap and on local species richness (Table 2 and Fig. 5), we found no indirect effects of ecological drivers mediated by niche overlap on local species richness. Our results, therefore, do not support our predictions related to *MTE* and *climatic stability* hypotheses and neither *species-energy* and *water* hypothesis.

Table 2. Direct effects on ant niche overlap (model 1) by ecological drivers (temperature, climatic stability, NPP and precipitation) and direct effects on

local species richness (model 2) by ecological drivers and niche overlap. Since our proxy of climatic stability was temperature seasonality, we inverted the estimate values because high temperature seasonality means high climatic instability. Indirect effects of ecological drivers mediated by niche overlap on local species richness are point out below. Bold values represent significant paths in model. R² represent the model explained variance of the response variables.

GLM Regressions	**Estimate**	***z-value***	***p-value***
Model 1: Niche Overlap ~			
Temperature	-0.079	-0.426	0.670
Climatic stability	0.074	0.436	0.663
NPP	0.074	0.463	0.643
Precipitation	-0.381	-2.914	**0.004**
R² = 0.17			
Model 2: Local species richness ~			
Temperature	0.001	0.002	0.999
Climatic stability	1.839	-6.299	**<0.001**
NPP	-0.104	-0.361	0.718
Precipitation	1.904	6.064	**<0.001**
Niche Overlap	0.155	0.550	0.582
R² = 0.68			
Indirect effects on Local species richness:	**Estimate**	***z-value***	***p-value***
Temperature	-0.012	-0.193	0.847
Climatic stability	-0.011	0.204	0.838
NPP	0.011	0.230	0.818
Precipitation	-0.059	-0.564	0.573

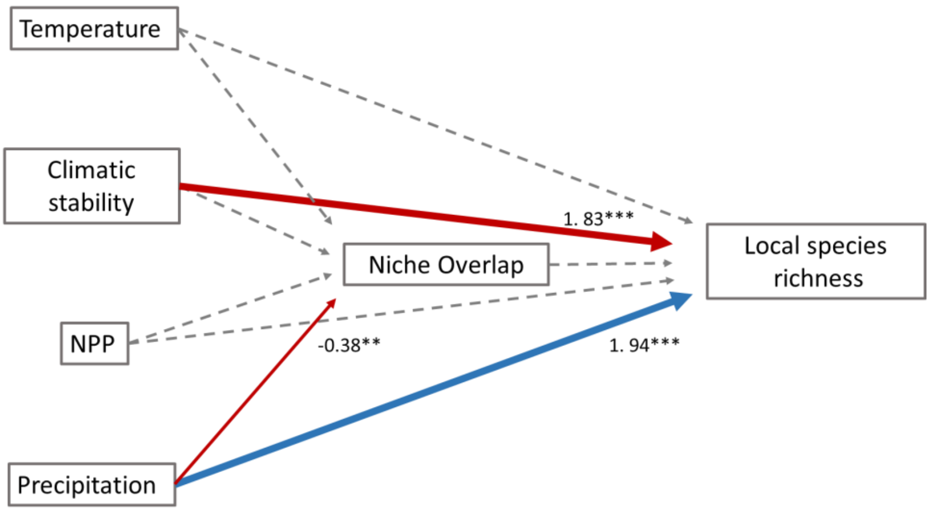


Figure 5. Relationship between paths in the model between ecological drivers, niche overlap and local species richness. Solid arrows represent significant relationships and the estimated effect sizes are next to arrows (*p

< 0.05, **p < 0.01, ***p < 0.001). We inverted the estimate signal for climatic stability because our proxy was temperature seasonality. High temperature seasonality means high climatic instability. Thickness of arrows represent the comparative effect size and positive effects are represented by blue arrows and negative ones are represented by red arrows. Traced grey lines represent non-significant paths.

Discussion

We disentangled the independent contribution of temperature, climatic stability, NPP and precipitation on the geographical variation of ant species richness and further assessed the effects of those ecological drivers on local species richness mediated by species niche overlap. We found support for *species-energy*, *water*, *metabolic theory of ecology* (*MTE*) and *climatic stability* hypotheses; however, most of the explained variation was related to the *water* and *climatic stability* hypotheses. Even though we found direct effects of precipitation on niche overlap, and precipitation and climatic stability on local species richness, we found no niche overlap mediation effects of ecological drivers on local species richness.

Species richness X ecological drivers

Species richness was higher in warmer, wetter, and more climatically stable and productive regions. However, based on the variance partitioning analysis, precipitation, followed by climatic stability, were the main drivers for variation of Brazilian ants. Hawkins et al. (2003) reported that temperature best explains the geographical variation in species richness in higher latitudes, but water factors are the main driver in low latitudes (i. e. tropical areas), which is in accord with our results that came through sampling only in tropical regions. Despite NPP and temperature positively influence the variation of many plants and animals across the globe (Hawkins et al. 2003, Buckley et al. 2012, Chu et al. 2019), including ants (Dunn et al. 2009, Jenkins et al. 2011, Kaspari et al. 2019), this finding is likely to happen because Brazilian biomes are considered more productive and warmer when compared with temperate regions at higher latitudes. Thus, NPP and temperature may not impose limiting constraints in the Neotropics.

We suggest that physiological constraints exerted by precipitation (via moisture) possibly may explain the geographic variation in neotropical biodiversity. This is supported by previous research showing strong effects on the geographical variation on population and species level for other animals and ants caused by precipitation (Pearce-Higgins et al. 2015, Gibb et al. 2015, Vasconcelos et al. 2018) and climatic stability (Arnan et al. 2014). Nevertheless, despite citing precipitation effects as a physiological constraint on animals, many studies proposed that the main mechanism promoting species richness are due to NPP effects, which positively influence speciation and negatively affect extinction rates (e.g. Hawkings 2003, Gibb et al. 2015, Vasconcelos et al. 2018). However, this is not supported by our results, as NPP and precipitation were weakly correlated while precipitation effects alone had the stronger influence.

We have two possible explanations for the higher species richness in wetter and more climatically stable regions. First, this could be a result of low extinction rates and more time for speciation. The latitudinal gradient of ant diversification is mainly due to time for speciation, but not speciation rates (Economo et al. 2018), and precipitation could be important for this process, as precipitation regimes have been important speciation refuges through time in South America ecosystems (Saupe et al. 2019). Climatic stability, in turn, could also contribute to reducing extinction rates (Fine, 2015). Second, and complementary, this could be a result of niche conservatism (Wiens et al. 2011) in relation to the dependence of wetter and climatically stable regions in Brazilian biomes. The origin and the majority of diversification of many current taxa occurred in the wet, warm and more climatically stable tropics (Wiens and Donoghue 2004). In this sense, low tolerance to climatic instability and drier environments could be challenging niche aspects for the majority of ant species. Similar processes were reported for current bird species that followed the past of precipitation regimes in Australia (Hawkins et al. 2006) and for Cerrado ants patterns that reflected the humid origin of this biome (Vasconcelos et al. 2018). Therefore, we think that patterns of ant species richness in the Neotropics are probably following the evolutionary history of the continent.

We found greater evidence for the role of precipitation and climatic stability on ant tolerance and ecological conditions requirements when observing the results for each habitat strata separately. For example, we may notice a less effect of precipitation and climatic stability in explaining the variance from epigaeic and arboreal strata to hypogaeic strata. This could happen because climate buffering and preservation of environmental humidity may increase from arboreal to hypogaeic strata. This possibility is supported by the fact that some ant traits vary across habitat strata – for example, thermal limits decrease and cuticle darkness differs from canopy to underground in order to prevent against desiccation risk (Kaspari et al., 2015; Law et al., 2019). On the other hand, temperature was the major driver influencing the hypogaeic stratum. This may indicate that temperature could be the most important ecological driver in regions that are more climatically stable and present satisfactory humidity levels.

Niche overlap mediation of the effects of ecological drivers on local species richness

Both precipitation and climatic stability directly influenced local ant species, however, these effects were not mediated by niche overlap. Even though the literature shows that more species can coexist in a local community if they have narrow niches and avoid potential competition (Chase and Leobold, 2003), we found no relationship here. Our study is in accord with Ricklefs and Marquis (2012) who did find a latitudinal gradient of niche overlap in herbivorous insects, but it did not match the variation in species richness. We suspect that this absence of relationship could be due to the stronger direct influence of precipitation and climatic stability on local species richness rather than due to the effect of niche overlap. It is also likely that these finding could be explained by other ecological interactions, such as mutualism and predation or local environmental heterogeneity – all of which not counted in our study.

Notwithstanding, we found less niche overlap in wetter regions. Our results differ from Chu et al. (2019), who found less niche overlap of tree species in warmer regions over a global data study. Possibly, the influence of ecological drivers on species co-evolution could also vary from latitudes as it does for species richness (*water-energy* hypothesis, Hawkings 2003, Evans et al. 2005) or vary between different taxa. At least for Neotropical ants, we suggest that the historical context could also shape patterns of niche overlap. A recent simulation study demonstrated that precipitation, rather than temperature, leads to high levels of Neotropical biodiversity due to temporal variability and spatially fragmented precipitation regimes that can generate species by allopatric speciation (Saupe et al. 2019). In this sense, considering that speciation events could be older in wetter regions, species could have more time to be set in particular niches due to past selective pressures.

Conclusion

Variation of Neotropical ant species richness is mainly due to precipitation regimes followed by climatic stability, probably due to niche conservatism that reflect the evolutionary history of biodiversity in the Neotropics. Vasconcelos et al (2018) also reported this historical reflection of precipitation role for ants in Cerrado biome. However, here we demonstrated that precipitation role is probably based on its physiological constraint but not due to productivity. Furthermore, it seems that water and climatic stability dependence are common requirements for ants in different biomes in Neotropics. In addition, no evidence was found of niche overlap mediating effects of ecological drivers on local species richness. However, we demonstrated that less niche overlap occurs in wetter regions that probably also followed the evolutionary history of ants in Neotropics. Since influence of ecological drivers can also vary from endothermic to ectothermic (Buckley et al. 2012), future studies are needed to confirm the same pattern for endothermic organisms. Finally, considering the negligence of current Brazilian government in relation to climate changes and with Amazon biome (Barlow et al. 2019), which in its turn are the major precipitation regulator for the entire South America (Zemp et al. 2014), biodiversity in Neotropics is endangered. This is very critical, mainly because if such physiological constraints were inherited from evolutionary time, no rapid adaptation changes could be possible for living organisms, leading many of them to extinction.

Acknowledgements

This work was funded by the Rufford Foundation's Small Grants (Project number: 21757-1) and Fundação de Amparo e Pesquisa de Minas Gerais (FAPEMIG, grant APQ-02551-16). We are thankful for the staff of each of the six protected areas where samples were carried out. We are also indebted to A.C. Souza, A.C. Reis, C. da Rosa, E.M.G.C. Silva, J.J.M. Aguiar, M.V. Mendes, M.A. Rabelo, M.A. Angotti, R.C.R. Souza, R.G. Cuissi and S. Farsura for their important help in the hard fieldwork. We are very grateful to the staff at the Laboratório de Sistemática de Formigas of Universidade Federal do Paraná for confirming ant identification, especially to A.C. Ferreira. We are also thank L.D.B. Faria for her help and advice on statistical analyses and Filipe França for critical reading. This study was part of CJ Lasmar's Ph,D. thesis at UFLA that was supported by Coordenação de Aperfeiçoamento Pessoal (CAPES, Finance code: 001).

References

Allen A. P. et al. 2006. Kinetic effects of temperature on rates of genetic divergence and speciation. – PNAS 103: 9130–9135

Arnan, X. et al. 2014. Ant functional responses along environmental gradients. – J. Anim. Ecol. 83: 1398–1408.

Baccaro, F. B. et al. 2015. Guia para gêneros de formigas do Brasil. INPA Publishing Company.

Barlow, J. et al. 2018. The future of hyperdiverse tropical ecosystems. – Nature. 559: 517–526.

Barlow, J. et al. 2019. Clarifying Amazonia's burning crisis. – Glob. Change Biol. 00:1–3

Bestelmeyer, B. T. et al. 2000 Field techniques for the study of ground-living ants: an overview, description, and evaluation. – In: Agosti D., Majer J. D. Tennant A., Schultz T. (eds) Ants: standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington, pp 122–144.

Bollen, K. A. and Stine, R. A. 1992. Bootstrapping goodness-of-fit measures in structural equation models. – Sociol. Method. Res. 21: 205–229.

Brown, J. H. 2014. Why are there so many species in the tropics? – J. Biogeogr. 41:8–22.

Buckley, L. B. et al. 2012. Broad-scale ecological implications of ectothermy and endothermy in changing environments. Global Ecology and Biogeography. – Global Ecol. Biogeogr. 21: 873–885.

Canedo–Júnior, E. O. et al. 2016. Can anthropic fires affect epigaeic and hypogaeic Cerrado ant (Hymenoptera: Formicidae) communities in the same way? – Rev. Biol. Trop. 64(1):95–104.

Chase, J. M. and Leibold, M. A. 2003. Ecological Niches: Linking Classical and Contemporary Approaches. – University of Chicago Press.

Chu, C. et al. 2019. Direct and indirect effects of climate on richness drive the latitudinal diversity gradient in forest trees. – Ecol. Lett. 22: 245–255.

Cleveland, C. C. et al. 2011. Relationships among net primary productivity, nutrients and climate in tropical rain forest: a pan-tropical analysis. Ecol. Lett. 14: 939–947.

Cleveland, C. C. et al. 2013. Patterns of new versus recycled primary production in the terrestrial biosphere. –PNAS. 110(31): 12733–12737.

Crawley, M. J. 2002. Statistical Computing, an Introduction to Data Analysis Using S–Plus. – John Wiley Sons.

Dunn, R. R. et al. 2009. Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. – Ecol. Lett. 12: 324–333.

Economo, E. P. et al. 2018. Macroecology and macroevolution of the latitudinal diversity gradient in ants. –Nat. Commun. 9: 1778.

Evans, K. L. et al. 2005. Species–energy relationships at the macroecological scale: A review of the mechanisms. – Biol. Rev. 80(1): 1–25.

Ferrante, L. and Fearnside, P. M. 2019. Brazil’s new president and ‘ruralists’ threaten Amazonia’s environment, traditional peoples and the global climate. – Environ. Conserv. 46(4): 261-263.

Fick, S. E. and Hijmans, R. J. 2017. Worldclim 2: New 1-km spatial resolution climate surfaces for a global land areas. – Int. J. Climat.

Fine, P. 2015. Ecological and evolutionary drivers of geographic variation in species diversity. – Annu. Rev. Ecol. Evol. S. 46: 369–392.

Folgarait, P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. – Biodivers. Conserv. 7: 1221–1244.

Fowler, D. et al. 2014. Niche filtering rather than partitioning shapes the structure of forest ant communities. J. Anim. Ecol. 83: 943–952.

Gibb H. et al. 2015. Climate mediates the effects of disturbance on ant assemblage structure. – Proc. R. Soc. B. 282: 20150418.

Gotelli N. et al. 2015. EcoSim in R. version 1. EcoSimRhttps://cran.r-project.org/web/packages/EcoSimR/index.html

Hawkins, B. A. et al. 2003. Energy, water, and broadscale geographic patterns of species richness. – Ecology. 84(12): 3105– 3117.

Hawkins, B. A. et al. 2006. Post-Eocene climate change, niche conservatism, and the latitudinal diversity gradient of New World birds. – J. Biogeogr. 33: 770–780.

Hillebrand, H. 2004. On the Generality of the Latitudinal Diversity Gradient. – Am. Nat. 163(2): 192–211.

Hölldobler, B. and Wilson, E. O. 1990. The Ants. – Harvard Univ. Press.

Jenkins, C. N. et al. 2011. Global diversity in light of climate change: The case of ants. – Divers Distrib. 17(4): 652–662.

Karger, D. N. et al. 2017. Climatologies at high resolution for the earth’s land surface areas. – Scientific Data. 4: 170122.

Kaspari, M. et al. 2015. Thermal adaptation generates a diversity of thermal limits in a rainforest ant community. – Glob. Change Biol., 21: 1092–1102.

Kaspari, M. et al. 2019. Species energy and Thermal Performance Theory predict 20-yr changes in ant community abundance and richness. – Ecology 100(12): e02888.

Kinlock, N. L. et al. 2018. Explaining global variation in the latitudinal diversity gradient: Meta-analysis confirms known patterns and uncovers new ones. – Global Ecol. Biogeogr. 27(1): 125–141.

Lasmar CJ et al. 2017. Testing the effect of pitfall-trap installation on ant sampling. – Insect. Soc. 64: 445–451.

Law, S. J. et al. 2019. Darker ants dominate the canopy: Testing macroecological hypotheses for patterns in colour along a microclimatic gradient. – J Anim Ecol. 2019; 00: 1– 13.

MacArthur, R. H. 1972. Geographical ecology: patterns in the distribution of species. – Harper & Row.

Mittelbach, G. G. et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. – Ecol. Lett. 10: 315–331.

Moreau, C. S. and Bell, C. D. 2013. Testing the museum versus cradle tropical biological diversity hypothesis: Phylogeny, diversification and ancestral biogeographic range evolution of ants. – Evolution. 67: 2240-2257.

Newbold T. et al. 2015. Global effects of land use on local terrestrial biodiversity. – Nature. 520: 45–50.

Pearce-Higgins et al. 2015. Geographical variation in species' population responses to changes in temperature and precipitation. – Proc. R. Soc. B. 282: 20151561.

Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. – Am. Nat. 100, 33–46.

Ribas C. R. et al. 2003. Tree heterogeneity, resource availability, and larger scale process regulating arboreal ant species richness. – Aust Ecol. 28:305–314.

Ricklefs, R. E. and Marquis, R. J. 2012. Species richness and niche space for temperate and tropical folivores. – Oecologia. 168, 213–220.

Rosseel, Y. et al. 2018. laavan an R package for structural equation modeling. version 0.6-5. https://cran.r-project.org/web/packages/lavaan/lavaan.pdf

Sandel B. et al. 2011. The influence of Late Quaternary climate change velocity on species endemism. – Science. 334: 660–64.

Saupe, E. E. et al. 2019. Spatio-temporal climate change contributes to latitudinal diversity gradients. – Nat. Ecol. Evol. 3: 1419–1429.

Schemske, D. W. et al. 2009. Is there a latitudinal gradient in the importance of biotic interactions? – Annu. Rev. Ecol. Evol. Syst. 40:245–69.

Schmidt, F. A. and Solar, R. R. C. 2010. Hypogaeic pitfall traps: methodological advances and remarks to improve the sampling of a hidden ant fauna. – Insect. Soc. 57(3): 261–266.

Schoener, T. W. 1974. Resource partitioning in ecological communities. – Science 185: 27-39.

Urban, M. C. 2015. Accelerating extinction risk from climate change. – Science. 348: 571–573.

Vasconcelos, H. L. et al. 2018. Neotropical savanna ants show a reversed latitudinal gradient of species richness, with climatic drivers reflecting the forest origin of the fauna. – J. Biogeogr. 45(1): 248–258.

Walsh, C. and Nally, R. C. 2015. hier.part: R package version 1.0-4. https://cran.r-project.org/web/packages/hier.part/hier.part.pdf

Wiens, J. J. and Donoghue, M. J. 2004. Historical biogeography, ecology and species richness. – Trends Ecol. Evol. 19:639–44.

Wiens, J. J. 2011. The niche, biogeography and species interactions. – Phil. Trans. R. Soc. 366: 2336–2350.

Wright, D. H. 1983. Species-energy theory: an extension of species-area theory. Oikos 41:496–506.

Zemp, D. C. et al. 2014. On the importance of cascading moisture recycling in South America. – Atmos. Chem. Phys. 14: 13337–13359.

Zhao, M and Running, S. W. 2010. Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. – Science. 329: 940–943.

Supplementary Appendix

Table 1. Collinearity between ecological drivers including current climate data and net primary productivity and climate data for the last glacial maximum (LGM). Temperature = Annual mean temperature; Precipitation = Annual precipitation; Climatic stability = Temperature seasonality; NPP = Net primary productivity. Each entry corresponds to correlation values (R) between a pair of ecological drivers based on Spearman correlation for non-normal distribution. Bold values ($p < 0.05$).

	Temperature	**Precipitation**	**Climatic stability**	**NPP**	**LGM Temperature**	**LGM Precipitation**	**LGM Climatic stability**
Temperature	1	0.20	**-0.55**	**-0.44**	**0.99**	-0.10	**-0.63**
Precipitation		1	0.01	**0.29**	0.22	**0.69**	0.14
Climatic stability			1	0.16	**-0.56**	-0.36	**0.96**
NPP				1	**-0.42**	**0.43**	0.13
LGM Temperature					1	0.13	**-0.63**
LGM Precipitation						1	-0.25
LGM Climatic stability							1

ARTIGO 2

DRIVERS OF THE GEOGRAPHICAL VARIATION IN ANT FORAGING ACTIVITY AND RESOURCE USE

Versão preliminar para submissão na revista Journal of Biogeography

Title: Drivers of the geographical variation in ant foraging activity and resource use

Authorship: Chaim J. Lasmar[1], Catherine L. Parr[2,3,4], Tom R. Bishop[2,3], Antônio C.M. Queiroz[1], Fernando A. Schmidt[5] and Carla R. Ribas[6]

1- Programa de Pós–Graduação em Ecologia Aplicada, Setor de Ecologia e Conservação, Laboratório de Ecologia de Formigas, Departamento de Biologia, Universidade Federal de Lavras, PO Box 3037, Lavras, MG, 37200-000, Brazil.
2- Department of Earth, Ocean and Ecological Sciences, University of Liverpool, Liverpool, U.K..
3- Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa
4- School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Wits, South Africa
5- Centro de Ciências Biológicas e da Natureza, Universidade Federal do Acre, Rio Branco, AC, Brazil
6- Laboratório de Ecologia de Formigas, Setor de Ecologia e Conservação, Departamento de Biologia, Universidade Federal de Lavras, PO Box 3037, Lavras, MG, 37200-000, Brazil

Abstract

Aim: Here we evaluated the influence of ecological factors (temperature, precipitation, climatic stability and net primary productivity) on ant foraging activity and relative resources use.

Location: Six Brazilian biomes. Amazon, Atlantic rainforest, Caatinga, Cerrado, Pampa and Pantanal.

Methods: We assessed ants’ response through a standardized sampling in 60 sites spread in six Brazilian biomes. We placed 4500 baited vials at one of three habitat strata (epigaeic, arboreal and hypogaeic) that could contain one of five liquid resources (sugar, lipids, amino acids, sodium and distilled water). We performed a model selection to assess the influence of ecological factors on ant foraging activity and relative resource use.

Results: Foraging activity was higher in warmer, wetter, more climatically stable and more productive environments. However, these patterns seem to be linked to species richness. Temperature and precipitation act positively in ant foraging performances whereas climatic stability and net primary productivity might act at the size of populations, which probably influenced the chance of finding resources. Energetic resources (sugar and lipids) were the main preferred resources by ants across our study, and ecological factors influence relative resources use in distinct ways. These influences could be due to two mechanisms, acting on resource demand regulation or shortfall limitation.

Main conclusions: We advanced the understanding of how ecological factors drive foraging activity and resource use through direct measures in the field. We suggest that ecological factors mediate ants role in the ecosystem functioning and so, many ecological process carried out by ants and possibly by other taxa are in danger front global climate change and human disturbance.

Keywords: Ants, Macroecology, Nutritional Ecology, Feeding activity, Neotropics

Introduction

Foraging is critical to the fitness of animals (Maynard Smith, 1978; Raubenheimer, Simpson, & Mayntz, 2009). Through foraging for resources, animals integrate themselves into the diversity of ecological interactions and nutrient cycles that make up functioning ecosystems (Folgarait, 1998; Tilman, Isbell, & Cowles, 2014). Species richness, distributions and abundance patterns are widely reported in the literature, and numerous mechanisms have been proposed to explain them (Brown, 2013 and references there in). Nevertheless, limited attention has been given to the drivers of animal foraging activity, and their decisions for particular resources. Knowledge on which factors limit or promote foraging activity at large scales will be helpful in a changing world where natural habitats and climates are changing at an unprecedented rate.

Existing data show that there is large variation in foraging activity patterns across space and time. For example, arthropod foraging activity is higher in the tropics than in the temperate zone, and is higher at low elevations compared to high (Peters, Mayr, Röder, Sanders, & Steffan-Dewenter, 2014; Tiede et al. 2017, Roslin et al., 2017). Animals also express seasonal changes in foraging activity (Wolda, 1978; Molleman, Remmel, & Sam, 2016). These spatial and temporal patterns have led to the development of a number of hypotheses aiming to explain them.

Net primary productivity (NPP), which is the fuel for all animals, is positively correlated with arthropod predation rates (Kaspari and Beurs, 2019). Temperature may have a similar effect, since it is a major constraint on life through its influence on biochemical reaction rates and animal metabolism (Brown, 2013). Consequently, higher temperatures tend to lead to animals being more active, moving faster and becoming more likely to find resources whilst foraging, up to a point (Gillooly et al., 2001; Stuble et al., 2013; Prather, Roeder, Sanders, & Kaspari, 2018). Precipitation events themselves may lead terrestrial animals (particularly small invertebrates) to decrease their activities due to the difficulty of foraging in the rain (Poulsen, 2008). On the other hand, foraging activity may be higher in wetter environments more generally due to decreased desiccation risk and increased resource availability (Levings, 1983; Kaspari & Weiser, 2000; Costa et al., 2018). Finally, these ecological factors can all change through time. Seasonality in temperature, productivity and rainfall can influence the availability of resources (Belchior, Sendoya, & Del-Claro, 2016; Costa et al., 2018) and the physiology of living organisms (Wolda, 1988; Baudier et al., 2018). However, few studies have assessed how these ecological factors drive the geographical variation in foraging activity patterns.

Geographical variation in foraging for specific resources can be caused by two related, but distinct, processes: resource shortfall and resource demand. Previous research has shown that if a resource is limiting (resource shortfall), then animals will dedicate a disproportionately high foraging effort to collect it (Csata & Dussutour, 2019). For example, sodium is often a limiting element in terrestrial systems, particularly in areas which are far from the sea, which is the main sources of sodium input (Kaspari, Yanoviak, & Dudley, 2008). Moreover, animals also targeted their efforts for particular resources in response to compensate for nutrient imbalances in the diet and according to their physiological requirements (resource demand) (Mayntz, Raubenheimer, Salomon, Toft, & Simpson, 2005; Raubenheimer, 2009). For example, climatic factors regulate the demand of sodium and sugar by increasing their demands at higher temperatures, in order to compensate for metabolic and excretion costs (Prather at al., 2018). Fowler, Lessard & Sanders (2014) went so far as to suggest that there is geographical variation in the degree of nutrient limitation experienced by animals. Therefore, in order to understand the geographical variation in the resource use, it is necessary to consider that both, resource shortfall and regulation of resource demand, may influence foraging decisions.

In terrestrial environments, ants are the most abundant living animals and are responsible for the majority of scavenging in tropical habitats (Hölldobler & Wilson 1990; Griffiths et al, 2018). Through their foraging activities, ants are essential components of terrestrial ecosystems as seed dispersers, scavengers, granivores, predators, and for plant defense and cycling of nutrients (Hölldobler and Wilson 1990; Folgarait, 1998; Blüthgen & Feldhaar, 2010; Tiede et al., 2017). Ants require a range of different macro and micronutrients for their development and their diet can be regulated by ecological factors (Arnan, Cerdá, & Retana, 2014; Prather et al., 2018). Sugar and lipids are the main source of energy for the entire colony, while amino acids are important for colony growth and development of larvae. Sodium is important for a number of physiological and metabolic processes (Blüthgen & Feldhaar, 2010; Csata & Dussutour, 2019).

Most studies of foraging activity patterns and nutritional ecology have been conducted at small spatial scales or in laboratories (Csata & Dussutour, 2019; but see Peters et al., 2014). Furthermore, most have not assessed foraging activity directly (e.g. counting the number of individuals in a trap and bite marks in fake plasticine animals; Kaspari & Beurs, 2019; Gibb, Grossman, Dickman, Decker, & Wardle, 2019). Understanding the influence of ecological factors on geographical variation in ant foraging activity patterns and their differential resource use will allow us to understand the role of ecological factors in influencing ant-mediated ecosystem function. Given this, we assessed the response of ant foraging activity and resource use to ecological factors, through a standardized sampling regime at a large spatial scale across six biomes in Brazil.

We asked how different ecological factors influenced (1) the occurrence of foraging ants, and (2) their relative use of different food resources. We expect that NPP, temperature, precipitation and climatic stability will positively influence the occurrence of foraging ants. We also expected that increasing temperatures will increase the relative use of sugar, amino acids and sodium due to the acceleration of ant metabolic rates with increasing temperature (Prather et al., 2018). Furthermore, we expect that low temperatures will increase the relative use of lipids because they are thermal isolates (Heinze, Foitzik, Fischer, Wanke, & Kipyatkov, 2003; Peters et al., 2014). Precipitation will decrease the relative use of sugar and lipids since precipitation generally increases the availability of plant-based carbohydrates (Costa et al., 2018). Low climactic stability will increase the relative use of lipids as it is easier to store and save for use in harsh periods (Heinze et al., 2003). Finally, high levels of NPP will decrease the relative use of sugar and lipids because NPP increases resource availability (Kaspari & Beurs, 2019; Gibb et al., 2019) and ants will choose other more limiting resources (Csata & Dussutour, 2019).

Material and Methods

Study area

We sampled in protected areas across six different biomes in Brazil which have different climates and vegetation types (Table 1). We carried out sampling in the rainy season of each biome, between November 2016 and March 2018. In each biome, we installed 10 transects which were separated by at least 800 m from each other totaling 60 transects across the study. Each transect was 740 m long and had 75 sampling points that were separated by 10 m from each other. At each sampling point, we provided one of five liquid food resources in one of three habitat strata (epigaeic, hypogaeic, and arboreal). Within each transect, we replicated each liquid food resource and strata combination five times. These combinations were spread along each transect in sequence. This gave five pseudoreplicates of each resource/habitat strata combination on each transect. In total, we had 750 sampling points per biome (75 sampling points x 10 transects) and 4500 sampling points across the study (750 x 6 biomes).

Table 1. Sampling sites characterization. Vegetation types of the sampled areas across six Brazilian biomes. Climate data were obtained from WorldClim Version 2 (Fick and Hijmans, 2017).

Biome and location	Vegetation type	Annual mean temperature (°C)	Annual minimum mean temperature (°C)	Annual maximum mean temperature (°C)	Annual precipitation (mm)	Precipitation of the driest month (mm)	Precipitation of the wettest month (mm)	Altitude (average) (m.a.s.l)	Sampling period
Amazon **Reserva Florestal de Humaitá (9°46'13"S, 67°37'7"W).**	Open rainforest with palm trees and bamboo	25.2	17.8	31.5	1,720	46	233	185	Nov/2016
Atlantic rainforest **Parque Estadual Intervales (24°17'13"S, 48°26'41"W).**	Montane dense rainforest	17.7	8.5	26.6	1,419	50	207	800	Mar/2018
Caatinga **Parque Nacional do Catimbau (8°30'19"S, 37°18'37.86"W).**	Shrublands	20.5	13.9	29	721	17	128	970	Jul/2017
Cerrado **Reserva Ecológica do IBGE and Jardim Botânico de Brasília (15°55'33"S, 47°52'59"W).**	Brazilian savannah; Cerrado *strictu senso*	20.1	11.5	27.5	1,519	8	263	1,100	Dec/2017
Pampa **Parque Estadual do Espinilho (30°11'25"S, 57°29'51"W).**	Humid stepic savannah	19.8	7.7	31.2	1,474	67	165	51	Nov/2017
Pantanal **Sesc Pantanal (16°31'22.59"S, 56°24'6.41"W)**	Different vegetation types varying from grasslands and natural forest remnants, also presenting natural floods	25.2	14.9	34.9	1,317	19	215	123	Apr/2017

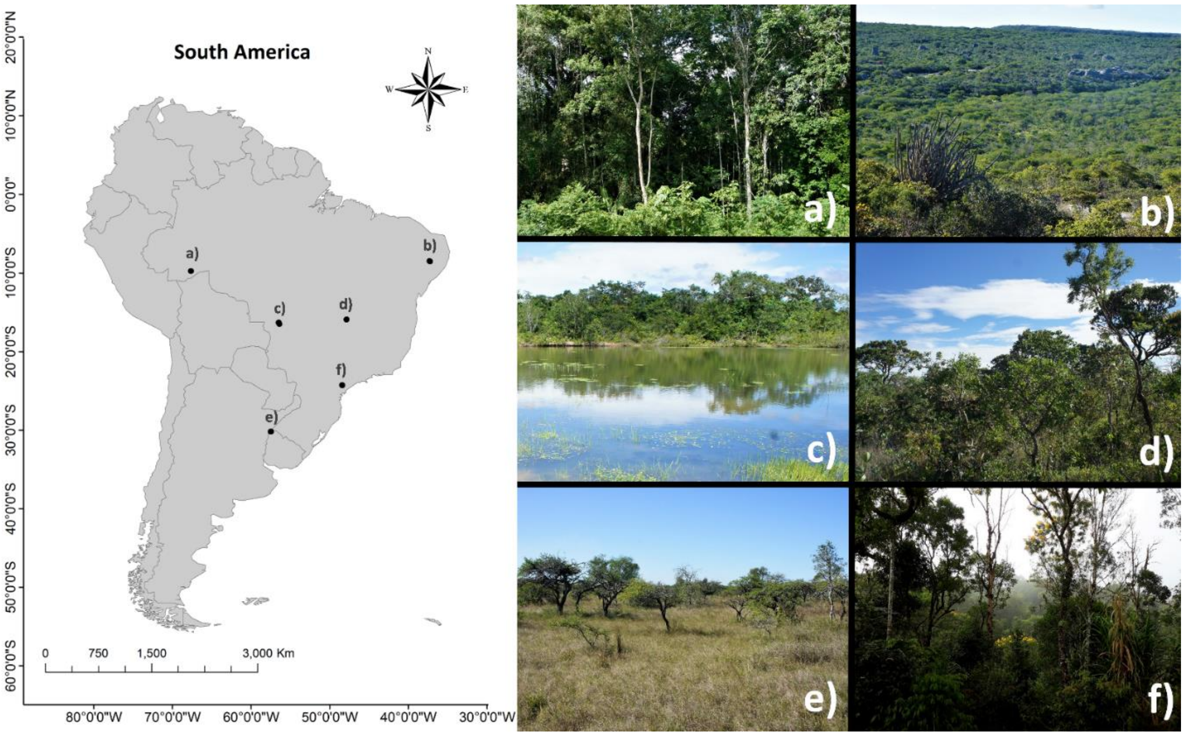


Figure 1. Location of the sampling sites across six Brazilian biomes: a) Amazon, b) Caatinga, c) Pantanal, d) Cerrado, e) Pampa and f) Atlantic rainforest.

Sampling of foraging ants

We placed the resources in 50-mL Fisher Scientific polypropylene centrifuge tubes with a 5 cm cotton ball containing 10 ml of the following solutions (distilled water/volume): 1% sodium (NaCl), 20% sugar (CHO, made with sucrose), 20% amino acids (AA, made with unflavored whey protein isolate), lipids (extra virgin olive oil), and distilled water, as a control (Fowler et al., 2014). Similar liquid resources have been used in previous studies (Fowler et al., 2014; Peters et al., 2014; Tiede et al., 2017).

In the epigaeic habitat strata, we placed the baited tubes horizontally on the ground. For arboreal habitat strata, we fixed the tubes horizontally, using a piece of adhesive and a string to keep the tube fixed at approximately 2 m above the ground in the closest tree trunk in the sampling point. For hypogaeic habitat strata, we placed the tubes in a plastic box that was 4.5 cm high, 8 cm wide and 15 cm long, containing four holes, each one in one side of the box and buried it 20 cm below the ground surface. We began placement of the baited tubes at 7:00 am at each site and left them open for 3 hours. After that, we closed the tubes with the cap in order to collect all the ants that visited it. However, in the Caatinga biome, we started to place the tubes at 1:00 pm because there was more rain in the morning in this area, which could decrease ant activity.

In the laboratory, we counted all the ant workers and identified them to genera following Baccaro et al. (2015), and whenever possible, to species level or morphospecies using relevant literature and matching with the ant reference collection of Laboratório de Ecologia de Formigas of the Universidade Federal de Lavras (UFLA). After that, we confirmed the identification at Laboratório de Sistemática de Formigas of the Universidade Federal do Paraná (UFPR). Voucher specimens are deposited in the reference collection of Laboratório de Ecologia de Formigas at UFLA and Entomological Collection Padre Jesus Santiago Moure of UFPR (DZUP).

Ecological factors

To obtain temperature, precipitation and climatic stability data, we accessed the WorldClim 2 database with a resolution of 1 km² (Fick & Hijmans, 2017) which represents average climate between 1970 and 2000. We extracted per transect, annual mean temperature (C°), annual precipitation (mm), temperature seasonality (standard deviation of annual mean temperature as a measure of climatic stability), precipitation seasonality (coefficient of variation of annual precipitation), monthly mean temperature (°C), and monthly precipitation (mm). We extracted these variables for the corresponding month that we sampled in each biome (Table 2).

We obtained net primary productivity (NPP) from MODIS NPP data representing the annual average of 2000 – 2015 years (MOD17) from the NASA Earth Observation System repository at the University of Montana (www.ntsg.umt.edu/), which improved MOD17 by cleaning it from cloud-contaminated pixels. The improved MOD17 uses a model that considers the difference between gross primary productivity and autotrophic respiration (Zhao and Running, 2010) and it is presents1 km spatial resolution.

Data analyses

Before analyzing the data, we checked for collinearity between our ecological factors ('Psych' package in R; Revelle, 2011; Supplementary appendix 1). We found strong association (correlation R > 0.65) between annual mean and monthly mean temperatures, annual and monthly precipitation, also between temperature seasonality and precipitation seasonality (Supplementary appendix 1, Table 1). Therefore, we only performed the subsequent analyses with monthly mean temperature, monthly precipitation, temperature seasonality (as a proxy of temperature, precipitation and climatic stability, respectively) and NPP.

To answer our first question about the influence of ecological factors on the occurrence of foraging ants, we constructed generalized linear models (GLM) where the proportion of visited tubes per transect was the response variable (n = 60 transects). Because our response variable was proportion data, we used a logit transformation to meet the Gaussian assumptions (Warton & Hui, 2011). A tube was classed as visited when there was at least one ant individual inside. Temperature, precipitation, climatic stability and NPP were explanatory variables. We used the *dredge* function ('MuMIn' package in R; Barton 2014) to run all the possible models, ranking them based on the Akaike criteria (AIC), considering only the models with ΔAICc < 2. We tested if the result remained the same with and without the control tubes. Since species richness and abundance may be correlated with ant foraging activity (Kaspari, Alonso & O'Donnel, 2000; Gibb et al., 2019) we also checked if our response variable (occurrence of foraging ants) was correlated with the number of ant workers and species richness at each transect by running a GLM. Once the correlation was detected, we extracted the residuals from the correlation of occurrence of foraging ants and ant species richness and performed another model selection using *dredge* function in order to determine how the occurrence of foraging ants was influenced by ecological factors controlling for its relationship with species richness.

To answer our second question on how ecological factors influence the use of different resources, we performed the same AIC selection using the dredge function (‘MuMIn’ package in R; Barton 2014). In this case, however, each resource type (Control, CHO, Lipids, Amino Acids and NaCl) was modelled as the response variable separately. Relative resource use, our response variable, was calculated as the number of visited tubes of a given resource on a transect, divided by the total number of visited tubes (including control) on a transect. Consequently, a relative use of 1 indicates that all foraging took place only on that resource, whilst a relative use of 0 means than no foraging took place on that resource and instead took place on other resource types. Consequently, the relative use indicates the use of a given resource type in relation to all others and it is not dependent on the different occurrences of foraging ants in transects. We used a logit transformation in relative resource use since it is also proportion data. Each GLM had temperature, precipitation, temperature seasonality and NPP as explanatory variables. Furthermore, as CHO, AA and NaCl solutions were made using distilled water, we performed another model selection that included the relative use of the control tubes (distilled water) as an extra explanatory variable. We expected that, if ants visited those resources only because of the water attraction, then the relative control use would be in the best model, positively influencing the response variable and, with no other explanatory variables. All the analyses were carried out in the R software 3.4.1 (R Development Core Team 2017).

Results

How do ecological factors influence the occurrence of foraging ants?

We sampled 26,752 ant workers belonging to 255 ant species and 40 genera across the study (Supplementary appendix 2). We obtained the same results for this question whether or not the control tubes were used when calculating the occurrence of foraging ants (Supplementary appendix, Table 1), therefore we only report results without control tubes. The best model explaining the occurrence of foraging ants included temperature, precipitation, temperature seasonality, and NPP (R^2 = 0.72; Table 2). The occurrence of foraging ants increased as precipitation, temperature and NPP increased and decreased as climatic stability decreased (Fig 2).

Since there were positive relationships between the proportions of visited tubes and both ant species richness and the number of ant workers (R^2 = 0.84; Fig. 3), we performed the model selection using the residuals of the relationship between occurrence of foraging ants and ant species richness and ecological factors. In this case, only precipitation was present in the best model and positively influenced the occurrence of foraging ants (R^2 = 0.09; Table 2). This could indicate that the influence of ecological factors on both foraging activity and species richness are linked, and that precipitation is the only factor that influences foraging activity regardless its relationship with species richness.

Table 2. Model selection using the *dredge* function (Barton, 2015) based on the Akaike information criterion (AICc) ranking across six Brazilian biomes. The generalized linear models were constructed for question 1 and 2 with the explanatory variables: temperature (monthly mean temperature, MMTemp), precipitation (monthly precipitation, MPrec), climatic stability (temperature seasonality, TSeas), net primary productivity (NPP). In question 1, we also performed the same model selection using the residuals from the correlation between occurrence of foraging ants and ant species richness. In question 2, the models were ran separately for four resources types represented as a solution of: 1% sodium (NaCl), 20% sugar (CHO, made with sucrose), 20% amino acids (AA, made with unflavored whey protein isolate), and lipids (extra virgin olive oil). We only considered and pointed out models equal or lower than Δ =2. Degrees of freedom of the model (d.f.), differences in AICc-values (Δ) and Akaike weight (ω) are shown.

Question 1: How do ecological factors influence the occurrence of foraging ants?

Model	d.f.	AICc	Δ	ω	Log Likelihood	Adjusted R²
MMTemp + MPrec + TSeas + NPP	6	57.2	0.00	0.996	-21.82	0.72
Question 1: using the residuals from the correlation between occurrence of foraging ants and ant species richness.						
Model	d.f.	AICc	Δ	ω	Log Likelihood	Adjusted R²
MPrec	3	21.8	0.00	0.391	-7.67	0.09
Question 2: How do ecological factors influence the use of different resources by foraging ants?						
CHO						
Model	d.f.	AICc	Δ	ω	Log Likelihood	Adjusted R²
MPrec + TSeas + NPP	5	68.3	0.00	0.57	-28.57	0.43
Lipids						
Model	d.f.	AICc	Δ	ω	Log Likelihood	Adjusted R²
MMTemp + MPrec + NPP	5	52.5	0.00	0.39	-20.71	0.49
MMTemp + MPrec	4	53.4	0.83	0.26	-22.32	0.47
MMTemp + MPrec + TSeas + NPP	6	54.2	1.62	0.17	-20.29	0.49
MMTemp + MPrec + TSeas	5	54.2	1.68	0.17	-21.55	0.48
AA						
Model	d.f.	AICc	Δ	ω	Log Likelihood	Adjusted R²
MMTemp + TSeas	4	138.4	0.00	0.45	-64.84	0.26
MMTemp + MPrec + TSeas	5	139.9	1.47	0.21	-64.38	0.26
MMTemp + TSeas + NPP	5	140.2	1.80	0.18	-64.54	0.26
NaCl						
Model	d.f.	AICc	Δ	ω	Log Likelihood	Adjusted R²
MMTemp + MPrec + TSeas + NPP	6	137.6	0.00	0.41	-62.01	0.54
MPrec + TSeas +NPP	5	137.9	0.27	0.36	-63.38	0.53

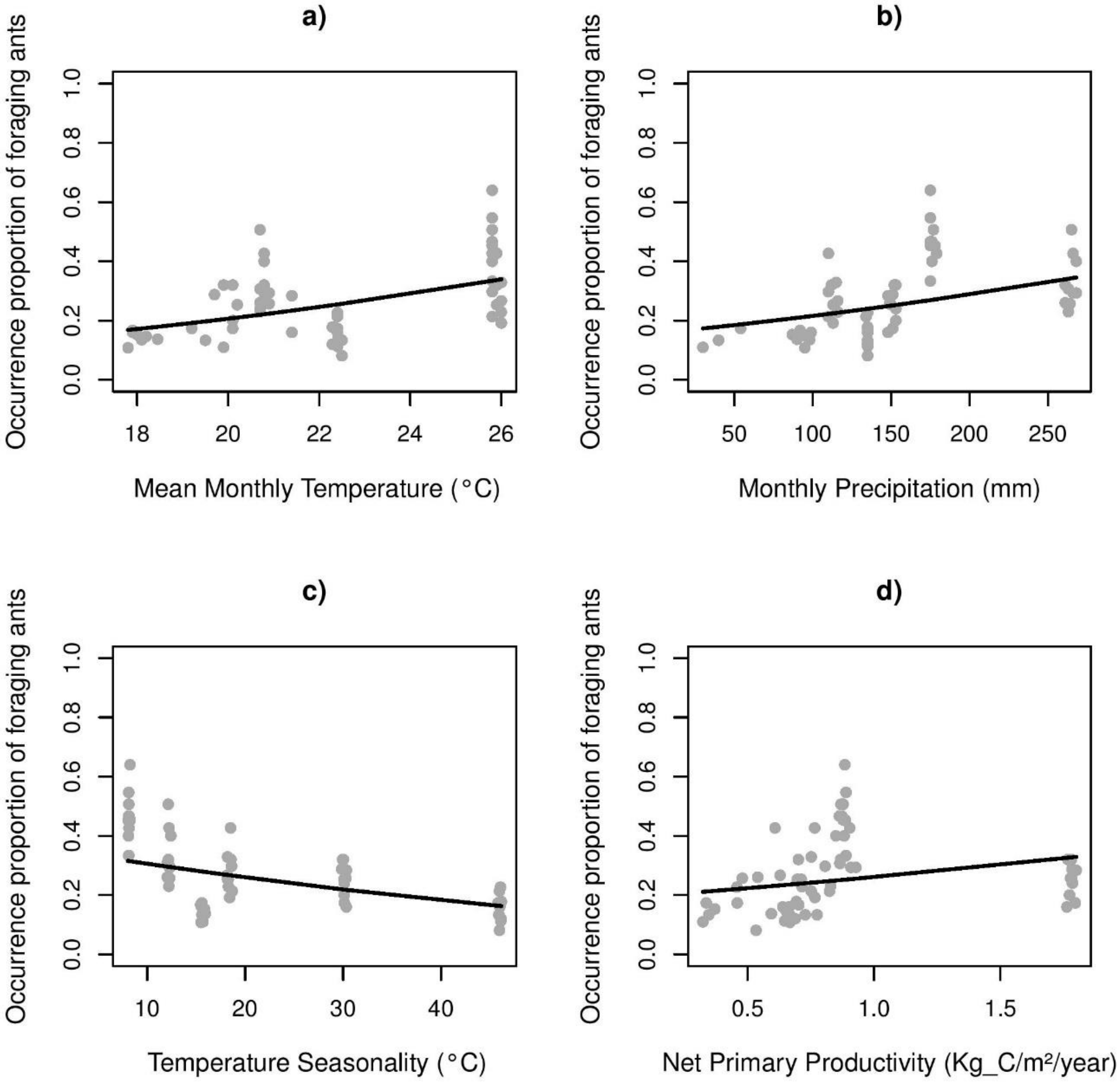


Figure 2. Generalized linear models (GLMs) between the proportion of occurrence of foraging ants (y-axes) and ecological factors. Points in the graphs are the proportion of visited tubes per transect and the black line represent the effects of a) temperature (mean monthly temperature); b) precipitation (monthly precipitation); c) climatic stability (temperature seasonality) and d) net primary productivity (NPP). Note that more climatically stable environment means an environment with low values of temperature seasonality.

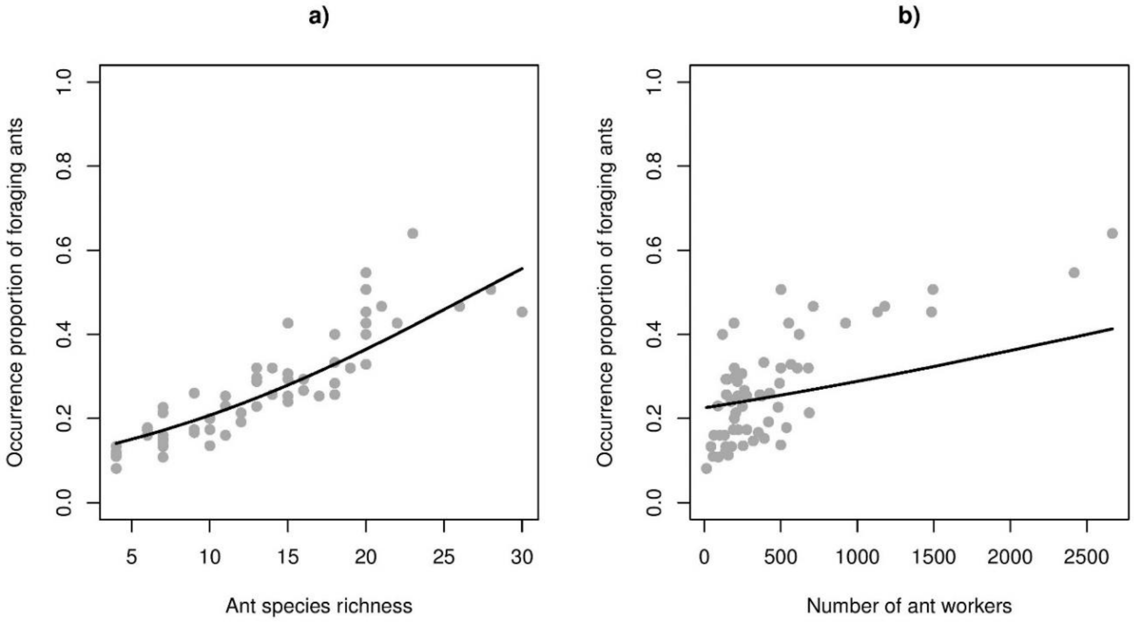


Figure 3. Generalized linear model (GLM) between the occurrence proportion of foraging ants a) number of ant species richness (F = 297.55; $p < 0.001$) and b) number of ant workers (F = 15.41; $p < 0.001$).

How do ecological factors influence the use of different resources by foraging ants?

The most visited resource type was sugar (CHO) represented by 44% of visited tubes over the whole study, followed by lipids with 40%, sodium (NaCl) with 23%, amino acids (AA) with 20% and distilled water (Control) with 6%. NaCl had a great variation in the number of visited tubes when comparing the biomes, ranging from the second least visited in Caatinga biome (five visits) to the most visited in Amazon (89 visits) (See Supplementary appendix, Table 2).

The best models (lowest AIC) for each type of resource are described in Table 2. Relative CHO use was positively influenced by temperature seasonality (Fig. 4c) and negatively influenced by precipitation (Fig. 4b) and NPP (Fig. 4d) ($R^2 = 0.44$). Relative lipid use was positively influenced by NPP (Fig. 4d) and negatively influenced by temperature (Fig. 4a) and precipitation (Fig. 4b) ($R^2 = 0.47$). Relative use of amino acid was positively influenced by temperature (Fig. 4a) and negatively influenced by temperature seasonality (Fig. 4c) ($R^2 =

0.27). Relative sodium use was positively influenced by temperature (Fig. 4a), precipitation (Fig. 4b) and NPP (Fig. 4d) and, negatively influenced by temperature seasonality (Fig. 4c) (R^2 = 0.55). Figures were constructed with the influence of each ecological factors on resource types (See Supplementary appendix, Fig. 2-5, for graphs per resource use).

No considerable changes were detected after controlling for relative control use (Supplementary appendix 1, Table 2), indicating that visits in CHO, AA and NaCl tubes were, at least mainly, by the resource itself attraction but not for water attraction.

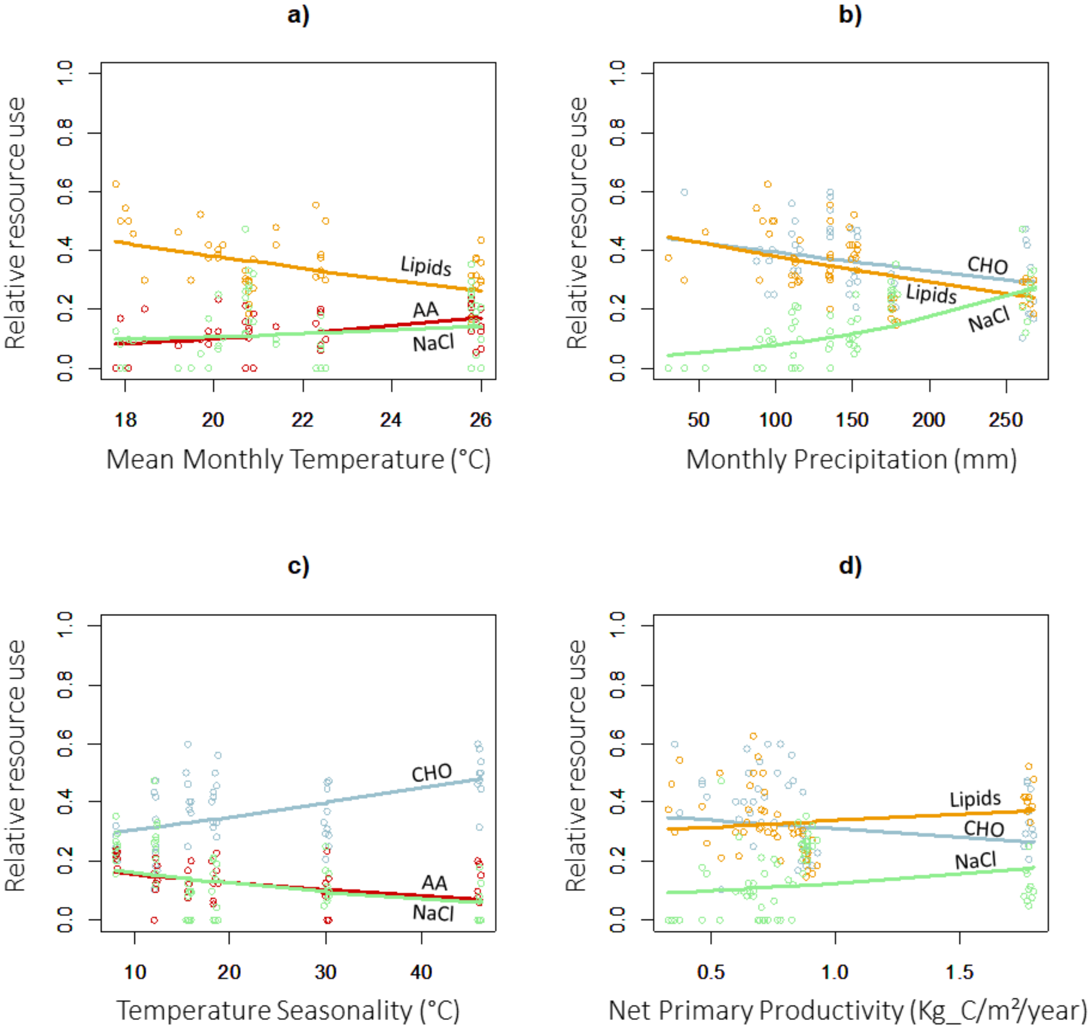


Figure 4. Generalized linear models (GLM) between relative use (y-axes) of sugar (CHO; Blue), lipids (Orange), amino acids (AA; Red) and sodium (NaCl; Green) and ecological factors. Points in the graphs represent the relative use in a given transect

and lines are the effects of a) temperature (mean monthly temperature) b) precipitation (monthly precipitation); c) climatic stability (temperature seasonality) and d) net primary productivity (NPP) on the respective resource type regarding its color. Note that more climatically stable environment means an environment with low values of temperature seasonality.

Discussion

Although geographical variation in foraging activity and resource use in animals has been documented, few studies have directly assessed what drives this variation in the field. Here, we highlight the importance of ecological factors in mediating ant foraging activity and resource use patterns, with likely implications for ecosystem functioning. In short, all the tested ecological factors (temperature, precipitation, climatic stability and NPP) explained 72% of the variation of the ant foraging activity. Moreover, ecological factors also explained the geographical variation in resource use.

How do ecological factors influence the occurrence of foraging ants?

Foraging activity is higher in hotter, wetter, more climatically stable and more productive environments (Fig. 2). Previous studies also found a positive influence of temperature (Stuble et al., 2013; Prather et al., 2018), precipitation (Kaspari & Weiser, 2000; Gibb et al., 2019) and NPP (Kaspari & Beurs, 2019) on foraging activity. These examples, however, come from small spatial scales or through indirect measures. Through the positive influence of temperature on metabolic rate, ants can move faster and capture more resources (Stuble et al., 2013; Prather et al., 2018); such metabolic acceleration is also common for other animals and plants (Gillooly et al., 2001; Barneche et al., 2008). It is likely that precipitation increases ant foraging activity directly by reducing physiological stress (Kaspari and Weiser, 2000; Gibb et al., 2019), and indirectly by increasing plant and animal resource availability (Levings, 1983; Costa et al., 2018; Gibb et al., 2019). Given that ants are typically described as thermophilic (Hölldobler & Wilson 1990), and that the majority of the Neotropical ant fauna originated and diversified following the expansion of hot and humid tropical forests (Moreau et al., 2013;

Price et al., 2014, Vasconcelos et al., 2018), the greater foraging activity in hotter and wetter environments could represent niche characteristics that have been conserved through evolutionary time.

It is possible that less climatically stable environments could have a negative effect on ant abundance (i.e. number of colonies) and colony size (i.e. number of ant workers) due to the reduced foraging activity in harsh periods (e.g. low temperatures and precipitation) (Kaspari et al., 2000). Although we do not have ant colony data, we show that the number of ant workers and foraging activity are positively correlated (Fig. 3). Conversely, ant abundance and the number of ant workers may be greater in more productive environments due to the increased energy and carbon available for individuals (Kaspari at al., 2000; Kaspari & Beurs, 2019). In this sense, the high number of ants in more climatically stable and productive environments might increase the probability of ants finding resources, which could reflect in more visited baits in such environments.

After controlling for ant species richness, precipitation was the most important factor explaining foraging activity. The drastic decrease in explained variance (from $R^2 = 0.72$ to $R^2 = 0.09$) suggests that patterns in foraging activity and species richness could be strongly linked. Even though this result is in according with other studies (e. g. Gibb et al., 2019), our data cannot determine whether foraging activity regulates species richness or vice versa, or even if ecological factors independently influence both parameters. It would be useful for future studies to address such causality.

How do ecological factors influence the use of different resources by foraging ants?

We observed a preference of ants for sugar and lipids across all six Brazilian biomes, which agrees with previous studies (e.g. Fowler et al., 2014; Peters et al., 2014). It could indicate that sugar and lipids (energetic resources) are the most important for ants regardless of the geographical region, even though other macro- and micro-nutrients are important for colony development (Blüthgen & Feldhaar, 2010). This preference for energetic resources has been hypothesized to explain the high dominance behavior of ants in protecting and monopolizing carbohydrate-rich resources (Grover, Kay, Monson, Marsh, & Holway, 2007).

As predicted, with increasing temperatures, ants increase the relative use of amino acids. This is possibly to supply colony growth (Porter 1988; Asano & Cassil, 2012). Furthermore, increasing temperatures increase the foraging for sodium as a response to the costs of metabolic rate acceleration and loss by excretion (Prather et al. 2018). Also as predicted, ants increase relative lipid use at lower temperatures because they are important components for thermal isolation (Heinz et al., 2003; Peters et al. 2014). Although at small spatial scales ants increase CHO and sodium consumption with increasing temperature (Prather et al., 2018), we found no pattern for relative CHO use as expected. This means that variation in CHO consumption due to temperature could be more sensitive at small spatial or because sodium consumption is more sensitive to temperature variation than CHO (Prather et al., 2018).

Ants increase the relative use of CHO and lipids in drier environments, but of sodium in wetter environments (Fig. 4b), which could indicate that ants are limited by different resources depending on precipitation levels. Ants could be limited by plant-based resources in drier environments, an explanation that could support the observations of greater interactions and frequencies of dominant ants in extrafloral nectaries in drier environments (Leal & Peixoto, 2016). Returning to the influence of precipitation on foraging activity, if ants forage more for plant sugar where it is in shortfall, high levels of precipitation will probably not stimulate foraging activity. Hence, this could indicate that reducing physiological stress is the main mechanism driving the greater occurrence of foraging ants in wetter environments. On the other hand, other resources seem to be limiting ants after CHO and lipids are in satisfactory levels in the ecosystem (e.g. sodium in wetter environments). Ants also increase their foraging effort when sodium levels in the environment are in shortfall (Kaspari et al., 2008). Thus, as sodium is water soluble, we suggest that high precipitation levels may easily leach it out from the environment, which may turn it a limiting resource.

Although we predicted high lipid use in less climatically stable environments due to its advantage for storage (Heinze et al., 2003), our results do not support this. Instead, ants increased the relative use of CHO in less climatically stable environments, while they increased the relative use of amino acids and sodium in more climatically stable environments (Fig. 4c). As seasonality could harm ant populations (Kaspari et al., 2000), obtaining more easily digestive energetic resources, such as sugar, could be more advantageous to redress harmful effects of harsh periods on ant abundance than lipid storage. However, where climate is more stable, ants might forage for a longer period of the year, which results in more foraging workers and possibly more colonies spread in the environment. In this case ants could become more limited by resources that improve ant colony size (e.g. AA) and resources that supply the high foraging activity costs (e.g. sodium). A similar trade-off between CHO and AA also occurs with ants at small spatial scales (Vidal, Silva, & Sendoya, 2018) and with primates at large spatial scales, depending on the degree of seasonality (Coleman and Hill, 2014).

As predicted, ants increased relative CHO use in less productive environments and increased the relative use for other limiting resources, such as sodium in more productive environments. However, contrary to our expectations, ants also increased the relative use of lipids in more productive environments (Fig. 4d). NPP is related to how much energy is available for animals (Kaspari at al., 2000). Thus, the relative use of CHO could increase in less productive environments to supply the energy deficit by ant assemblages. However, for the opposite pattern of relative lipid use, we have two possible explanations. First, considering that dominant ants can restrict sugar sources (Kay, 2004), subdominant and submissive species could avoid such conflict by directing the forage effort to lipids, of which energetic benefits could be higher than CHO’s. Another aspect to consider is that arthropods at higher trophic levels are lipid-limited (Wilder, Norris, Lee, Raubenheimer, & Simpson, 2013, Peters et al., 2014). Since higher NPP may increase species populations at different trophic levels (Kaspari, Ward, & Yuan, 2004), there are probably more scavenger and predator ants in more productive environments, which are related to the high consumption of lipid-rich resources (Rosumek et al., 2018).

Finally, considering that foraging activity is higher in more productive environments, the demand for sodium could increase to supply the resulted sodium losses by excretion (Prather et al., 2018), similar to the effects of climatic stability. Interestingly, the same factors that influenced the occurrence of foraging ants (and in the same direction) also influenced the relative use of sodium. We suggest that besides the influence of ecological factors on sodium demand and shortfall presented here, sodium is also in greater demand where foraging activity is higher. Thus, sodium could be a critical limiting resource that probably constrains foraging activity performances as it does in decomposition and carbon cycle processes in tropical forests (Kaspari, Yanoviak, Dudley, Yuan, & Clay, 2009; Kaspari, Clay, Donoso, & Yanoviak, 2014).

Conclusion

From laboratories to small regions and mountains or through indirect measures and in this study across a continental scale through direct measures, we move a step forward in our understanding of the geographical variation in foraging activity and resource use. The majority of variation in ant foraging activity can be explained by ecological factors. However, this may be confounded by species richness, which it would be useful future studies assess the causality of the positive relationship between foraging and species richness. Furthermore, different food resources are selected in different environments through the influence of ecological factors that can act on resource shortfall or on resources demand. In this sense, ecological processes carried out by ants, through their foraging activity and decisions for particular resources, may be constrained by changes in climate and NPP. Thus, considering the existence of the influence of ecological factors on the variation of foraging activity and on the resources use for other taxa (e.g. Barneche et al., 2008, Kissling, Sekercioglu, & Jetz, 2012; Coleman and Hill, 2014), we suggest that the observed patterns can be generalized (especially for ectotherms). Finally, as tropical ectotherms are the most sensitive animals to climate changes (Deutsch et al, 2008) and governmental policies for biodiversity conservation and global climate change are neglected, especially in Brazil (Urban, 2015; Ferrante and Fearnside, 2019), several ecological processes can be endangered.

Acknowledgements

This work was funded by the Rufford Foundation's Small Grants (Project number: 21757-1) and Fundação de Amparo e Pesquisa de Minas Gerais (FAPEMIG, grant APQ-02551-16). We are thankful for the staff of each of the six protected areas where samples were carried out. We are also indebted to A.C. Souza, A.C. Reis, C. da Rosa, C.V. Oliveira, E.M.G.C. Silva, I.W.G. Carvalho, J.J.M. Aguiar, M.V. Mendes, M.A. Rabelo, M.A. Angotti, M.M.G. Imata, R.C.R. Souza, R.G. Cuissi and S. Farsura for their important help in the hard fieldwork. We are very grateful to the staff at the Laboratório de Sistemática de Formigas of Universidade Federal do Paraná for confirming ant identification, especially to R.M. Feitosa and A.C. Ferreira. We are also thank H.M. Griffiths for her help and advice on statistical analyses and C.A. Nunes for critical reading. This study was part of CJ Lasmar's Ph.D. thesis at UFLA that was supported by Coordenação de Aperfeiçoamento Pessoal (CAPES, Finance code: 001).

References

Arnan, X., Cerdá, X. & Retana, J. (2014), Ant functional responses along environmental gradients. *Journal of Animal Ecology, 83,* 1398-1408.

Asano, E., & Cassill, D. L. (2012). Modeling temperature-mediated fluctuation in colony size in the fire ant, *Solenopsis invicta*. *Journal of Theoretical Biology, 305,* 70–77.

Baccaro, F. B., Feitosa, R. M., Fernandez, F., Fernandes, I. O., Izzo, T. J., Souza, J. L. P., Solar, R. (2015) *Guia para gêneros de formigas do Brasil*. INPA Publishing Company, Manaus, Brasil.

Barneche, D. R., Floeter, S. R., Ceccarelli, D. M., Frensel, D. M., Dinslaken, D. F., Mário, H. F., & Ferreira, C. E. (2009). Feeding macroecology of territorial damselfishes (Perciformes : Pomacentridae). *Marine Biology, 156,* 289–299.

Barton, K. (2014). *MuMIn: Multi-model inference*. R package version 1.10.5. https://cran.r-project.org/package=MuMIn

Baudier, K. M., D'Amelio, C. L., Malhotra, R., Michael P. O'Connor, M. P. & Sean O'Donnell1, S. (2018). Extreme Insolation: Climatic Variation Shapes the Evolution of Thermal Tolerance at Multiple Scales. *The American Naturalist*, 192 (3), 347–359.

Belchior C., Sendoya S. F., Del-Claro K. (2016) Temporal Variation in the Abundance and Richness of Foliage-Dwelling Ants Mediated by Extrafloral Nectar. *Plos one,* 11(7): e0158283.

Blüthgen, N., & Feldhaar, H. (2010). Food and Shelter: How Resources Influence Ant Ecology: In Lach, L., Parr, C. L., & Abbot, K. L. *Ant Ecology*. Oxford, Oxford University Press.

Brown, J. H. (2014), Why are there so many species in the tropics? *Journal of Biogeography, 41*, 8–22.

Csata E., & Dussutour, A. (2019). Nutrient regulation in ants (Hymenoptera: Formicidae): a review. *Mymecological News*, *29*, 111–124.

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

Coleman B. T., & Hill, S. A. (2014). Biogeographic Variation in the Diet and Behaviour of Cercopithecus mitis. *Folia Primatologica, 85,*319–334.

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences May* 2008, *105*, 6668-6672.

Dussutour, A., & Simpson, S.J. (2012) Ant workers die young and colonies collapse when fed a high-protein diet. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 2402–2408.

Ferrante, L., & Fearnside, P. M. (2019). Brazil's new president and 'ruralists' threaten Amazonia's environment, traditional peoples and the global climate. *Environmental Conservation*, *46*(4), 261-263.

Fick, S. E., & Hijmans, R. J. (2017). Worldclim 2: New 1-km spatial resolution climate surfaces for a global land areas. *International Journal of Climatology*.

Folgarait, P. J. (1998). Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodiversity and Conservation*, *7*, 1221–1244.

Fowler, D., Lessard, J. P., & Sanders, N.J. (2014) Niche filtering rather than partitioning shapes the structure of forest ant communities. *Journal of Animal Ecology*, 83, 943–952.

Gibb, H., Grossman, B. F., Dickman, C. R., Decker, O., & Wardle, G. M. (2019) Long-term responses of desert ant assemblages to climate. *Journal of Animal Ecology*, *88*, 1549– 1563.

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., & Charnov, E. L. (2001) Effects of Size and Temperature on Metabolic Rate. *Science*, *293*, 2248-2251

Griffiths, H. M., Ashton, L. A., Walker, A. E., Hasan, F., Evans, T. A., Eggleton, P., & Parr, C. L. (2018). Ants are the major agents of resource removal from tropical rainforests. *Journal of Animal Ecology*, *87*, 293–300.

Grover, C. D., Kay, A. D., Monson, J. A., Marsh, T. C., & Holway, D. A. (2007). Linking nutrition and behavioural dominance: carbohydrate scarcity limits aggression and activity in Argentine ants. Proceedings. Biological sciences, 274(1628), 2951–2957. doi:10.1098/rspb.2007.1065

Heinze, J., Foitzik, S., Fischer, B., Wanke, T., & Kipyatkov, V. E. (2003) The significance of latitudinal variation in body size in a holarctic ant, Leptothorax acervorum. *Ecography*, *26*, 349-355.

Hölldobler, B. & Wilson, E.O. (1990). *The Ants*. Harvard University Press, Cambridge, MA.

Kaspari, M., Alonso, L. & O'Donnell, S. (2000) Three energy variables predict ant abundance at a geographical scale. *Proceedings of the Royal Society of London B*, *267*, 485-489.

Kaspari, M., & Weiser, M. D. (2000). Ant Activity along Moisture Gradients in a Neotropical Forest. *Biotropica*, *32*, 703-711.

Kaspari, M., Ward, P., & Yuan, M. (2004) Energy gradients and the geographic distribution of local ant diversity. *Oecologia*, *140*, 407–413.

Kaspari, M., Yanoviak, S.P. & Dudley, R. (2008) On the biogeography of salt limitation: a study of ant communities. *Proceedings of the National Academy of Sciences USA, 105,* 17848–17851.

Kaspari, M., Yanoviak, S.P., Dudley, R., Yuan, M., & Clay, N.A. (2009) Sodium shortage as a constraint on the carbon cycle in an inland tropical rainforest. *Proceedings of the National Academy of Sciences USA*, *106*, 19405– 19409.

Kaspari, M., Clay, N. A., Donoso, D. A. & Yanoviak, S. P. (2014) Sodium fertilization increases termites and enhances decomposition in an Amazonian forest. *Ecology*, *95*, 795-800.

Kaspari, M., & Beurs, K. (2019) On the geography of activity: productivity but not temperature constrains discovery rates by ectotherm consumers. *Ecosphere, 10*(2), e02536.

Kay, A. (2004) The relative availabilities of complementary resources affect the feeding preferences of ant colonies. *Behavioral Ecology, 15*, 63–70.

Kissling, W. D., Sekercioglu, C. H., & Jetz, W. (2012) Bird dietary guild richness across latitudes, environments and biogeographic regions. *Global Ecology and Biogeography*, *21*, 328-340.

Leal, L. C., & Peixoto, P. E. C. (2016) Decreasing water availability across the globe improves the effectiveness of protective ant-plant mutualisms: a meta-analysis. *Biological Reviews*, 92(3),1785-1794.

Levings, S. C. (1983) Seasonal, annual, and among-site variation in the ground ant community of a deciduous tropical forest: Some causes of patchy species distributions. *Ecological Monographs*, *53*(4), 435-455.

Maynard Smith, J. (1978) Optimization theory in evolution. *Annual Review of Ecology and Systematics*, *9*, 31–56.

Mayntz, D., Raubenheimer, D., Salomon, M., Toft, S., & Simpson S. J. (2005) Nutrient-Specific Foraging in Invertebrate Predators. *Science*, *307*, 111-113.

Molleman, F., Remmel, T., & Sam, K. (2016) Phenology of Predation on Insects in a Tropical Forest: Temporal Variation in Attack Rate on Dummy Caterpillars. *Biotropica*, *48*: 229-236.

Moreau, C. S., & Bell, C. D. (2013) Testing the museum versus cradle tropical biological diversity hypothesis: phylogeny, diversification, and ancestral biogeographic range evolution of the ants. *Evolution*, *67,* 2240-2257.

Peters, M. K., Mayr, A., Röder, J., Sanders, N. J. and Steffan-Dewenter, I. (2014) Variation in nutrient use in ant assemblages along an extensive elevational gradient on Mt Kilimanjaro. *Journal of Biogeography*, 41, 2245-2255.

Porter S. D. (1988) Impact of temperature on colony growth and developtemal rates of the ant, *Solenopsis invicta*. *Journal of Insect Physiology, 34*, 1127-1133.

Poulsen, B. O. (1996) Relationships between frequency of mixed-species flocks, weather and insect activity in a montane cloud forest in Ecuador. *Ibis*, *138*, 466-470.

Prather, R. M., Roeder, K. A., Sanders, N. J., & Kaspari, M. (2018) Using metabolic and thermal ecology to predict temperature dependent ecosystem activity: a test with prairie ants. *Ecology*, *99*, 2113-2121.

Price, S. L., Powell, S., Kronauer, D. J. C., Tran, L. A. P., Pierce, N. E., & Wayne, R. K. (2014). Renewed diversification is associated with new ecological opportunity in the Neotropical turtle ants. *Journal of Evolutionary Biology*, *27*, 242–258.

Stuble, K. L., Pelini, S. L., Diamond, S. E., Fowler, D. A., Dunn, R. R., & Sanders. N. J. (2013) Foraging by forest ants under experimental climatic warming: a test at two sites. *Ecology and Evolution*, 3, 482–491.

R Core Team (2017) *R: A language and environment for statistical computing. R Foundation for Statistical Computing*, Vienna, Austria. https://www.R-project.org/.

Raubenheimer, D., Simpson, S. J., & Mayntz, D. (2009) Nutrition, ecology and nutritional ecology: toward an integrated framework. *Functional Ecology*, *23*, 4-16.

Revelle W. (2011*) psych: Procedures for Psychological, Psychometric, and Personality Research*. R package version 1.01.9. Available: http://personality-project.org/r/psych.manual.pdf.

Roslin, T., Hardwick, B., Novotny, V., Petry, W. K., Andrew, N. G., Asmus, A., … Slade, E. M. (2017) Higher predation risk for insect prey at low latitudes and elevations. *Science*, *356*, 742–744.

Rosumek, F. B., Blüthgen, N., Brückner, A., Menzel, F., Gebauer, G., & Heethoff, M. (2018) Unveiling community patterns and trophic niches of tropical and temperate ants using an integrative framework of field data, stable isotopes and fatty acids. *PeerJ*, *6*, e5467.

Tiede, Y., Schlautmann, J., Donoso, D. A., Wallis. C. I. B., Bendix, J., Brandl, R. & Nina Farwig, N. (2017). Ants as indicators of environmental change and ecosystem processes. *Ecological Indicators*, *83*, 527-537.

Tilman, D., Isbell, F., & Cowles, J. M. (2014) Biodiversity and Ecosystem Functioning. *Annual Review of Ecology, Evolution, and Systematics*, *45*, 471–93.

Urban, M. C. (2015) Accelerating extinction risk from climate change. *Science*, *348*, (6234), 571-573.

Vidal, M. C., Silva, A. K., & Sendoya, S. (2018) Foraging preferences of ants on a heterogeneous Brazilian sandy shore habitat. *Ecological entomology, 44,* 283-286.

Yanoviak, S. P., & Kaspari, M. (2000) Community structure and the habitat templet: ants in the tropical forest canopy and litter. *Oikos*, 89, 259–266.

Warton, D. I., & Hui, F. K. C. (2011). The arcsine is asinine: the analysis of proportions in ecology. *Ecology*, 92, 3–10.

Wilder, S. M., Norris, M., Lee R. W., Raubenheimer, D. & Simpson, S. J. (2013) Arthropod food webs become increasingly lipid-limited at higher trophic levels. *Ecology Letters*, *16*, 895–902.

Wolda, H. (1978) Seasonal fluctuations in rainfall, food and abundance of tropical insects. *Journal of Animal Ecology*, *47*,369–381

Wolda, H. (1988) Insect seasonality: Why? *Annual Review of Ecology and Systematics*, *19*, 1-18.

Zhao, M., & Running, S. W. (2010) Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science, 329,* 940–943.

Supplementary Appendix 1

Figure 1. Collinearity between ecological factors. AMTemp = annual mean temperature; APrec = annual precipitation; MMTemp = Monthly mean temperature, MPrec = Monthly precipitation; TSeas = temperature seasonality, PSeas = precipitation seasonality; NPP = net primary productivity.

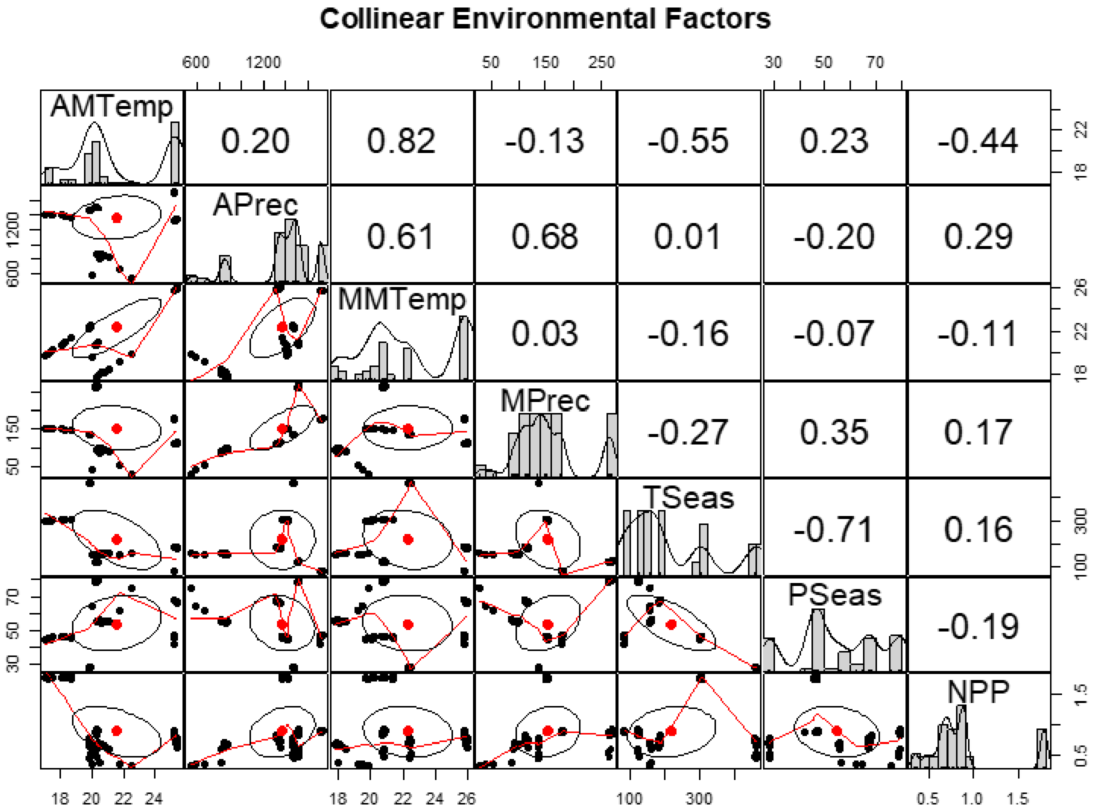


Figure 2. Generalized linear models (GLMs) between relative use of sucrose (CHO) (y-axes) and ecological factors. Points in the graphs represent the relative use in a given transect and black lines are the effects of **a)** monthly precipitation (MPrec); **b)** temperature seasonality (TSeas) and; **c)** net primary productivity (NPP).

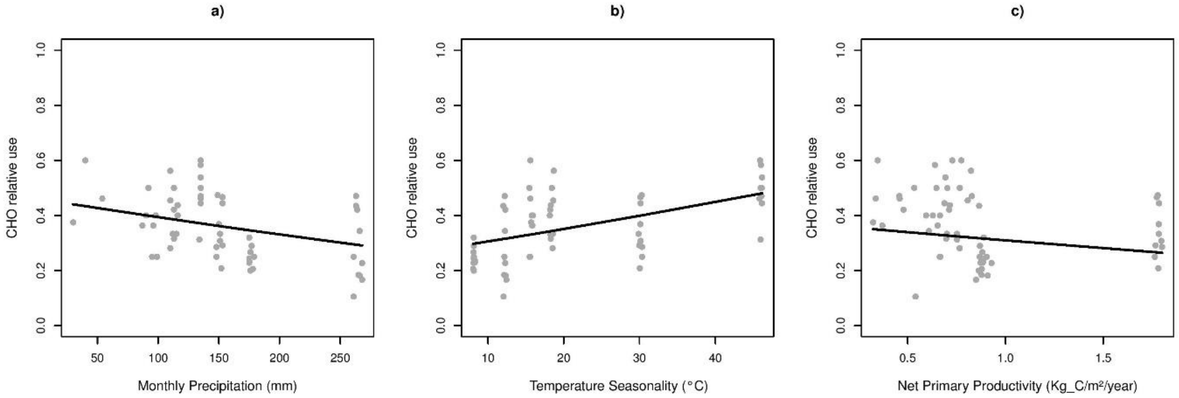


Figure 3. Generalized linear models (GLM) between relative use of lipids (y-axes) and ecological factors. Points in the graphs represent the relative use in a given transect an the black lines are the effects of **a)** mean monthly temperature (MMT); **b)** monthly precipitation (MPrec) and **c)** net primary productivity (NPP).

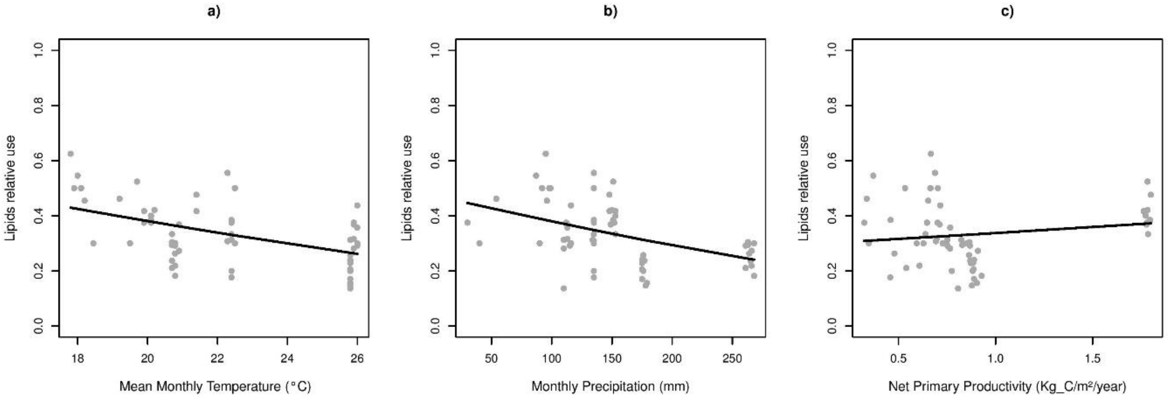


Figure 4. Generalized linear models (GLM) between relative use of amino acids (AA) (y-axes) and ecological factors. Points in the graphs represent the relative of use in a given transect and the black lines are the effects of **a)** monthly mean temperature (MTemp) and **b)** temperature seasonality (TSeas).

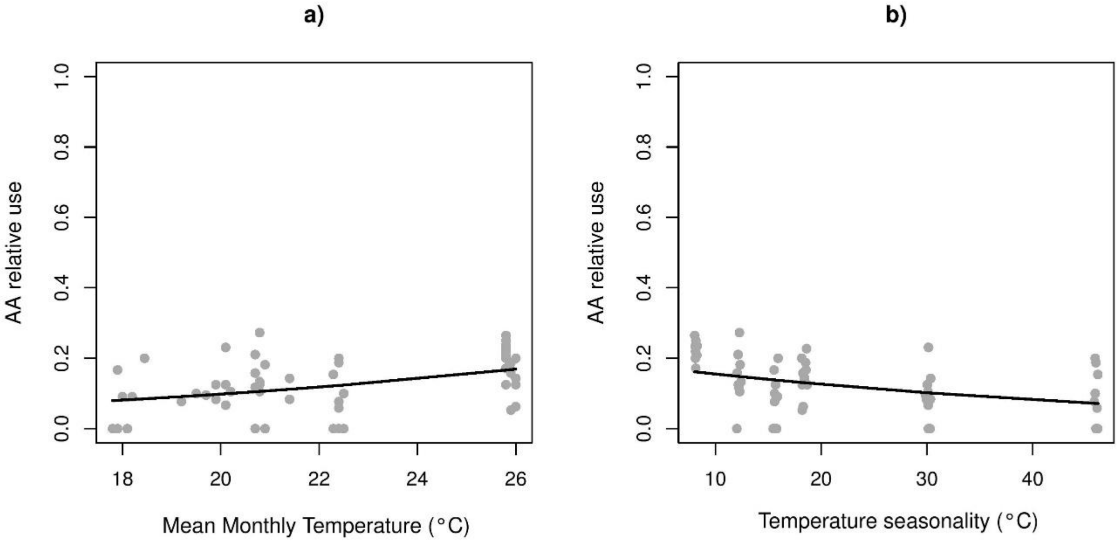


Figure 5. Generalized linear models (GLM) between relative use of sodium (NaCl) (y-axes) and ecological factors. Points in the graphs represent the relative of use in a given transect and the black lines are the effects of. a) mean monthly temperature (MMT); b) monthly precipitation (MPrec); c) temperature seasonality (TSeas) and d) net primary productivity (NPP).

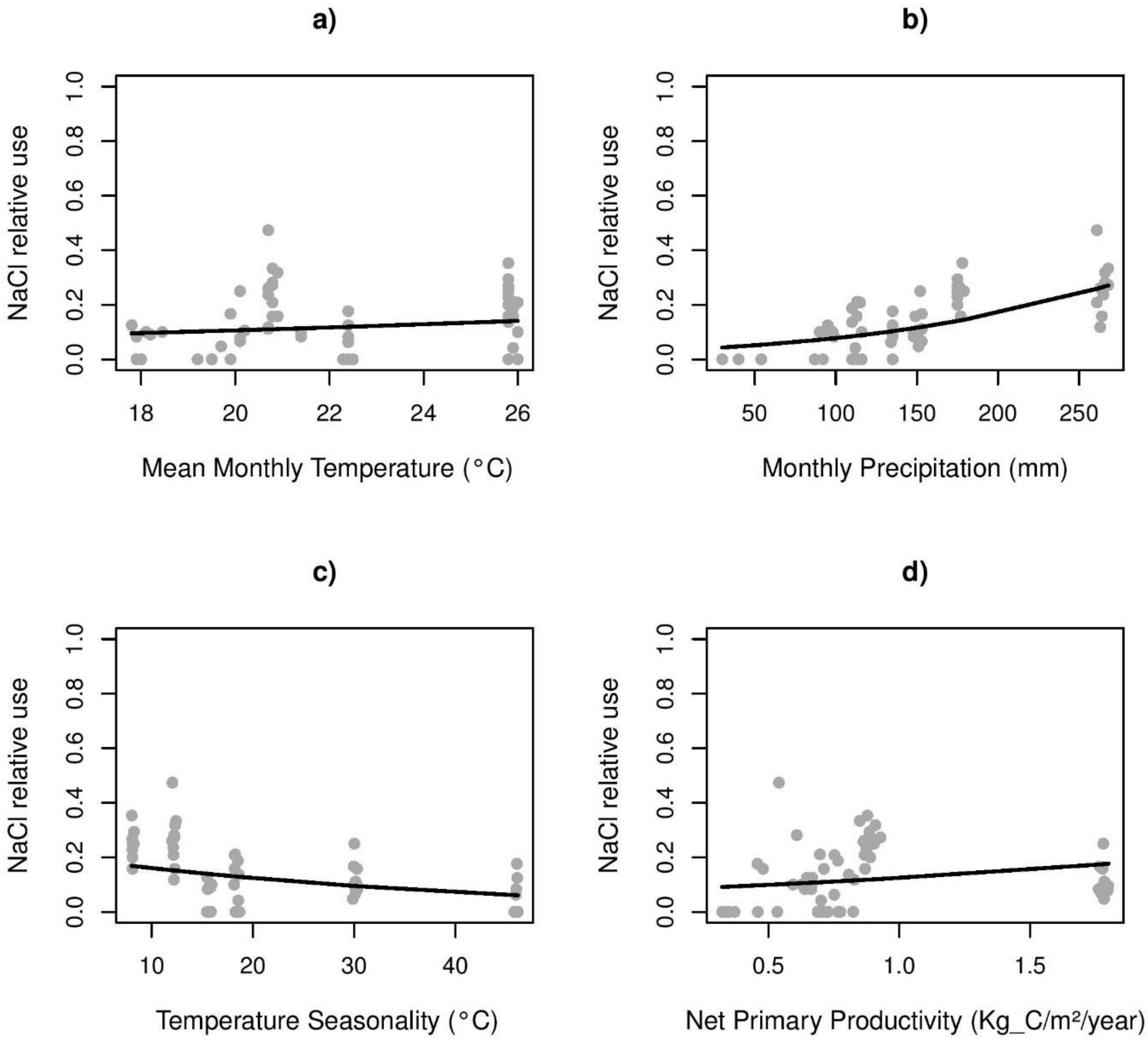


Table 1. Model selection considering the occurrence of foraging ants in control tubes (distilled water) and controlling for relative distilled water use, using the Dredge function (Barton, 2015) based on the Akaike information criterion (AICc) ranking, across six Brazilian biomes. For question 1 and 2, the generalized linear models were constructed with the explanatories variables: temperature (monthly mean temperature, MMTemp), precipitation (monthly precipitation, MPrec), climatic stability (temperature seasonality, TSeas), net primary productivity (NPP). In question 2, the models were ran separately for four resources types represented as a solution (distilled water/volume) of : 1% sodium (NaCl), 20% sugar (CHO, made with sucrose), 20% amino acids (AA, made with unflavored whey protein isolate), and only distilled water as control. To control for relative distilled water use in other resources (NaCl, CHO and AA), we also added the relative use of distilled water (Control) as an additional explanatory variable, in order to verify if patterns remain the same. We only considered and pointed out models equal or lower than Δ = 2. Degrees of freedom of the model (d.f.), differences in AICc-values (Δ) and Akaike weight (ω).

Question 1: How do ecological factors influence the occurrence of foraging ants?

Model	d.f.	AICc	Δ	ω	Log Likelihood	Adjusted R²
MMTemp + MPrec + TSeas + NPP	6	52.1	0.00	0.996	-19.24	0.72

Question 2: How do ecological factors influence the use of different resources by foraging ants?

Distilled water (Control)

Model	d.f.	AICc	Δ	ω	Log Likelihood	Adjusted R²
MMTemp + MPrec	4	130.4	0.00	0.40	-60.65	0.17
MMTemp + MPrec + TSeas	5	131.6	1.54	0.18	-60.22	0.17

CHO

Model	d.f.	AICc	Δ	ω	Log Likelihood	Adjusted R²
MPrec + TSeas + NPP + Control	6	58.9	0.00	0.50	-22.65	0.52
MMTemp + MPrec + TSeas + NPP + Control	7	60.9	1.97	0.18	-22.34	0.52

AA

Model	d.f.	AICc	Δ	ω	Log Likelihood	Adjusted R²
MMTemp + TSeas	4	138.4	0.00	0.25	-64.84	0.26
MMTemp + TSeas + Control	5	138.7	0.30	0.21	-63.80	0.27
MMTemp + MPrec + TSeas	5	139.9	1.47	0.12	-64.38	0.26
MMTemp + TSeas + NPP	5	140.2	1.80	0.10	-64.54	0.26

NaCl

Model	d.f.	AICc	Δ	ω	Log Likelihood	Adjusted R²
MMTemp + MPrec + TSeas + NPP	6	137.6	0.00	0.27	-62.01	0.54
MPrec + TSeas +NPP	5	137.9	0.27	0.23	-63.38	0.53
MPrec + TSeas + NPP +Control	6	138.8	1.14	0.15	-62.58	0.53
MMTemp + MPrec + TSeas + NPP +Control	7	139.3	1.72	0.11	-61.59	0.54

Table 2. Number of tubes visited by at least one ant individual at different biomes and different solutions (distilled water/ volume) of resources: 1% sodium (NaCl), 20% sugar (CHO, made with sucrose), 20% amino acids (AA, made with unflavored whey protein isolate), and lipids (extra virgin olive oil) and distilled water, as a control. For each resource type, there were 150 tubes placed in each biome. Below there is a percentage of visiting in the whole experiment.

	CHO	**Lipids**	**AA**	**NaCl**	**Control**
Amazon	86	73	78	89	23
Atlantic rainforest	63	77	17	23	6
Caatinga	42	48	9	5	1
Cerrado	66	63	36	66	15
Pampa	56	37	10	6	5
Pantanal	80	64	31	24	7
Percentage of visited tubes across the study	44%	40%	20%	23%	6%

Supplementary appendix 2

Table 1. Ant species list sampled in six Brazilian biomes: Amazon, Atlantic rainforest, Caatinga, Cerrado, Pampa and Pantanal. In general, the most diverse genera were *Pheidole* (97 species) followed by *Camponotus* (25), *Solenopsis* (24), *Crematogaster* (17), *Brachymyrmex* (9), *Linepithema* (7), *Pseudomyrmex* (6), *Nylanderia* (6), *Cephalotes* (5) and *Neoponera* (5).

Amazon		
Ant species	**Number of individuals**	**Number of baited tube visited**
Atta sexdens	25	1
Azteca sp. 2	98	3
Brachymyrmex sp. 1	198	1
Brachymyrmex sp. 3	47	3
Brachymyrmex sp. 9	1	1
Camponotus aff. *brevis*	13	1
Camponotus burtoni	2	1
Camponotus depressus	71	9
Camponotus latangulus	4	2
Camponotus sp. 2	3	3
Camponotus sp. 3	20	3
Camponotus sp. 7	21	2
Carebara sp. 1	1	1
Cephalotes atratus	167	10
Cephalotes pavonii	20	3
Crematogaster aff. *snellingi*	24	1
Crematogaster aff. *sotobosque*	76	3
Crematogaster brasiliensis	1	1
Crematogaster carinata	4415	69
Crematogaster flavosensitiva	173	4
Crematogaster gr. *limata* sp. 1	1588	37
Crematogaster limata	26	5
Crematogaster torosa	3	1
Crematogaster sp. 3	265	5
Dolichoderus bidens	160	2
Dolichoderus debilis	1069	9
Dolichoderus rugosus	16	1
Dolichoderus septemspinosus	225	6
Ectatomma brunneum	5	4
Ectatomma edentatum	2	2
Gigantiops destructor	1	1
Labidus coecus	26	1
Labidus sp. 1	5	1
Mayaponera constricta	1	1

Megalomyrmex emeryi	34	2
Megalomyrmex aff. *balzani*	218	10
Neoponera carinulata	1	1
Neoponera obscuricornis	1	1
Neoponera unidentata	3	2
Neoponera villosa	1	1
Nylanderia fulva	9	2
Nylanderia sp. 1	96	8
Nylanderia sp. 3	79	17
Nylanderia sp. 4	3	1
Ochetomyrmex semipolitus	264	17
Odontomachus haematodus	1	1
Pachycondyla crassinoda	3	1
Pheidole aff. *bufo* sp. 1	13	3
Pheidole aff. *laevifrons*	135	6
Pheidole aff. *longiseta* sp. 2	12	1
Pheidole aff. *mendicula*	3	1
Pheidole aff. *radoszkowskii* sp. 1	395	27
Pheidole biconstricta	323	5
Pheidole cataractae	1	1
Pheidole cf. *flavens*	47	1
Pheidole fimbriata	1	1
Pheidole lemur	44	1
Pheidole midas	345	4
Pheidole sp. 17	3	1
Pheidole sp. 19	1	1
Pheidole sp. 1	310	36
Pheidole sp. 10	18	1
Pheidole sp. 11	1	1
Pheidole sp. 12	34	3
Pheidole sp. 1b	1	1
Pheidole sp. 1c	49	5
Pheidole sp. 1d	1	1
Pheidole sp. 1f	2	1
Pheidole sp. 20	4	1
Pheidole sp. 3	2	1
Pheidole sp. 5a	43	1
Pheidole synarmata	36	6
Pheidole cf. *trageri*	195	7
Pheidole cf. *wallacci*	97	8
Pheidole zelata	46	1
Pseudomyrmex oculatus	1	1
Pseudomyrmex tenuis	2	2
Sericomyrmex mayri	1	1
Solenopsis sp. 9	178	4
Solenopsis sp. 1	470	39

Solenopsis sp. 2	4	1
Solenopsis virulens	4	2
Solenopsis bicolor	144	7
Tapinoma ramulorum	3	1
Trachymyrmex bugnioni	2	2
Trachymyrmex sp. 10	1	1
Wasmannia auropuncata	604	20
Total	**13,017**	**468**

Atlantic rainforest		
Ant species	**Number of individuals**	**Number of baited tube visited**
Acromyrmex subterraneus	2	1
Brachymyrmex sp. 7	29	6
Brachymyrmex sp. 10	1	1
Gnamptogenys striatula	7	5
Heteroponera inermis	1	1
Heteroponera mayri	1	1
Labidus coecus	62	1
Linepithema leucomelas	45	3
Linepithema micans	9	4
Linepithema pulex	1	1
Megalomyrmex iheringi	49	2
Nylanderia sp. 4	11	5
Oxyepoecus punctifrons	18	2
Pachycondyla striata	8	6
Pheidole sp. 49a	210	3
Pheidole aff. *caulicola*	21	2
Pheidole aff. *longiseta* sp. 1	431	19
Pheidole ambigua	244	3
Pheidole sp. 131	57	2
Pheidole aper	1	1
Pheidole gibba	48	1
Pheidole guelelmimuelleri	6	1
Pheidole lucculenta	54	5
Pheidole sarcina	339	50
Pheidole senilis	102	10
Pheidole sospes	379	27
Pheidole sp. 49	115	8
Pheidole sp. 52	5	1
Pheidole sp. 54	54	8
Pheidole sp. 53b	9	1
Pheidole sp. 54a	4	2
Pheidole sp. 54b	5	2
Pheidole sp. 56	31	2
Pheidole sp. 8a	33	9

Pheidole sp. 8b	29	1
Pheidole synarmata	14	1
Pheidole tristis	341	6
Solenopsis sp. 10	84	14
Solenopsis sp. 18	1	1
Solenopsis sp. 3	18	10
Solenopsis sp. 7	267	2
Solenopsis sp. 8	9	5
Wasmmania lutzi	15	4
Total	**3,170**	**239**

Caatinga

Ant species	**Number of individuals**	**Number of baited tube visited**
Camponotus aff. *Cingulatus*	4	1
Camponotus blandus	6	1
Camponotus crassus	76	7
Camponotus sp. 27	2	1
Dinoponera quadriceps	21	20
Dorymyrmex aff. *biconis*	492	14
Ectatomma edentatum	31	17
Pheidole nubila	180	13
Pheidole cf. bruesi	437	15
Pheidole claviscapa	6	1
Pheidole sp. 31	34	4
Pheidole sp. 63	88	6
Pheidole sp. 64	1	1
Pheidole aff. *trageri*	27	1
Solenopsis sp. 23	2	1
Solenopsis sp. 1	6	3
Solenopsis sp. 13	785	18
Solenopsis sp. 19	14	6
Solenopsis tridens	1	1
Wasmannia auropunctata	4	1
Total	**2,217**	**132**

Cerrado

Ant species	**Number of individuals**	**Number of baited tube visited**
Acanthostichus laticornis	5	1
Acanthostichus quadratus	2	1
Azteca sp. *5*	1	1
Azteca sp. 1	1	1
Blepharidatta conops	4	2
Brachymyrmex sp. 2	1	1
Camponotus arboreus	23	4

Camponotus crassus	130	64
Camponotus melanoticus	15	4
Camponotus renggeri	2	2
Camponotus sp. 11	15	2
Camponotus sp. 17	15	5
Camponotus sp. 20	1	1
Camponotus sp. 22	1	1
Camponotus novogranadensis	14	11
Camponotus trapeziceps	1	1
Cephalotes persimilis	3	2
Cephalotes betoi	36	19
Cephalotes pusillus	67	24
Crematigaster crinosa	2	1
Crematogaster aff. *torosa*	1	1
Crematogaster bruchi	4	1
Ectatomma brunneum	1	1
Ectatomma edentatum	2	1
Gnamptogenys sulcata	1	1
Linepithema sp. 1	1	1
Linepithema pr. *gallardoi*	30	8
Linepithema pulex	11	4
Nesomyrmex spininodis	1	1
Nylanderia sp. 7	1	1
Pheidole sp. 5e	93	9
Pheidole gertrudae	109	5
Pheidole jujuyensis	1	1
Pheidole oxyops	25	2
Pheidole sp. 31a	13	1
Pheidole sp. 16	45	1
Pheidole sp. 22	1	1
Pheidole sp. 28	99	3
Pheidole sp. 31	251	14
Pheidole sp. 32	1	1
Pheidole sp. 34	501	13
Pheidole sp. 37	2	1
Pheidole sp. 39	76	1
Pheidole sp. 40	3	1
Pheidole sp. 30	2	1
Pheidole sp. 5d	11	5
Pheidole sp. 5h	77	7
Pheidole sp. 5f	6	2
Pheidole sp. 5g	10	2
Pheidole sp. 5i	32	5
Pheidole susannae	151	6
Pseudomyrmex gr. *pallidus* sp. 1	1	1
Pseudomyrmex kuenckeli	1	1

Pseudoponera gilberti	1	1
Solenopsis sp. 13	101	2
Solenopsis sp. 16	22	1
Solenopsis sp. 10	3	1
Solenopsis gr. *geminata* sp. 17	119	1
Solenopsis sp. 3	36	5
Tranopelta gilva	3	3
Wasmannia auropunctata	10	2
Total	**2,198**	**268**

	Pampa	
Ant species	**Number of individuals**	**Number of baited tube visited**
Brachymyrmex sp. 8	5	2
Brachymyrmex sp. 9	5	2
Camponotus crassus	2	2
Camponotus mus	1	1
Camponotus punctulatus minutior	2	2
Camponotus renggeri	29	2
Camponotus sp. 28	1	1
Crematogaster cisplatinalis	1	1
Crematogaster crinosa	3	1
Crematogaster quadriformiformis	11	2
Crematogaster torosa	15	4
Hypoponera sp. 2	1	1
Linepithema humile	5	1
Nylanderia fulva	502	25
Nylanderia sp. 7	4	1
Nylanderia sp. 9	12	1
Pheidole aberrans	1	1
Pheidole humeridens	224	5
Pheidole laevinota	540	28
Pheidole sp. 5j	19	2
Pheidole sp. 69	43	2
Pheidole sp. 70	110	10
Pseudomyrmex gr. *oculatus* sp. 1	1	1
Solenopsis gr. geminata sp. 17	871	18
Solenopsis sp. 21	8	4
Solenopsis gr. *geminata* sp. 22	1	1
Wasmmania auropunctata	21	2
Total	**2,438**	**123**

	Pantanal	
Ant species	**Number of individuals**	**Number of baited tube visited**
Azteca aff. alfari	11	3

Brachymyrmex sp. 2	2	1
Brachymyrmex sp. 5	32	3
Brachymyrmex sp. 6	16	4
Camponotus blandus	4	2
Camponotus crassus	8	5
Camponotus melanoticus	7	1
Camponotus senex	13	3
Camponotus sp. 11	17	3
Camponotus sp. 17	1	1
Camponotus sp. 26	1	1
Camponotus novogranadensis	22	9
Centromyrmex brachycola	1	1
Cephalotes attratus	1	1
Crematogaster aff. *obscurata*	1	1
Crematogaster aff. *wardi*	39	10
Crematogaster torosa	125	7
Dorymyrmex sp. 1	23	2
Ectatomma brunneum	70	24
Ectatomma edentatum	10	4
Ectatomma permagnum	7	7
Ectatomma planidens	62	13
Gnamptogenys striatula	1	1
Hypoponera sp. 1	1	1
Labidus coecus	122	1
Linepithema angulatum	192	2
Monomorium floricola	2	2
Brachymyrmex brasiliensis	25	2
Neoponera verenae	1	1
Nylanderia sp. 3	2	2
Nylanderia sp. 4	89	17
Pachycondila harpax	1	1
Paraponera clavata	1	1
Pheidole aff. *radoszkowskii* sp. 2	59	7
Pheidole aff. *flavens*	134	1
Pheidole fracticeps	439	24
Pheidole gigaflavens	75	2
Pheidole mendicula	30	2
Pheidole obscurithorax	57	5
Pheidole oxyops	39	3
Pheidole sp. 1a	53	1
Pheidole sp. 1e	4	2
Pheidole sp. 22	1	1
Pheidole sp. 23	9	1
Pheidole sp. 28	1	1
Pheidole sp. 30	1	1
Pheidole sp. 5b	15	3

Pheidole sp. 5c	32	1
PheIdole sp. 9	59	2
Pheidole subarmata	335	8
Pheidole tambopatae	200	6
Pseudomyrmex gracilis	2	2
Pseudomyrmex tenuis	4	4
Solenopsis sp. 10	8	2
Solenopsis sp. 11	93	15
Solenopsis sp. 12	10	1
Solenopsis sp. 13	176	2
Solenopsis sp. 5	2	2
Solenopsis sp. 8	351	13
Solenopsis sp. 14	115	1
Solenopsis subistituta	3	2
Tranopelta gilva	2	1
Wasmannia auropuncata	396	17
Wasmannia rochai	96	7
Total	**3,712**	**278**

CONCLUSÃO GERAL

Todos os fatores ecológicos em estudo (temperatura, produtividade primária líquida, precipitação e estabilidade climática) explicam a variação geográfica da riqueza de espécies nos biomas brasileiros. Porém, a maior parte dessa variação foi devida à precipitação e depois à estabilidade climática. Não foi encontrada mediação da sobreposição de nicho nos efeitos dos fatores ecológicos na riqueza local de espécies.

Dos laboratórios às pequenas escalas espaciais, ou até medidas indiretas da atividade de forrageio, a tese avança no conhecimento sobre o efeito de fatores ecológicos na atividade de forrageamento e do uso do recurso avaliando diretamente esses padrões em grandes escalas espaciais. Os fatores ecológicos (temperatura, produtividade primária líquida, precipitação e estabilidade climática) explicam grande parte variação da atividade de forrageio das formigas e o uso de diferentes recursos. Nestes últimos, os fatores ecológicos podem agir tanto na limitação por escassez do recurso quanto na demanda deles.

Estudar a influência de fatores ecológicos na variação dos padrões geográficos de riqueza de espécies e atividade de forrageamento pode nos ajudar a fazer previsões em relação às ameaças à biodiversidade. Além disso, conhecendo os padrões de riqueza e sua variação geográfica e testando fatores ecológicos relacionados aos mesmos, podemos entender como e por que existem maior biodiversidade em certas regiões do Brasil. Já em relação a atividade de forrageamento, podemos entender o papel dos fatores ecológicos nesta que é a base dos diversos processos ecossistêmicos que acontecem.

Um dos achados mais relevantes foi a influência da precipitação nos padrões de riqueza, sobreposição de nicho e atividade de forrageamento desmembrada da influência da produtividade primária líquida. Juntamente com a estabilidade climática, os resultados apontam que, muito provavelmente, os padrões encontrados podem refletir o passado evolutivo da biodiversidade na América do Sul, que se originou em um ambiente climaticamente estável e úmido. Por exemplo, a dependência de certos níveis de umidade pode ter sido um aspecto do nicho ecológico conservado no tempo evolutivo. Isso pode ter refletido no nosso estudo tanto na quantidade de espécies que há em uma região, quanto na diversificação de diferentes formas das formigas usarem os recursos ecológicos e também na melhor performance em forragear em ambientes mais úmidos.

Por fim, considerando o crescente extermínio da biodiversidade no Brasil em prol de um modelo de desenvolvimento econômico que mais beneficia a países desenvolvidos somado à negligência dos governos brasileiros, passados e principalmente do atual, a biodiversidade brasileira está ameaçada. Além disso, se os padrões vistos aqui são resultado do passado evolutivo das espécies, elas não poderão se adaptar às rápidas mudanças ambientais causadas, por exemplo, por mudanças no uso do solo ou climáticas. Dessa forma, muitas espécies poderão entrar em extinção, além de haver uma provável mudança nos processos ecológicos desempenhados pelos animais, o que acarretaria uma perda de serviços ecológicos para o ser humano. Assim, os conhecimentos teóricos alcançados com a tese também poderão servir de base para a aplicação científica na conservação da biodiversidade Brasileira.

APÊNDICE:

Relato de experiência referente ao trabalho de divulgação realizado durante as campanhas de campo

Precisamos falar das formigas

Sempre que coletamos amostras para nossos estudos e extraímos dados de um local, deixamos muito pouco para a população que ali vive, até mesmo em relação ao que fomos fazer lá. Muitos biólogos, ecólogos e mirmecólogos certamente já foram questionados por moradores locais em suas atividades de campo: "Mas o que vocês fazem no mato?"; "Vocês estão catando lixo?". Especificamente, para mirmecólogos são essas as perguntas mais comuns: "Coletam formiga? Meu Deus, na minha casa está cheio, por que não coletam lá?"; "Mas você veio lá de Minas Gerais pra coletar formiga aqui? Pra quê?"; "Formiga? Como faço para matar aquelas amarelinhas miudinhas que vivem no açúcar?". Essas perguntas frequentes e acompanhadas de um certo espanto nos motivaram a fazer este trabalho de divulgação.

Durante o projeto: "*Environmental factors and community structuring mechanisms upon ant community in distinct Brazilian Biomes*", viajamos pelos seis biomas brasileiros entre os anos de 2016 e 2018 coletando em Unidades de Conservação. Além das coletas do material biológico em campo, dedicamos um tempo a mais (um a dois dias) nas comunidades e cidades dos arredores das unidades de conservação para conversar e apresentar para as pessoas o que realmente fazemos. Nosso público-alvo foram os estudantes de escolas rurais, municipais e Institutos Federais. Escolhemos esses locais por já representarem um espaço de troca de saberes e onde encontraríamos um maior número de pessoas reunidas para nos ouvir.

No Pantanal, visitamos o Instituto Federal do Mato Grosso – Núcleo Avançado do Pantanal, próximo a Poconé – MT, que atendia alunos de todas as idades, adultos, adolescentes e crianças. No Pampa, visitamos a Escola Estadual Nilza Correa Pereira na cidade de Barra do Quaraí - RS e a escola rural Manoel Imas dos Santos, que atendiam alunos do ensino fundamental. No Distrito Federal (Cerrado), visitamos o Instituto Federal de Brasília – Campus São Sebastião, que atendia alunos do ensino médio. E, finalmente, na Mata Atlântica, visitamos a Escola Estadual Boa Vista, próxima ao município de Ribeirão Grande – SP, que atendia alunos do ensino fundamental. Infelizmente, não conseguimos visitar nenhuma escola no bioma Amazônia porque a unidade de conservação se situava numa área remota e isolada, e nem no bioma Caatinga, pois coletamos no período de férias dos estudantes. No total, conversamos com aproximadamente 750 estudantes e professores (Figura 1).

Figura 1. Trabalho de divulgação do projeto *“Environmental factors and community structuring mechanisms upon ant community in distinct Brazilian Biomes”*. As visitas foram feitas nas instituições: Instituto Federal Instituto Federal do Mato Grosso – Núcleo Avançado do Pantanal próximo a Poconé – MT (**a** e **c**); Escola Estadual Nilza Correa Pereira, Barra do Quaraí – RS (**d**) e escola rural Manoel Imas dos Santos, próximo a Barra do Quaraí (**b**); Instituto Federal de Brasília – Campus São Sebastião, Distrito Federal (**e**); Escola Estadual Boa Vista, próxima a Ribeirão Grande – SP (**f**).

Sempre que entrávamos nas salas de aula, após nos apresentarmos, fazíamos a seguinte pergunta: “O que vocês sabem sobre as formigas?”. A partir daí, recebíamos diferentes respostas. A maioria, na visão dos estudantes, estava relacionada a alguma coisa negativa sobre as formigas. Ressaltamos algumas pouquíssimas exceções nas escolas rurais, onde ouvimos aspectos positivos, como, por exemplo, que as formigas cuidam das plantas. A partir daí nós começávamos a falar da biologia das formigas e de suas funções ecológicas, ressaltando a importância das mesmas para o meio ambiente de uma forma mais informal e acessível. Nesse momento, nós também mostrávamos as formigas que coletamos enquanto estávamos por ali.

Uma vez que falávamos aos estudantes o que as formigas fazem no ecossistema, nós introduzíamos o assunto do nosso projeto. Explicávamos o que são biomas e a importância de conservarmos cada um deles. Também falávamos dos objetivos do nosso projeto de uma forma simplificada, explicando o porquê de estarmos usando formigas para avaliar padrões de diversidade de espécies a atividade de forrageamento.

No geral, tivemos uma boa receptividade por parte dos estudantes e das escolas. Estudantes e professores nos disseram que não sabiam que formigas poderiam fazer tantas coisas. Assim, esperamos encorajar outros pesquisadores a saírem das unidades de conservação e das universidades para falarem e divulgarem para a população o que fazemos. Isso é urgentemente necessário em tempos de descrença e negacionismo da ciência, o que resulta em coisas do tipo “terraplanismo” e em ignorância em relação ao meio ambiente, em geral. Além do mais, a comunidade científica está sendo fortemente atacada e, já que, infelizmente, não é possível trazer toda a população brasileira para a universidade, nós devemos ir a ela.