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DIVERSIDADE DE FORMIGAS DE SOLO NO CERRADO – DETERMINANTES HIERÁRQUICOS ENTRE ESCALAS ESPACIAIS

JONAS BROCHADO MARAVALHAS

2018

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

Orientador: Prof. Dr. Heraldo Luís de Vasconcelos

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Ata da defesa de TESE DE DOUTORADO junto ao Programa de Pós-Graduação em Ecologia e Conservação de Recursos Naturais - Instituto de Biologia da Universidade Federal de Uberlândia.

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Às **14 horas** do dia **26** de **fevereiro** do ano de **2018, no auditório do Bloco 8C** – Campus Umuarama, da Universidade Federal de Uberlândia reuniu-se a Banca Examinadora, designada pelo Colegiado do Programa de Pós-Graduação em Ecologia e Conservação de Recursos Naturais, composta pelos Doutores: **Ricardo Ildefonso de Campos (UFV), Ricardo de Castro Solar (UFMG), Natália Mundim Tôrres (UFU), Mario Moura (UFU) e Helrado Luís de Vasconcelos (UFU)** orientador(a) do(a) candidato(a).

Iniciando os trabalhos, o(a) Presidente da mesa, Dr(a). Helrado Luís de Vasconcelos apresentou a Comissão Examinadora e o(a) candidato(a), agradecendo a presença do público e concedendo ao(à) Discente a palavra para a exposição do seu trabalho. A duração da apresentação do(a) Discente, o tempo de arguição e resposta foram estabelecidos conforme as normas do Programa.

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Em face do resultado obtido, a Banca Examinadora considerou o(a) candidato(a) _A__ provado(a), sugerindo novo título para o trabalho (quando couber):

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Dedico esta tese à Tatiane, minha parceira
na trajetória espaço-temporal da vida.

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Acts in what Hutchinson (1965) has called the 'ecological theatre' are played out on various scales of space and time. To understand the drama, we must view it on the appropriate scale.

J. A. Wiens, 1989

Resumo

Compreender por que determinadas regiões diferem em número e identidade de espécies é um dos principais objetivos da ecologia e biogeografia, representando tanto um desafio teórico como uma urgente necessidade na biologia da conservação. Esta tese tem por objetivo estudar os padrões de diversidade (alfa) e de dissimilaridade (beta) de formigas de solo no Cerrado. Estes padrões foram analisados em diferentes escalas espaciais, pois a montagem de comunidades depende de fatores ecológicos e evolutivos que operam em escalas espaço-temporais hierárquicas. No primeiro capítulo desta tese a densidade de espécies e a diversidade (independente da abundância) foram calculadas em quatro escalas espaciais, sendo então modeladas por fatores que remetem a uma dentre quatro hipóteses: i) espécies-energia; ii) heterogeneidade; iii) fatores históricos e geográficos; e iv) fatores locais. Os resultados mostram que locais com maior produtividade primária (hipótese de espécies-energia) estão associados a uma maior diversidade de espécies, pois climas favoráveis levam a menores taxas de extinção e, logo, a um maior banco regional. Os resultados indicam ainda que as espécies do banco são possivelmente filtradas por características do solo (hipótese de fatores locais), por meio de um controle da abundância de formigas. No segundo capítulo foi analisada a dissimilaridade composicional (beta diversidade) e seus componentes de troca (substituição de espécies entre amostras) e aninhamento (mudança composicional devido a diferenças de riqueza). Estas métricas foram calculadas em cinco escalas que variam em termos de grão (resolução da unidade amostral) e extensão (dispersão espacial das amostras). Os padrões encontrados foram relacionados, em cada escala, a cinco fatores: i) diferenças no banco de espécies; ii) heterogeneidade topográfica; iii) heterogeneidade da estrutura da vegetação; iv) presença de vegetação densa; e v) quantidade de areia no solo. Conforme esperado a beta diversidade (e seus componentes) foi maior em escalas espaciais menores, diminuindo em escalas intermediárias; inesperadamente, porém, os valores aumentaram novamente na maior escala. Maiores bancos de espécies resultaram em menor aninhamento e maior troca, esta também sendo negativamente afetada pela quantidade de areia no solo. A influência do banco de espécie de formigas de solo, no entanto, diminuiu com o aumento da escala, e a heterogeneidade da vegetação foi o principal determinante dos padrões de troca e aninhamento em maiores escalas, indicando uma maior importância de processos de alocação de espécies. Os estudos que compõem esta tese mostram a importância de considerar a escala espacial ao analisar padrões de biodiversidade, já que ela determina a importância relativa dos fatores ecológicos e evolutivos que geram esses padrões. Compreender como diferentes fatores interagem através de escalas é, portanto, fundamental para que medidas eficazes de conservação sejam aplicadas para remediar a crise global de biodiversidade.

Palavras-chave: Macroecologia, Biogeografia, Gradiente latitudinal de diversidade, Comunidades de Formicidae, Alfa e beta diversidade, Troca, Aninhamento, Cerrado.

Abstract

To understand why certain regions differ in the number and identity of occurring species is one of the major goals in ecology and biogeography, representing both a theoretical challenge and an urgent conservation need. This thesis aims at studying the patterns of diversity (alpha) and dissimilarity (beta) of ground-dwelling ants in the Cerrado savannas. These patterns were analyzed at different spatial scales, since the assembly of communities depend on ecological and evolutionary factors that operate at hierarchical spatial and temporal scales. In the first chapter of this thesis the species density and diversity (abundance-independent) were calculated at four spatial scales and then modelled by factors related to one of four general hypotheses: i) species-energy; ii) heterogeneity; iii) geographical/historical factors; and iv) local factors. The results show that localities with higher net primary productivity (species-energy hypothesis) are associated to higher diversity of species, since favorable climate lead to lower rates of local extinctions and, thus, more species in the regional banco. On the other hand, the species in the banco are filtered by edaphic characteristics (local factors hypothesis) that control ant abundances. In the second chapter the patterns of compositional dissimilarity (beta diversity) and its components of turnover (species replacement) and nestedness (dissimilarity due to richness differences) were analyzed across five spatial scales that vary in terms of spatial grain (spatial resolution of the sampling unit) and extent (spatial dispersion of samples). The patterns found were then related, in each scale, to five environmental factors: i) species banco sizes; ii) heterogeneity in topography; iii) heterogeneity in the structure of the vegetation; iv) presence of closed habitat vegetation; and v) sand content in the soil. As expected, beta diversity was highest at the smallest spatial scale and decreased with increasing scale, showing a further increase at the largest spatial scale. More species in the regional banco resulted in lower nestedness and higher turnover, the latter being also negatively affected by the amount of sand in the soil. The influence of these factors, however, reduced with increasing scale, being accompanied by an increase in the importance of heterogeneity in vegetation structure. This point to a greater importance of species sorting processes at larger spatial scales. The studies of the present thesis demonstrate the importance of incorporating spatial scale in the analysis of biodiversity patterns, since scale determine the relative importance of the ecological and evolutionary factors that generate these patterns. Understanding how these factors interact is, thus, fundamental to appropriately design conservation strategies that counter the effects of the global biodiversity crisis.

Key-words: Macroecology, Biogeography, Latitudinal gradient in diversity, Formicidae communities, Alpha and beta diversity, Species turnover, Nestedness, Cerrado.

Sumário

Introdução

Estudar padrões geográficos de biodiversidade e compreender os mecanismos que os geram é um tema central na ecologia, biogeografia e evolução (Gaston, 2000; Sutherland *et al.*, 2013). O gradiente latitudinal de diversidade (GLD), por exemplo, é um dos mais antigos padrões ecológicos reconhecidos, sendo caracterizado pela maior diversidade bilógica nas regiões tropicais e um empobrecimento gradual em direção às regiões polares. Este padrão é verdadeiro para a grande maioria dos grupos taxonômicos, em ambientes terrestres e marinhos e em diferentes períodos geológicos (Rohde, 1992; Willig *et al.*, 2003; Hillebrand, 2004). Estas variações na diversidade biológica, no entanto, não são causadas pela latitude em si, mas sim por fatores históricos, climáticos, ambientais e estocásticos que determinam a ocorrência das espécies no espaço e que apresentam marcada variação latitudinal (Hawkins & Diniz-filho, 2004). Diversas hipóteses oferecem explicações para o GLD e, apesar de séculos de pesquisa, ainda não há um consenso sobre qual fator é o principal causador desse conspícuo padrão ecológico. Uma potencial explicação para o GLD é a integração entre tempo, área e clima, i.e., regiões tropicais tem maior área e experimentaram maior favorabilidade climática por um maior período de tempo, comparado às regiões temperadas (Wright, 1983; Rosenzweig, 1995; Jetz & Fine, 2012; Fine, 2015). Esta integração de fatores resultou num acúmulo de espécies, evidenciado pela presença de linhagens mais antigas nos trópicos (Marin & Hedges, 2016).

Dessa forma, o número de espécies que ocorre em uma região pode ser determinado por fatores históricos (Ricklefs, 1987; Whittaker *et al.*, 2001), como o histórico de retração/contração de geleiras (Dobrovolski *et al.*, 2012) ou de formações vegetais (Werneck *et al.*, 2012) durante variações climáticas no Quaternario. A riqueza de espécies pode ser determinada também por fatores estocásticos (Chase, 2014) ou determinísticos, como – por exemplo – a quantidade de energia que entre em um sistema, o que depende do clima (relação espécies-energia, Connell & Orias, 1964; Pianka, 1966; Wright, 1983; Hawkins *et al.*, 2003; Willig *et al.*, 2003). Outras hipóteses, como a maior favorabilidade ou menor estresse ambiental (Pianka, 1966; Rohde, 1992), taxas evolutivas (Rohde, 1992; Currie *et al.*, 2004) e heterogeneidade ambiental (Tews *et al.*, 2004) podem ajudar a explicar o gradiente latitudinal de espécies, embora não sejam amplamente sustentadas como explicação universal (Willig *et al.*, 2003). Por fim, um dos consensos que surge deste rico debate é que a diversidade biológica se organiza, no espaço e no tempo, por meio de processos hierárquicos (Ricklefs, 1987; Wiens, 1989; Levin, 1992).

Escalas espaciais possuem dois componentes, o grão, e a extensão. O grão (ou foco) é a resolução da menor unidade amostral, enquanto que a extensão mede a dispersão das unidades amostrais no espaço geográfico (Wiens, 1989). A teoria hierárquica da diversidade (Figura 1) assume que fatores operando em grandes escalas espaciais (e temporais) definem padrões globais e regionais de biodiversidade; porém processos locais, em última instância, filtram o número de espécies do banco regional em assembleias de organismos coexistentes (Whittaker *et al.*, 2001; Hortal *et al.*, 2010; Vellend, 2010). Fatores geográficos e históricos são importantes determinantes dos padrões de diversidade em escalas globais e continentais (Willig *et al.*, 2003; Field *et al.*, 2009; Ricklefs & He, 2016); no entanto, dentro destas arenas evolutivas, padrões regionais de diversidade são limitados pelo equilíbrio entre a entrada de energia e água no ecossistema (Hawkins *et al.*, 2003). Este equilíbrio limita os padrões geográficos de produtividade, que determina os padrões regionais de diversidade biótica por meio de diversos mecanismos (Evans *et al.*, 2005; Fine, 2015). Na escala da paisagem, dinâmicas de metacomunidades – dentre elas os efeitos de massa e a dinâmicas de manchas – tornam-se importantes determinantes dos padrões de ocorrência de espécies no tempo e no espaço (Shmida & Wilson, 1985; Leibold *et al.*, 2004; Braga *et al.*, 2017). Por fim, em escalas menores, fatores locais como tipo de habitat podem ser importantes determinantes dos padrões de diversidade, pois condicionam o resultado de interações bióticas (Parr *et al.*, 2005), bem como regulam a alocação de espécies no espaço (Shmida & Wilson, 1985; Huston, 1999). Vale ressaltar também a importância de processos neutros, que podem influenciar padrões de diversidade em escalas menores (Chase, 2014).

Padrões de biodiversidade são bem conhecidos para muitos organismos em diversos ecossistemas e servem de referência para desenvolver estratégias de conservação, utilizando informações de taxa mais bem estudados como modelo para outros organismos. Esta abordagem, no entanto, favorece a conservação de grupos carismáticos, que nem sempre são úteis na priorização da conservação (Caro & O'Doherty, 1999; Andelman & Fagan, 2000). Existem, portanto, grandes lacunas no conhecimento dos padrões de diversidade em larga escala, como o viés taxonômico, pois invertebrados são sub-representados nos estudos de variações de diversidade em macroescala (Hawkins *et al.*, 2003; Willig *et al.*, 2003), mesmo que estes organismos representem a maior parte da diversidade biótica do planeta, porém ainda pouco conhecida (Mora *et al.*, 2011). De forma semelhante, há um viés geográfico, já que existem relativamente poucos estudos realizados na América do Sul e Ásia (Field *et al.*, 2009), de modo que informações sobre a distribuição de espécies nestas regiões são bastante deficientes. Preencher essas lacunas não é uma tarefa simples, já que o uso de coleções científicas e de dados publicados apresenta um viés para áreas mais populosas, mais acessíveis ou próximas a centros de pesquisa; além da falta de padronização amostral e da dificuldade de identificação correta das espécies. Coletas padronizadas em larga escala geográfica realizadas e identificadas por parataxonomistas superam alguns obstáculos, porém exigem grande investimento financeiro e laboral e podem falhar na detecção de espécies crípticas (Basset *et al.*, 2000).

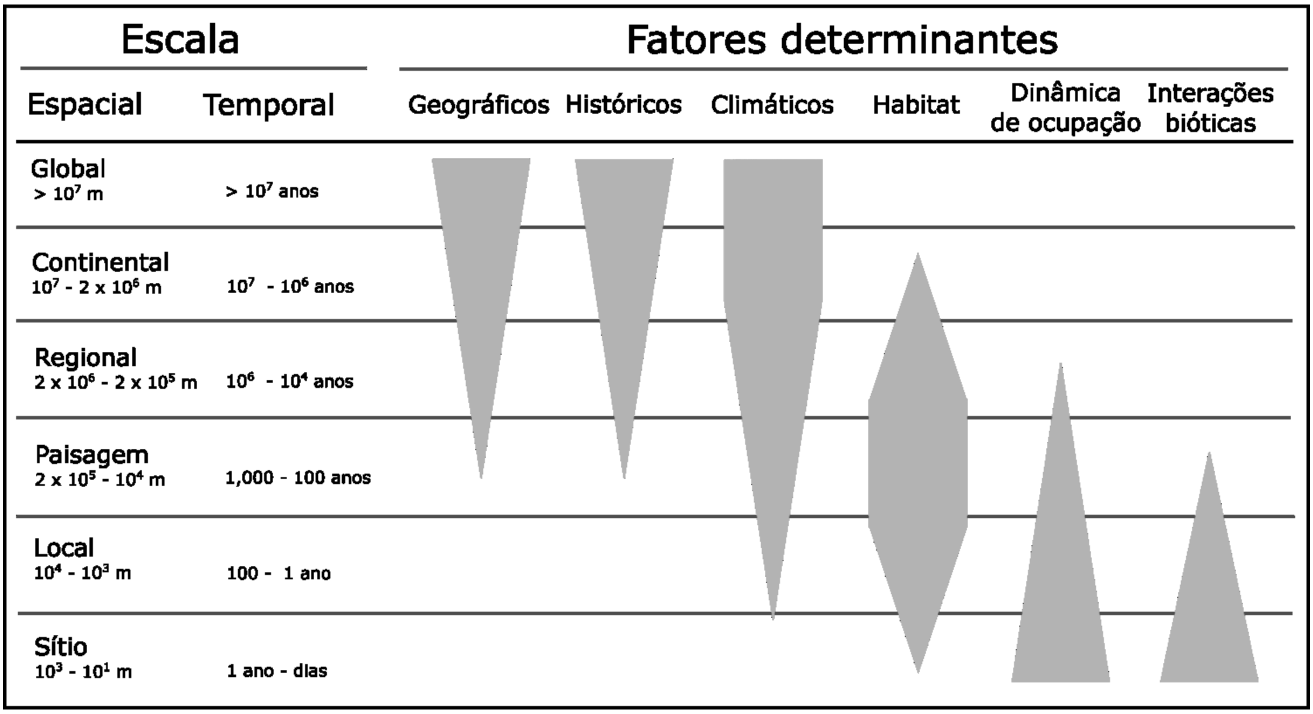

Figura 1. Diagrama esquemático dos fatores ecológicos e evolutivos que podem explicar padrões macroecológicos de diversidade. Figuras em cinza representam a importância relativa (proporcional à espessura da figura) de cada fator em determinar os padrões de diversidade em diferentes escalas espaciais (classificação segundo Pearson & Dawson, 2003) e temporais (classificação segundo Willis & Whittaker, 2002). Imagem compilada a partir de informações presentes em diversas fontes (Whittaker *et al.*, 2001; Willis & Whittaker, 2002; Pearson & Dawson, 2003; Hortal *et al.*, 2010; Fine, 2015).

O Cerrado é a segunda maior ecorregião Neotropical, com extensão original de aproximadamente dois milhões de km^2 do território brasileiro e partes da Bolívia e Paraguai (Ratter *et al.*, 1997), sendo considerada a savana mais biodiversa no mundo (Klink & Machado, 2005). O domínio do Cerrado é a principal fronteira agrícola atualmente no Brasil, e a conservação dessa ecorregião está seriamente ameaçada pelo crescimento das áreas urbanas e principalmente pelo rápido avanço do agronegócio no Brasil (Klink & Moreira, 2002). Por volta de 40% da área da ecorregião do Cerrado foi convertida em pastagens ou culturas (Sano *et al.*, 2010) enquanto apenas 3,1% da sua área se encontram sobre proteção integral (MMA - Ministério do Meio Ambiente, 2017). Devido à alta diversidade biológica, aos altos níveis de endemismos e à rápida perda de habitat, o Cerrado é considerado um *hotspot* de conservação global (Myers *et al.*, 2000), e, apesar da prioridade de proteção, a conservação dessa ameaçada ecorregião é extremamente desafiadora (Strassburg *et al.*, 2017).

Diversas características do Cerrado podem ajudar a explicar seu alto grau de diversidade, heterogeneidade e endemismo (Ratter *et al.*, 1997; Klink & Machado, 2005). Por exemplo, a alta diversidade de plantas tem sido atribuída às variações climáticas no Quaternário e à origem antiga do Cerrado (Ratter *et al.*, 1997). Por outro lado, o Cerrado faz conexão com todos as principais ecorregiões brasileiros, e o intercâmbio de espécies entre essas ecorregiões também pode ter contribuído para uma alta diversidade (Silva, 1995; Silva & Bates, 2002). Já para animais ectotérmicos, como répteis Squamata, a alta proporção de espécies endêmicas no Cerrado foi associada à radiação em platôs elevados de grande antiguidade (Nogueira *et al.*, 2011). De fato, a riqueza de Squamata no Cerrado está relacionada à estabilidade ambiental (Costa *et al.*, 2007) e climática, ou seja, a regiões de refúgio durante as flutuações do Quaternário (Werneck *et al.*, 2012). Por fim, padrões de diversidade no Cerrado também estão associados à grande heterogeneidade ambiental, ou seja, aos altos níveis de troca de espécies entre diferentes fisionomias (e.g., Pacheco & Vasconcelos, 2012) e entre diferentes localidades (e.g., Ratter *et al.*, 2003).

Formigas são insetos sociais presentes em praticamente todos os ecossistemas terrestres e um dos mais bem estudados grupos de invertebrados (Dunn *et al.*, 2007). Elas possuem ampla gama trófica (Davidson *et al.*, 2003), ocupam diversos estratos (Vasconcelos & Vilhena, 2005), contribuem com grande parte da biomassa animal (Fittkau & Klinge, 1973), são importantes herbívoros, dominam recursos e estruturam comunidades de outros artrópodes por predação ou competição (Holldobler & Wilson, 1990; Chomicki & Renner, 2017), além de desempenharem inúmeros serviços e desserviços ecossistêmicos (Del Toro *et al.*, 2012). Formigas no Cerrado brasileiro apresentam um gradiente latitudinal invertido, i.e., mais espécies são encontradas nas regiões centrais e sul do que nas regiões norte, e este padrão foi associado a uma maior favorabilidade climática nas regiões meridionais (Vasconcelos *et al.*, 2018). Esse padrão também foi atribuído à estreita relação evolutiva entre espécies de formigas Neotropicais e climas úmidos (Campos *et al.*, 2011; Vasconcelos *et al.*, 2018). Estes resultados contrastam com os encontrados para faunas associadas a ambientes secos, como as formigas da savana australiana (Andersen *et al.*, 2015) ou do Chaco (Delsinne *et al.*, 2010).

Este trabalho pretende descrever os padrões de diversidade de formigas que forrageiam no solo na região do Cerrado e determinar quais fatores ecológicos são responsáveis por esses padrões. Para tal, coletas padronizadas foram conduzidas em 29 locais distribuídos no domínio do Cerrado (Figura 2, Tabela 1). A partir desse banco de dados (ver tabela 1 do Anexo), a diversidade alfa e beta de formigas foram calculadas em múltiplas escalas espaciais, para testar a importância relativa dos diferentes fatores ecológico e evolutivos que afetam a biodiversidade entre escalas. Abaixo os objetivos específicos de cada capítulo.

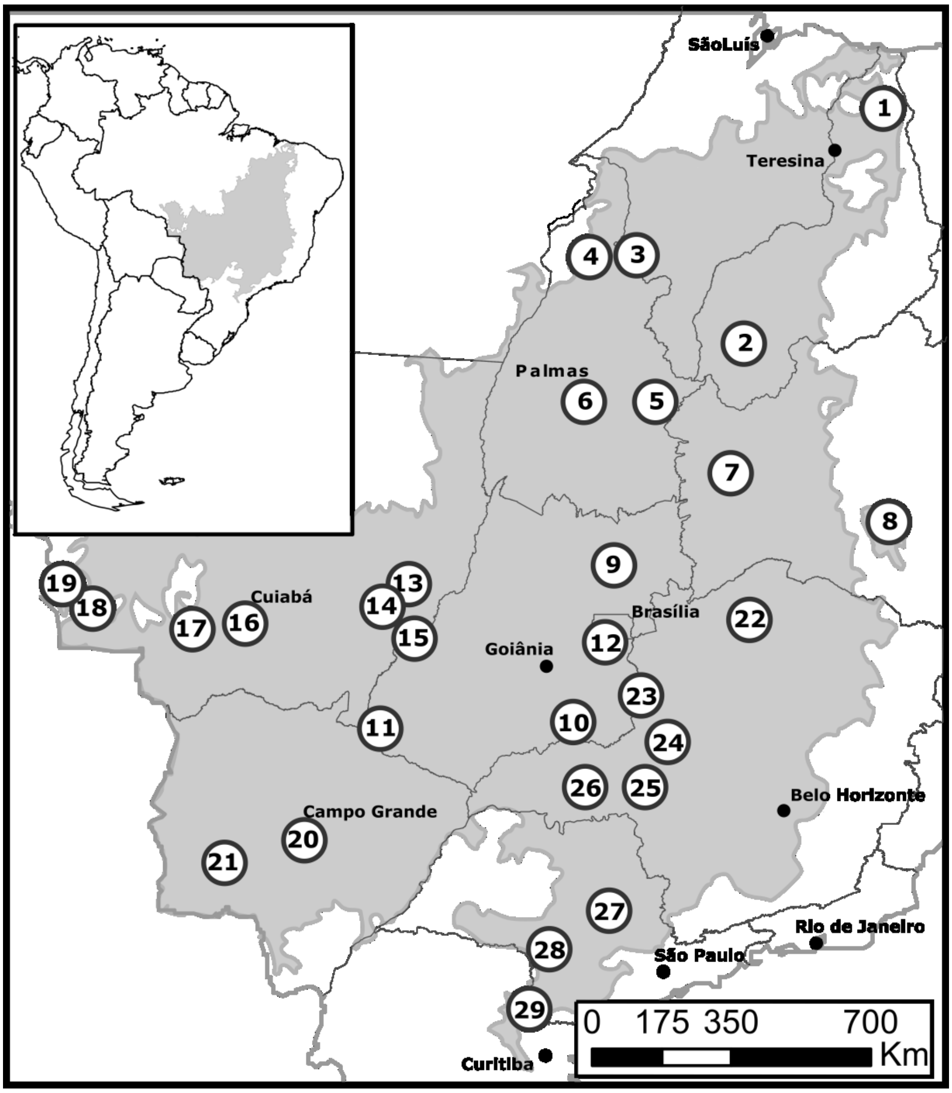

Figura 2. Mapa da distribuição do Cerrado (área cinza) mostrando as 29 localidades onde coletas padronizadas foram realizadas para amostrar a fauna de formigas de solo. Informações relevantes de cada localidade podem ser vistos na Tabela 1. O mapa da distribuição do Cerrado foi gerado a partir da sobreposição de mapas de distribuição de 1,454 espécies de plantas típicas do Cerrado, baseado na informação de especialistas em relação à bacia hidrográfica de ocorrência de cada espécie.

Tabela 1. Informações de 29 localidades em que coletas padronizadas da fauna de solo de formigas foram realizadas no domínio do Cerrado. Estado e município de coleta; tipo e nome da Unidade de Conservação; ID mapa: códigos conforme mapa na Fig. 2; data da coleta; latitude e longitude (do centroide dos transectos) em graus decimais; elevação (NMM); *Área equivale à área ocupada (em hectares) do mínimo polígono convexo formado entre os três transectos de cada localidade. Tipos de UC: PARNA: Parque Nacional; APA: Área de Proteção Ambiental; PE: Parque Estadual; EE: Estação Ecológica.

Estado/Município	Tipo/Nome da área protegida	ID mapa	Data	Latitude	Longitude	Elevação	Área* (ha)
Piauí							
Piripiri	PARNA Sete Cidades	1	Dez. 2013	-4.099	-41.710	224.0	300.7
Bom Jesus	Reserva Legal	2	Nov. 2010	-9.285	-44.721	620.0	2956.4
Maranhão							
Carolina	PARNA Chapada das Mesas	3	Out. 2015	-7.215	-47.319	257.3	303.2
Tocantins							
Araguaína	APA Nascentes do Araguaína	4	Out. 2015	-7.231	-48.138	241.7	9.0
Jalapão	PE Jalapão	5	Nov. 2012	-10.570	-46.747	422.0	191.3
Palmas	Reserva Legal	6	Nov. 2012	-10.527	-48.351	227.7	30.2
Bahia							
Barreiras	Reserva Legal	7	Mai. 2011	-12.150	-45.159	697.7	6.8
Mucugê	PARNA Chapada Diamantina	8	Jun. 2011	-12.964	-41.470	1036.3	84.7
Goiás							
São Jorge	PARNA Chapada dos Veadeiros	9	Abr. 2015	-14.139	-47.766	1134.7	275.5
Caldas Novas	PE Serra de Caldas Novas	10	Nov. 2011	-17.786	-48.669	985.0	111.3
Mineiros	PARNA Emas	11	Fev. 2012	-17.909	-53.009	837.0	14.0
Distrito Federal							
Brasília	APA Gama-Cabeça de Veado	12	Abr. 2011	-15.957	-47.933	1130.7	135.6

continua na próxima página

tabela 1, continuação

Estado/Município	Tipo/Nome da área protegida	ID mapa	Data	Latitude	Longitude	Elevação	Área* (ha)
Mato Grosso							
Nova Xavantina	Reserva Legal	13	Mai. 2011	-14.708	-52.348	306.7	114.4
Novo São Joaquim	Reserva Legal	14	Mai. 2011	-15.079	-52.788	329.7	29.0
Barra do Garças	PE Serra Azul	15	Mai. 2011	-15.851	-52.268	526.3	24.6
Cuiabá	PARNA Chapada dos Guimarães	16	Jun. 2011	-15.354	-55.968	206.3	8418.6
Cáceres	EE Serra das Araras	17	Out. 2011	-15.656	-57.214	235.3	66.3
Vila Bela da S. Trindade	Reserva Legal	18	Fev. 2014	-15.054	-59.779	211.7	54.9
Vila Bela da S. Trindade	PE Serra de Ricardo Franco	19	Fev. 2014	-14.908	-60.065	598.3	23.2
Mato Grosso do Sul							
Campo Grande	APA Córrego Ceroulas	20	Jul. 2012	-20.426	-54.728	547.3	69.8
Bonito	Reserva Legal	21	Jul. 2012	-20.966	-56.520	410.3	44.3
Minas Gerais							
Pandeiros	APA Bacia do Rio Pandeiros	22	Jul. 2011	-15.494	-44.683	693.3	16.2
Paracatu	RPPN Acangau	23	Abr. 2011	-17.191	-47.066	873.0	87.8
Presidente Olegário	Reserva Legal	24	Jun. 2011	-18.200	-46.489	944.3	221.5
Patrocínio	Reserva Legal	25	Jun. 2011	-19.192	-47.044	568.3	158.4
Uberlândia	EE Panga	26	Jan. 2012	-19.173	-48.397	793.0	50.7
São Paulo							
São Carlos	Reserva Legal	27	Out. 2011	-21.968	-47.863	848.0	71.7
Águas de Santa Bárbara	EE Santa Bárbara	28	Dez. 2014	-22.799	-49.254	635.3	62.6
Paraná							
Jaguariaíva	EE Cerrado	29	Jan. 2015	-24.188	-49.665	873.3	26.8

a) Capítulo 1. Analisar os padrões de densidade de espécies (riqueza média e total) e de diversidade (índice α de Fisher) de formigas de solo no Cerrado. Estas métricas de diversidade foram calculadas em diferentes escalas espaciais, de modo a testar se os fatores que determinam a montagem das comunidades seguem hierarquias determinadas pela escala espacial. As escalas vão desde pares de pontos amostrais, com distância de 40 m entre pontos, até três transectos distribuídos em uma localidade, com pelo menos 1 km de distância entre transectos. Quatro hipóteses comumente relacionadas a padrões geográficos de diversidade foram testadas: i) espécies-energia, ii) heterogeneidade ambiental, iii) fatores geográficos/históricos e iv) fatores locais. A importância relativa de dez variáveis preditoras, relacionadas às hipóteses, foram analisadas por meio de inferência multi-modelo. Espera-se que em escalas maiores haja uma grande influência de fatores históricos e climáticos nos padrões de diversidade, e que esta influência diminuirá em escalas menores, com um aumento da importância de fatores locais (Fig. 1, Ricklefs, 1987; Whittaker *et al.*, 2001; Hortal *et al.*, 2010).

b) Capítulo 2. Analisar os padrões de diversidade beta de formigas de solo no Cerrado. Neste caso, as escalas espaciais foram organizadas seguindo um quadro teórico proposto para avaliar padrões geográficos de beta diversidade, i.e., uma perspectiva de janela deslizante, em que tanto o grão quanto a extensão das amostras variam sistematicamente (Fig. 3; Barton *et al.*, 2013). Além disso, os valores de beta diversidade ($\beta_{sør}$ baseado no índice de dissimilaridade de Sørensen) foram particionados aditivamente entre os componentes de troca (β_{sim} baseado no índice de dissimilaridade de Simpson) e de dissimilaridade resultante de aninhamento (ou simplesmente aninhamento, $\beta_{nes} = \beta_{sør} - \beta_{sim}$) (Fig. 4; Baselga, 2010). Em cada escala espacial, variações na troca e aninhamento foram relacionadas a cinco fatores que podem explicar os padrões de beta diversidade: i) o banco regional de espécies, ii) heterogeneidade na vegetação, iii) variação elevacional, iv) proporção de ambientes fechados e v) quantidade de areia no solo. Nessa abordagem espera-se que a diversidade beta seja alta em escalas locais, pois a adição de novas amostras resulta numa alta troca de espécies devido à seleção de habitat ou a fatores estocásticos de ocupação (Huston, 1999; Whittaker *et al.*, 2001).

Com o aumento da escala, um número proporcionalmente maior de espécies (em relação ao banco) pode ser encontrado em cada amostra, logo, valores mais baixos de beta diversidade podem ser encontrados entre unidades amostrais na escala da paisagem (Ricklefs, 2004; Barton *et al.*, 2013). Além disso, espera-se que a troca e o aninhamento sejam determinados por fatores distintos, visto que esses componentes da beta diversidade são causados por processos antitéticos.

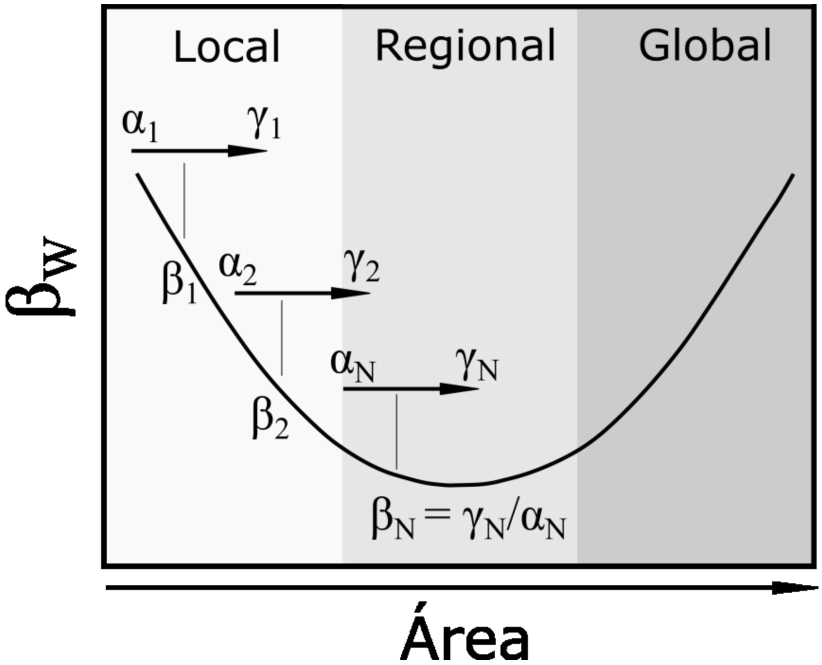

Figura 3. Quadro teórico de escalonamento espacial da beta diversidade. Neste quadro o grão e a extensão espacial das amostras variam sistematicamente, i.e., uma janela deslizante (Barton *et al.*, 2013). Os valores esperados de beta diversidade são derivados de relação trifásica entre o número de espécies e área e, resumidamente, espera-se que: i) em escalas locais a beta diversidade seja alta, pois a variação composicional entre amostras resulta em um rápido aumento da riqueza com a adição de novas amostras; ii) em escalas regionais os valores de beta sejam baixos, visto que, com novas amostras, menos espécies novas são encontradas em relação às espécies do banco regional; e iii) em escalas globais os valores de beta sejam altos, pois as amostras tem maior probabilidade de serem tiradas de bancos regionais distintos (devido à fatores geográficos e históricos) e, portanto, a dissimilaridade entre amostras é alta. Figura traduzida livremente a partir de Barton *et al.* (2013).

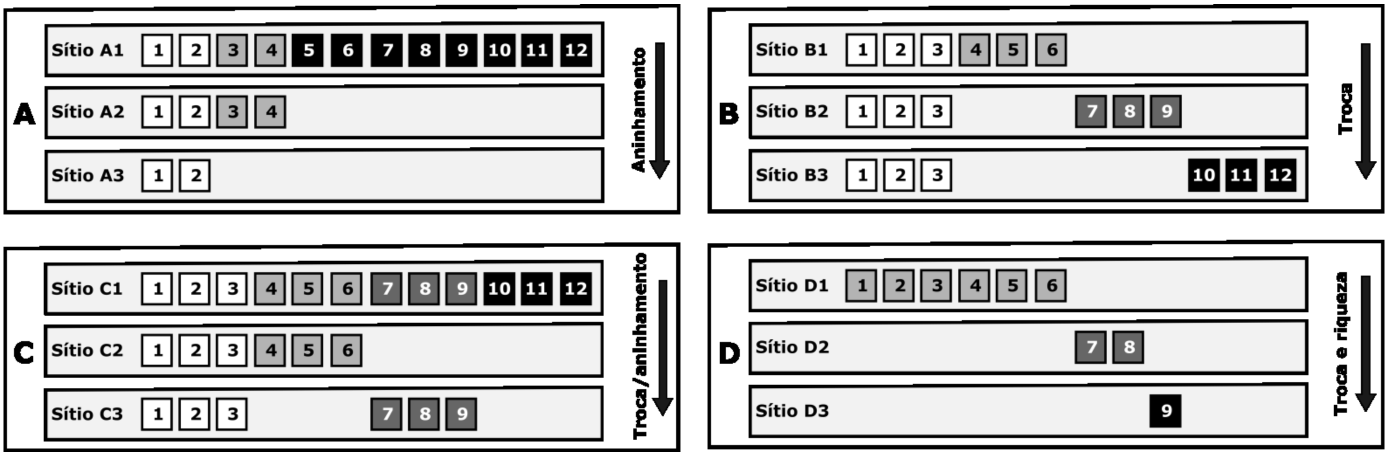

Figura 4. Representação de quatro comunidades hipotéticas (A-D) com três sítios de coleta cada. Sítios da comunidade A são completamente aninhados, pois A2 e A3 são subconjuntos do sítio mais rico, A1. Na comunidade B os sítios apresentam troca de espécies, pois eles têm mesma riqueza (seis espécies cada), três espécies compartilhadas entre sítios e três espécies exclusivas em cada sítio, resultando em troca. Na comunidade C há tanto troca quanto aninhamento, pois C2 e C3 são subconjuntos de C1 (dissimilaridade por aninhamento), porém algumas espécies são substituídas entre C2 e C3. Na comunidade D também há troca de espécies e diferenças de riqueza, porém não há aninhamento, pois sítios mais pobres não são subconjuntos do sítio mais rico em espécies. Figura traduzida livremente de Baselga (2010).

Capítulo 1 – Ant diversity in a Neotropical savanna region: hierarchical processes acting at multiple spatial scales

Jonas Brochado Maravalhas & Heraldo Luís de Vasconcelos

Introduction

One of the major goals in ecology and evolution is to map global patterns of biotic diversity and to understand the mechanisms that drive them (Gaston, 2000; Sutherland *et al.*, 2013). This is of special concern given the accelerated rate of biodiversity loss and the overwhelming challenges of meeting global and regional conservation requirements (Whittaker *et al.*, 2005; Pouzols *et al.*, 2014). The latitudinal gradient of diversity (LGD) is probably the most striking ecological pattern of our planet, with biological diversity of major taxonomic groups increasing from the Poles towards the Equator in nearly all ecosystems (Willig *et al.*, 2003; Hillebrand, 2004). However, a great number of ecological and evolutionary hypotheses, which are interdependent and often difficult to falsify, have been proposed as a general explanation to diversity gradients (Currie, 1991; Hillebrand, 2004; Evans *et al.*, 2005; Fine, 2015).

One consensus stems from the plethora of hypothesized drivers of spatial patterns in diversity is the idea that biodiversity is organized by hierarchical processes acting at different temporal and spatial scales (Ricklefs, 1987; Wiens, 1989; Whittaker *et al.*, 2001; Hortal *et al.*, 2010; Vellend, 2010). The number of species occurring within a locality is the balance between regional processes of diversification and dispersal, which influences the size of the species pools, and local processes that influence habitat use and the outcome of biotic interactions, and thus control local extinctions (Ricklefs, 1987; Huston, 1999; Willis & Whittaker, 2002; Kneitel & Chase, 2004; Ricklefs & Jenkins, 2011). At the largest spatial scales, i.e., global and continental, processes that occur at temporal scales of millions of years have driven the patterns of lineages distributions and rates of biotic diversification and extinction. These include, for instance the effect of area, time and past climatic conditions. Area is known to affect species richness by buffering the likelihood of extinctions and by supporting a higher turnover of species, since larger areas tend to have higher habitat variability (Rosenzweig, 1995). The historical stability of favorable climatic conditions over large areas is likely to be the main driver of the ubiquitous LGD (Wright, 1983; Rosenzweig, 1995; Jetz & Fine, 2012), which is evidenced by the persistence of relatively older lineage ages in tropical vs. temperate regions (Marin & Hedges, 2016). Moreover, historical factors such as the uplift of mountains, aridification events and cycles of glacial expansion and retraction are likely to influence the processes of speciation, extinction and dispersal at continental scales (Whittaker *et al.*, 2001; Ricklefs & Jenkins, 2011; Marin & Hedges, 2016).

Within these geographical realms, or evolutionary arenas, the regional patterns of diversity are almost exclusively driven by the balance between energy and water, which limits autotrophs productivity within a given area (Connell & Orias, 1964; O'Brien, 1993; Hawkins *et al.*, 2003; Field *et al.*, 2009). This led to the search for one single mechanism that would provide the link between climate and diversity, which has proven to be elusive (Pianka, 1966; Rohde, 1992; Currie *et al.*, 2004) in part due to inadequacies in dealing with scale (Evans *et al.*, 2005). The abundance-extinction mechanism states that higher productivity sustains higher population sizes and avoids local extinctions, resulting in higher species richness (Connell & Orias, 1964; Wright, 1983). This mechanism is expected to be more common at larger grains, while at smaller grains, the sampling mechanism is likely to occur (Evans *et al.*, 2005). The latter posits that productivity limits the number of individuals that can thrive in a certain area. These individuals are sampled from a pool of species, and thus, by chance, the more individuals being sampled the more species will be found in that area (Kaspari *et al.*, 2003; Evans *et al.*, 2005). Large-scale abiotic factors conditions sets limits to the size of species pools within large geographical regions, but as scales become finer, the number of potentially occurring species are filtered by biotic, abiotic or neutral factors that ultimately determine how species coexist in space. At the landscape scale, diversity patterns are determined by metacommunity processes which depend on species dispersal abilities, heterogeneity in habitat conditions and species competitive abilities (Leibold *et al.*, 2004). At local spatial scales, microhabitat type, heterogeneity or disturbances influence the interaction of species with the physical habitat and with other species (Ricklefs, 1987; Huston, 1999; Kneitel & Chase, 2004).

The ability to relate patterns and process that drive species coexistence, as well as to effectively protect biodiversity, is hampered by issues such as unclear definitions of the spatial scale of analysis, differences in modelling approaches and inadequacies of theory (Whittaker *et al.*, 2005). In addition, macroecological patterns of diversity are usually derived from superposition of species range maps, and relatively few studies have actually used standardized sampling to estimate the species richness of a determined taxon over large geographical areas (Hawkins *et al.*, 2003). This is especially true for invertebrates, which are underrepresented in macro-scale diversity studies (Hawkins *et al.*, 2003; Willig *et al.*, 2003), despite the fact that the largest proportion of global biodiversity is composed of invertebrate species (Mora *et al.*, 2011). There is also a major geographical bias, with more studies done in Europe and North America compared to Asia and South America (Field *et al.*, 2009).

The Brazilian Cerrado is the second largest Neotropical ecoregion, spanning over two million hectares of central Brazil, and is part of the 'diagonal of dry formations' of South America (Werneck, 2011). Variation in soil conditions, water availability and history of fires within the region result in the coexistence of multiple vegetation forms, from treeless grasslands to closed woodlands and dry forest (Eiten, 1972; Oliveira-Filho & Ratter, 2002). However, over 60% of the area of natural Cerrado remnants is comprised of a xeromorphic savanna vegetation (Sano *et al.*, 2010), which is characterized by the coexistence of a herbaceous layer of grasses and shrubs and a discontinuous canopy of small trees (Eiten, 1972; Oliveira-Filho & Ratter, 2002). The distribution of Cerrado physiognomies likely suffered shifts during climatic fluctuations of the Quaternary (Salgado-Labouriau *et al.*, 1997; Bueno *et al.*, 2017). However, patches of the usually dominant vegetation formation are thought to have persisted within some areas (Haffer, 1969). These refuges may have prevented local extinctions, providing sources for recolonization of typical Cerrado species when climatic conditions returned to normality (Werneck *et al.*, 2012; Bueno *et al.*, 2017). Moreover, the presence of species from multiple biomes within the Cerrado may be an evidence of the historical and contemporary relationship between this and other major Neotropical biomes (Silva & Bates, 2002). Despite the importance of historical events, large-scale patterns of diversity in the Cerrado have also been attributed to high levels of species turnover, which may promote high biodiversity at local, landscape and regional scales (Ratter *et al.*, 2003; Pacheco & Vasconcelos, 2012). The maintenance of this rich ecosystem, however, face serious threats, since over 40% of the original extent of the Cerrado has been converted into pastures, croplands and other land uses (Sano *et al.*, 2010). Moreover, only 2.8% of the Cerrado area is strictly protected, with additional 5.3% of indigenous and sustainable use reserves (MMA, 2017). The Cerrado is considered a conservation hotspot (Myers *et al.*, 2000; Olson & Dinerstein, 2002) and despite the awareness raised by this, the fate of the most diverse tropical savanna is daunting (Klink & Machado, 2005; Strassburg *et al.*, 2017).

Ants are among the most ubiquitous organisms in terrestrial ecosystems, contributing to a large portion of total animal biomass in tropical forests (Fittkau & Klinge, 1973). Ants play diverse ecological roles, since they can occupy various trophic levels (Davidson *et al.*, 2003) and are often enrolled in multiple biotic interactions, either between ant species or with other organisms (Parr & Gibb, 2010; Chomicki & Renner, 2017). These organisms are responsible for multiple ecosystem services and disservices and are fundamental in the functioning of terrestrial ecosystems (Del Toro *et al.*, 2012). Ant communities are sensitive to disturbance and habitat variability and thus are important bioindicators of ecosystem change (Andersen & Majer, 2004). Macro-scale patterns of ant diversity are known to be dependent on temperature, rainfall and/or productivity, especially at large spatial scales (Kaspari *et al.*, 2003; Dunn *et al.*, 2009; Jenkins *et al.*, 2011). Finally, ant taxonomy and systematic, although not completely resolved, is becoming increasingly better defined (Ward, 2007), thus contributing to more precise ecological data. Therefore, ants are an ideal macroecological model (Dunn *et al.*, 2009), especially if one is interested in analyzing the interaction of processes that drive biodiversity at different spatial scales.

In this study, we asked the following questions: i) Which factors drive local patterns of ground-dwelling ant diversity in Neotropical savannas? ii) Do these factors exert abundance-dependent or abundance-independent effects on ant diversity? iii) Does the strength of these effects vary with the spatial scale in which diversity is estimated? To answer these questions we conducted standardized samplings of the ant fauna in a set of sites scattered over the Cerrado region. At each site we measured ant species density (mean and total species richness within localities) and the diversity (Fisher's α, a diversity index corrected for abundance differences) at four hierarchical spatial scales. Scales varied in terms of grain, i.e., the spatial resolution of the sampling unit; and represented an increase in area from 0.01 ha at the smallest scale, to *ca.* 70 ha at the largest scale.

We chose ten correlates related to four non-exclusive hypotheses that may explain patterns of biotic diversity at different spatial scales: i) the species-energy hypothesis states that climatic factors limit the per-unit-area productivity, so that higher productivity areas have increased population sizes, which buffer local extinctions and resulted in increased pool of species (Wright, 1983; Rohde, 1992; Evans *et al.*, 2005). Although temperature is also commonly associated to the species-energy hypothesis, a previous analysis of this dataset found that temperature is a poor predictor of ant species richness (Vasconcelos *et al.*, 2018); Therefore, the species-energy hypothesis was tested with the correlates mean annual rainfall and net primary productivity; ii) heterogeneity is regarded as a major driver of species richness patterns (Tews *et al.*, 2004) being spatially structured in a hierarchical fashion (Kotliar & Wiens, 1990) and thus promoting species coexistence at different spatial scales (Stein *et al.*, 2014). We used the heterogeneity in greenness (EVI), the diversity of land covers and the proportion of closed habitats to test the environmental heterogeneity hypothesis; iii) geographical and historical factors are also regarded as major determinants of species richness patterns, particularly at large spatial scales (Willis & Whittaker, 2002; Hortal *et al.*, 2010). For instance, the mid-domain effect (Colwell *et al.*, 2004) predicts that the random overlap of species ranges result in higher species diversity at mid domains, which corresponds to the core area of a two-dimensional region. Also, many studies have shown that the core regions of the Cerrado savannas experienced less climatic and environmental fluctuations during the Pleistocene, and were likely to be refugial areas (Werneck *et al.*, 2012; Bueno *et al.*, 2017). To test the geographical/historical hypothesis we used the historical difference in precipitation, as well as the geographical position (core or periphery) within the Cerrado; iv) local environmental characteristics are related to possible effects of factors at inferior spatial hierarchies – such as habitat structure, disturbance and biotic interactions – that filter regional species pools into local assemblages (Huston, 1999; Hortal *et al.*, 2010). For instance, edaphic conditions (Peck *et al.*, 1998; Bestelmeyer & Wiens, 2001) and habitat structure (Andersen & Majer, 2004; Pacheco & Vasconcelos, 2012) are known to affect local patterns of ant diversity and composition. As measures of local environmental factors we used two principal component axes of soil properties, as well as a greenness index (NDVI).

We expect a greater importance of climatic, historical and geographical factors in determining patterns of ant biodiversity at larger spatial scales; while at smaller scales we expect a greater influence of local environmental factors such as soil texture and vegetation structure. Moreover, we expect environmental heterogeneity to affect ant biodiversity patterns at multiple scales. Finally, by analyzing both the species density (abundance-dependent) and diversity (abundance-independent) of ants, it is possible to unveil some of the mechanisms by which different ecological end evolutionary factors affect spatial patterns of biotic diversity.

Material and methods

Study region and sampling

The study was conducted within the Cerrado region in a total of 29 localities, which span over 20 degrees of latitude, 18.6 degrees of longitude and an elevational variation of nearly 1,000 m (Fig. 1) (Further information on the surveyed localities may be found in Vasconcelos *et al.*, 2018)). The region harbors a mosaic of vegetation forms, ranging from treeless grasslands to xeromorphic forests, but the dominant formation is a savanna (hereafter referred to as *cerrado*) characterized by the coexistence of a ground layer with grasses and herbs, and a discontinuous canopy of small and scattered trees (Eiten, 1972).

We selected well preserved areas of typical cerrado vegetation in each locality and established three transects with about 1 km of distance between them (Fig. 1). Two sampling plots were then delimited along each transect, with 120 m of spacing between plots. Each plot consisted of four sampling points (40 m spacing), where four pitfall traps were buried at ground level in a 2.5 m x 2.5 m grid (Fig. 1). Traps consisted of a 250 mL plastic cup filled to a third of its volume with a solution of water and detergent. Traps remained open for 48 hours after which the contents of the four cups in each sampling point were combined and preserved in 96º ethanol. This resulted in four samples in each plot, eight samples in each transect, 24 samples per site and 696 samples in the whole study area.

Samples were sorted in the laboratory with the aid of a stereomicroscope, where all ant species found in each sample were mounted. The specimens were identified to genus and to species – whenever possible – or assigned to a unique morphospecies code by comparing with reference specimens deposited at the Zoological Collection of the Federal University of Uberlandia. Although commonly collected in ground-level pitfall traps, for the purpose of the present analysis we did not consider the records of ant species that nest/feeds mainly in trees, following the classification of Vasconcelos *et al.* (2018).

Spatial scales of analysis

We analyzed the patterns of ground-dwelling ant biodiversity at four hierarchical spatial scales that vary in terms of grain (or focus). Grain size is a fundamental feature of a given scale, and is related to the spatial resolution of the smallest unit of analysis, in comparison to the extent, which is the geographical distribution of samples (Wiens, 1989). Ant biodiversity at the smallest spatial scale (SS1) is the mean number of species found at every pair of samples (12 pairs per locality; grain = distance between samples = 40 m); at SS2 we estimated the mean number of species at plots (four samples per plot, six plots per locality; grain = 120 m); at SS3 we estimated the mean number of species at transects (eight samples per transect, three transects per locality; grain = 360 m); and at SS4 we estimated the total number of species at each locality (24 samples per locality; grain varied across localities due to the spatial arrangement of transects). In each spatial scale we calculated ant species density and diversity. Species density is related to the number of species occurring within an area and, in the present analysis, may correspond to alpha (mean number of species found within each sampling unit, as in SS1, SS2 and SS3) or gamma (total number of species, as in SS4) diversity components (Whittaker, 1960). To account for possible bias in ant abundances recorded between localities we further calculated, in each scale, the diversity of ant species based on Fisher's α index.

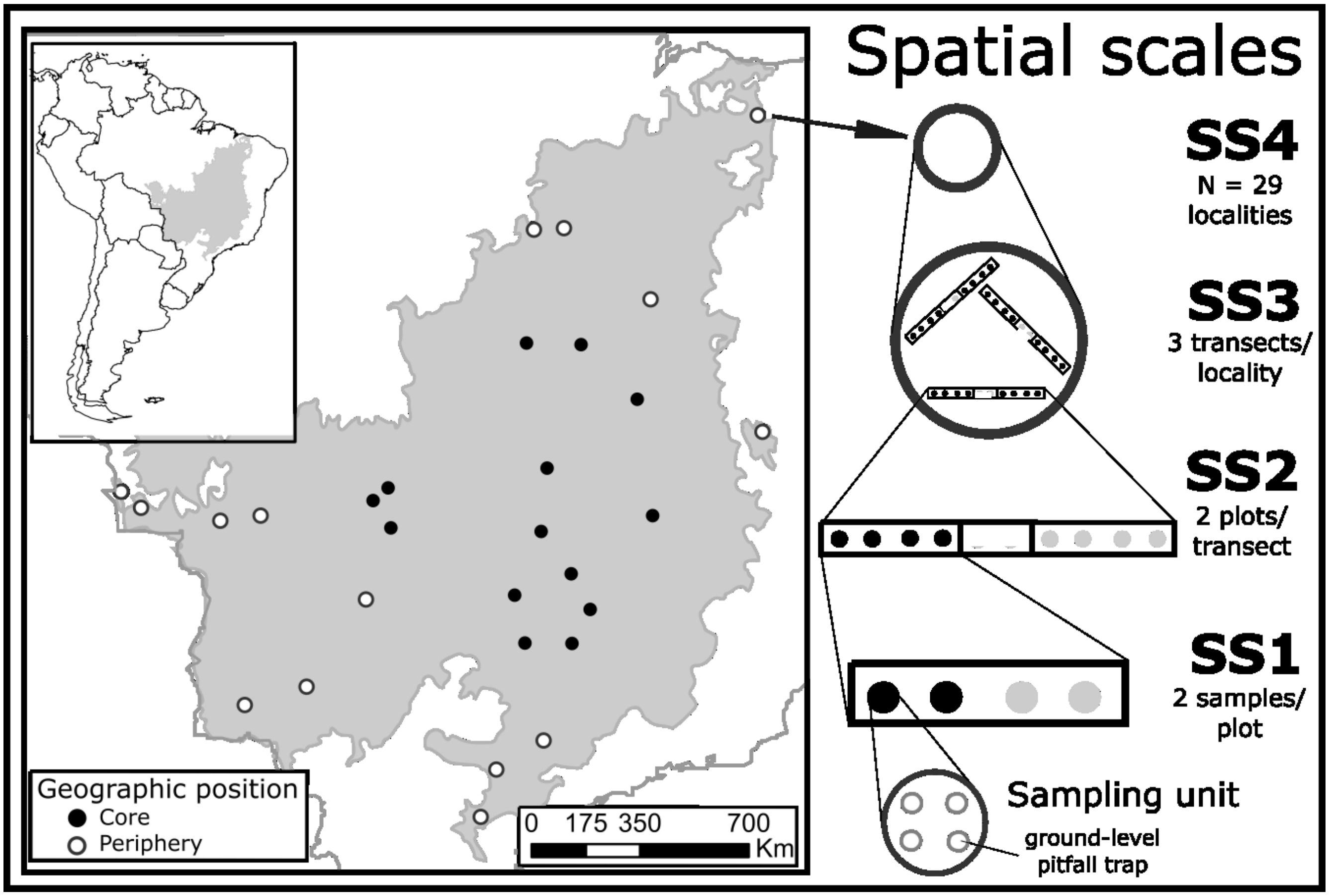

Figure 1. Map of the 29 localities within the domain of the Cerrado savannas (gray area) where standardized samples were conducted to assess ground-dwelling ant biodiversity patterns. Right side box shows a schematic representation of the standardized protocol applied in each of the localities and the spatial scales (SSs) in which ant biodiversity was analyzed. We measured ant biodiversity as the mean number of species found in each locality at four hierarchical scales that varied systematically in terms of grain size (spatial resolution of sampling unit). SS1: 12 sampling pairs (grain = distance between samples = 40 m); SS2: 6 plots (four samples per plot, grain = 120 m); SS3: three transects (eight samples per transect, grain = 360 m); as well as the total number of species per locality (SS4 grain varied across localities due to the spatial arrangement of transects). The sampling unit consisted of four pitfall traps buried to ground level in a 2.5 m grid, which were left exposed for 48 hours and then combined into a composite sample. In each corresponding scale, black circles represent sampling units that were used to calculate biodiversity values, while gray circles are units that were not considered. In the Cerrado map, localities where further classified into core (full circles) or periphery (empty circle) depending on its location within the Cerrado region. The map of the Cerrado domain was generated by overlapping distribution maps of 1,454 typical plant species. These maps represent the limits of the watersheds in which any given plant species was recorded, based on knowledge of various specialists (WWF-Brasil, 2015).

We followed the formula '$S = \alpha \ln\left(1 + \frac{N}{\alpha}\right)$', where S is the number of species, N is the abundance and α is the constant of interest. The number of species records was used as a measure of ant abundance, given that ants are social insects and the colony is considered the individual. Thus, the count of ant workers captured is not a biologically realistic measure of ant abundance, while the count of ant colonies was not feasible due to time constraints. As with species density, diversity was calculated as the mean (from SS1 to SS3) or total (SS4) Fisher's α diversity. It is worth mentioning that Fisher's α is a spatially ambiguous diversity measure, representing a scale that is larger than the one in which the species richness was estimated, i.e., it estimates the total number of species occurring in an undefined scale where all occurring species were recorded (Colwell & Coddington, 1994; Kaspari *et al.*, 2003).

Predictor variables

To extract the variables of interest, we used geoprocessing tools to create buffers of 400 m radius around the first sampling point of each transect in each locality. Within buffer we created ca. 40 equally spaced points from which we extracted the values of interest using the software ArcGis (ESRI, 2012). A total of 10 variables were used as correlates of ant species density and diversity, each related to one of four general hypotheses that may explain patterns of biotic diversity across spatial scale. The hypotheses and corresponding correlates were: i) species-energy hypothesis: mean annual precipitation (bio 12 from WorldClim database; Hijmans *et al.*, 2005) and net primary productivity (NPP) (MOD17; Zhao *et al.*, 2005). ii) heterogeneity hypothesis: for the diversity of land cover we extracted the land cover classification (only natural vegetation: IGBP classes 6 to 11, MCD12Q1; Friedl *et al.*, 2010) of each point within buffers and calculated the Shannon index of diversity of land classes in each locality. The heterogeneity in greenness is the complement of homogeneity, which is based on the similarity in enhanced vegetation index between any pixel (~1 km resolution) and its adjacent pixels (Tuanmu & Jetz, 2015). Although sampling took place in typical savanna vegetation, different physiognomies could also occur within our sampling area. Therefore, the variable closed habitats represents the proportion of points (in each buffer) that fell within forest and woodland land cover classifications (IGBP classes 2 to 8, MCD12Q1, Friedl et al., 2010). iii) geographical and historical hypothesis: the historical difference in rainfall is a measure of climatic stability over time, based on the difference in mean annual rainfall between current conditions (CR) and conditions during the Last Glacial Maximum (LGM). It was calculated as the mean of three available scenarios: historical difference in rainfall = [(CR - LGM1) + (CR - LGM2) + (CR - LGM3)] / 3 (WorldClim; Hijmans *et al.*, 2005). Geographical position describes how central a locality is regarding the distribution of the Cerrado region. Core localities are in the central distribution of the biome, while periphery localities are near the boundaries of the Cerrado with other biomes. We chose this geographical classification because it may be a surrogate of different ecological and evolutionary processes operating in a given region (e.g. Pironon *et al.*, 2017), the distinction of which is beyond the scope of this study. iv) local environment hypothesis: Soil PCA1 and soil PCA2 were created with principal component analysis using three measures of soil granulometry: the proportion of silt particles (diameter between 0.002 mm and 0.05 mm; parts per ton), sand particles (diameter between 0.05 mm and 2 mm; parts per ton) and the volumetric percentage of coarse fragments in the soil (diameter > 2 mm) (spatial resolution of 250 m; Hengl *et al.*, 2017). Soil PCA1 was positively correlated to coarse fragments and silt and negatively correlated to sand; while soil PCA2 was positively correlated to coarse fragments and sand. As a further descriptor of local environmental condition, the greenness index is the mean normalized difference vegetation index (calculated from Landsat 08 spectral bands; NASA LP DAAC, 2016) within buffers.

Statistical analyses

The relative importance of predictor variables in driving the patterns of species density and diversity was estimated at each spatial scale. For that we used multimodel inference, an information-theory analysis with increasing use in the ecological literature (Johnson & Omland, 2004). This analysis is based on the Akaike's Information Criterion (AICc, corrected for small samples, see Brewer *et al.*, 2016), which measures how well a model predicts the variation of the response variable and penalizes models with too many predictors (Jørgensen, 2004). AICc weights provide measures of the probability that a given model is indeed the best among the candidate models (Jørgensen, 2004). We used model averaging, which uses the population of models (created by combining all variables of interest) to estimate the relative importance of each variable (Banner & Higgs, 2017). We used *all subsets* regression analysis and conditioned the averaging procedure to consider models with a cumulative sum of AICc weights higher than 0.95. To account for possible spatial structure within our study region, we used Moran's eigenvector maps (MEMs; Dray *et al.*, 2006). These maps describe spatial structures within a set of georeferenced locations, and a given MEM can be selected based on its ability to minimize spatial autocorrelation in the residuals (Dray *et al.*, 2006). Finally, we used commonality analysis (Peres-Neto & Legendre, 2010; Ray-Mukherjee *et al.*, 2014) to additively partition the total variation explained by a model composed of environmental and spatial variables into fractions of variation explained uniquely by each environmental and spatial variable, as well as the fraction of explained variation shared between variables. Multimodel inference analysis were run in R (R Core Team, 2015) using package 'MuMIn' and commonality analysis was run using the package 'yhat'. SAM software (Rangel *et al.*, 2010) was used to calculate the principal components of soil conditions and to generate and select MEMs.

Results

The survey of the ground-dwelling ant fauna (24 samples per locality) resulted in 9,921 records of a total of 350 ant species/morphospecies, which belong to 65 genera and eight subfamilies. Ant species density and diversity showed considerable variation across localities (Fig 2) and scales (Fig. 3). Across scale, mean (± standard deviation) species density was 22.07 (± 5.75) at SS1, 31.99 (± 7.81) at SS2, 48.93 (± 11.55) at SS3 and 78.93 (± 19.23) at SS4. Mean (± standard deviation) diversity was 44.71 (±12.38) at SS1, 30.92 (±8.01) at SS2, 27.09 (±7.26) at SS3 and 29.13 (±8.52) at SS4 (Fig 3).

Model averaging revealed that soil conditions, most notably soil PCA2, were important predictors of species density, but their importance decreased with increasing scales (Fig. 4). We found lower density of ground-dwelling ant species in localities with higher amounts of sand and coarse fragments in the soil, and a weaker but also negative effect of silt content. At the largest scale, net primary productivity (NPP) became the better predictor of species density and, as expected, there was higher species density in higher productivity localities. Although with a relatively minor influence, geographical position also affected species density at the largest spatial scale, with increased density of ant species found at the core than at the periphery of the Cerrado region (Fig. 4).

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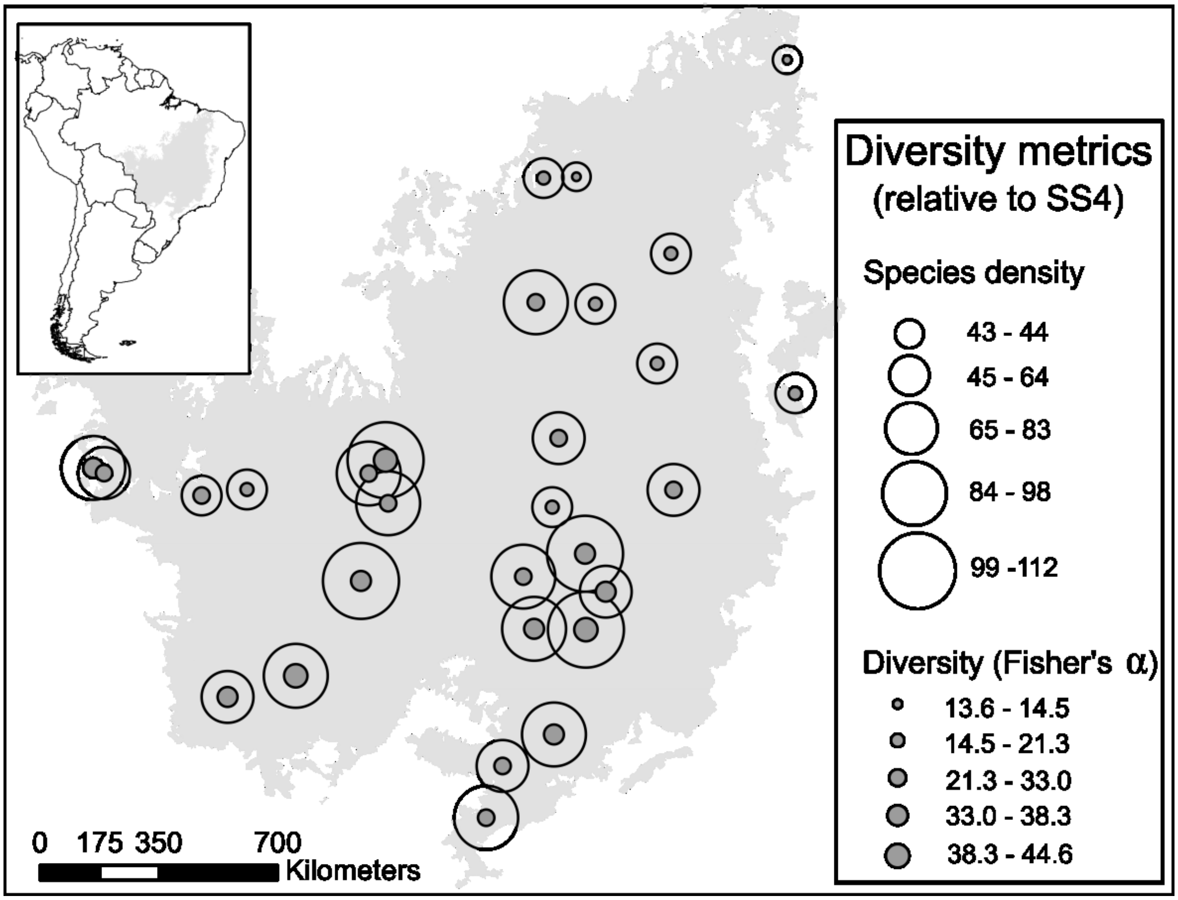

Figure 2. Graphic representation of the variation in ground-dwelling ant species density (total species richness) and diversity (Fisher's α) found at 29 localities in which standardized sampling of the ground-dwelling ant fauna was conducted. For simplicity we only present the values of species density and diversity at the largest spatial scale (SS4). The gray area represents the domain of the Cerrado savannas.

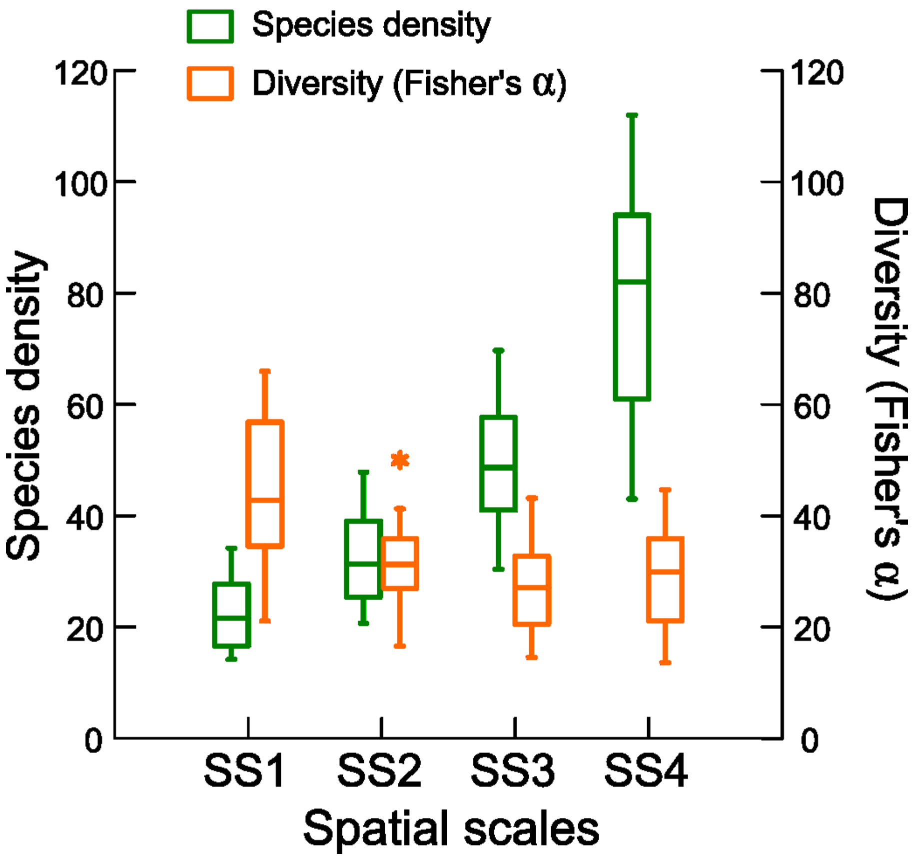

Figure 3. Box plot (median, 1st and 3rd quartiles) of ground-dwelling ant species density (mean and total species richness) and diversity (Fisher's α) in 29 Cerrado savanna localities. In each locality, species density and diversity was calculated at four hierarchical spatial scales: SS1: 12 pairs of samples (each sample constitutes four pitfall traps buried to ground level); SS2: 6 plots (four samples per plot); SS3: three transects (two plots per transect); and SS4 (three transects per locality).

By correcting for differences in abundance (Fisher's α diversity), we found a similar, albeit reduced effect of soil PCA2 in ant diversity in comparison to species density (Fig. 4). More sand and a greater amount of coarse fragments in the soil (soil PCA2) were associated with decreased ant diversity, and the importance of this variable was lower at larger scales. On the other hand, the importance of NPP was much greater for diversity than for species density. However, there was no clear scale-dependency in the importance of NPP in driving diversity, with the influence being of similar magnitude from SS2 to SS4. Agreeing with the results found for species density, higher ant diversity was found at the core compared to the periphery localities, and this effect was also strongest at the largest spatial scale. The remaining correlates showed a moderate to weak importance in driving diversity patterns within our study region (Fig. 4) (Complete model-averaged results may be found in table S1 of Supporting Information). Given that soil PCA2, NPP and geographical position were the variables that most influenced the patterns of species density and diversity across scales, we considered only these variables in the commonality analysis. Furthermore, one Moran's eigenvector map (MEM) significantly reduced residual spatial autocorrelation in our dataset and was used to assess the spatial structure of data in the commonality analysis.

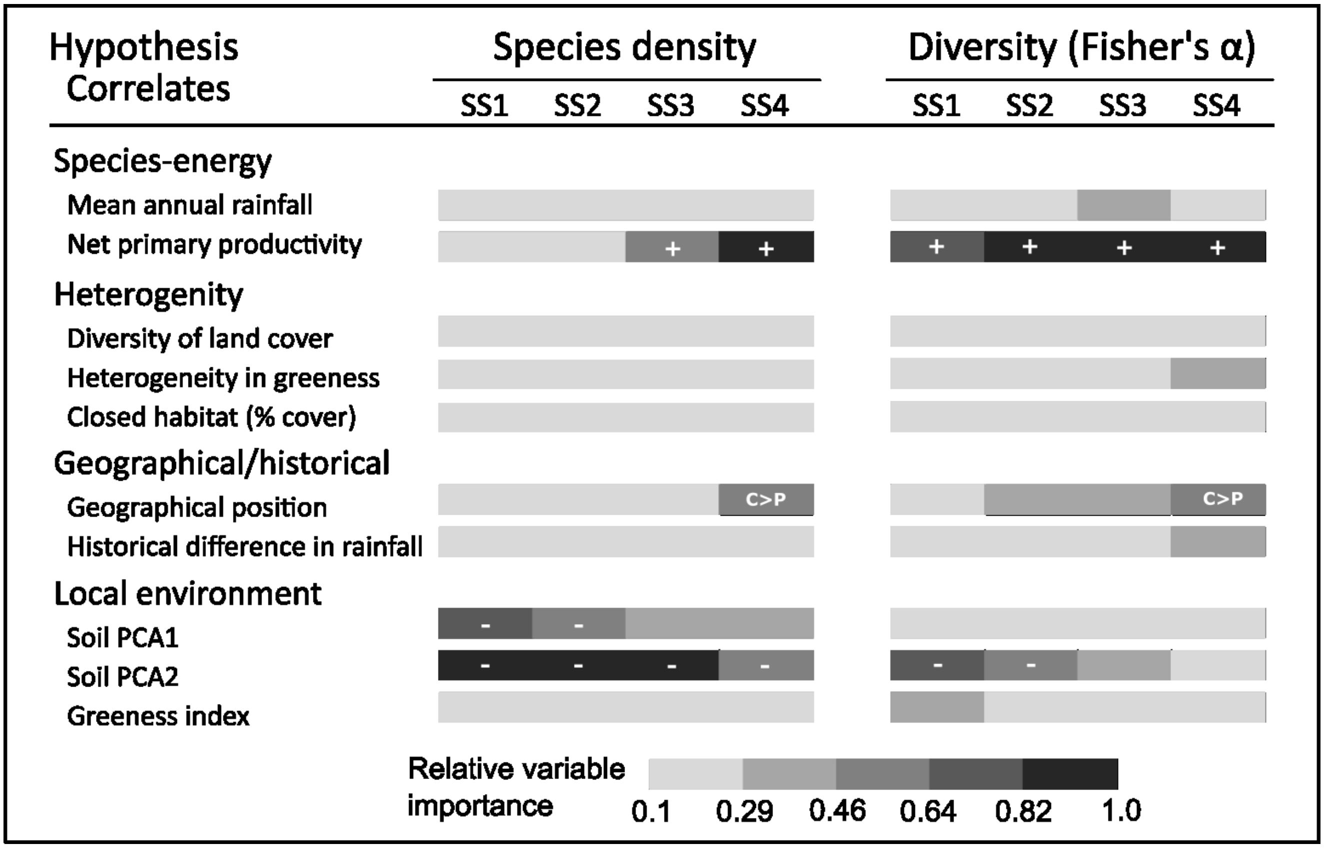

Figure 4. Summary of the relative variable importance of a set of ten correlates related to four hypotheses that may explain diversity gradients. We used model averaging (based on AICc weights) to determine the importance of these correlates in explaining the variation in ant species density and diversity across four spatial scales. For relative importance values greater than 0.46, the sign of the averaged regression coefficient is indicate, while C > P means that ant biodiversity was higher in core than in periphery areas in the Cerrado.

We found a strong spatial structure in our data, as revealed by the high proportion of explained variation shared between environmental variables and MEM (Fig. 5). This spatially structured effect was highest for NPP and for the variation shared between environmental correlates (most of which corresponds to the variation shared between NPP and PCA2, see table S2 of Supporting Information). Soil PCA2, on the other hand, showed the highest proportion of uniquely explained variation among the environmental correlates, indicating that the effect of soil on ant species density and diversity is not spatially autocorrelated. Moreover, the unique explained variation of MEM increased from SS1 to

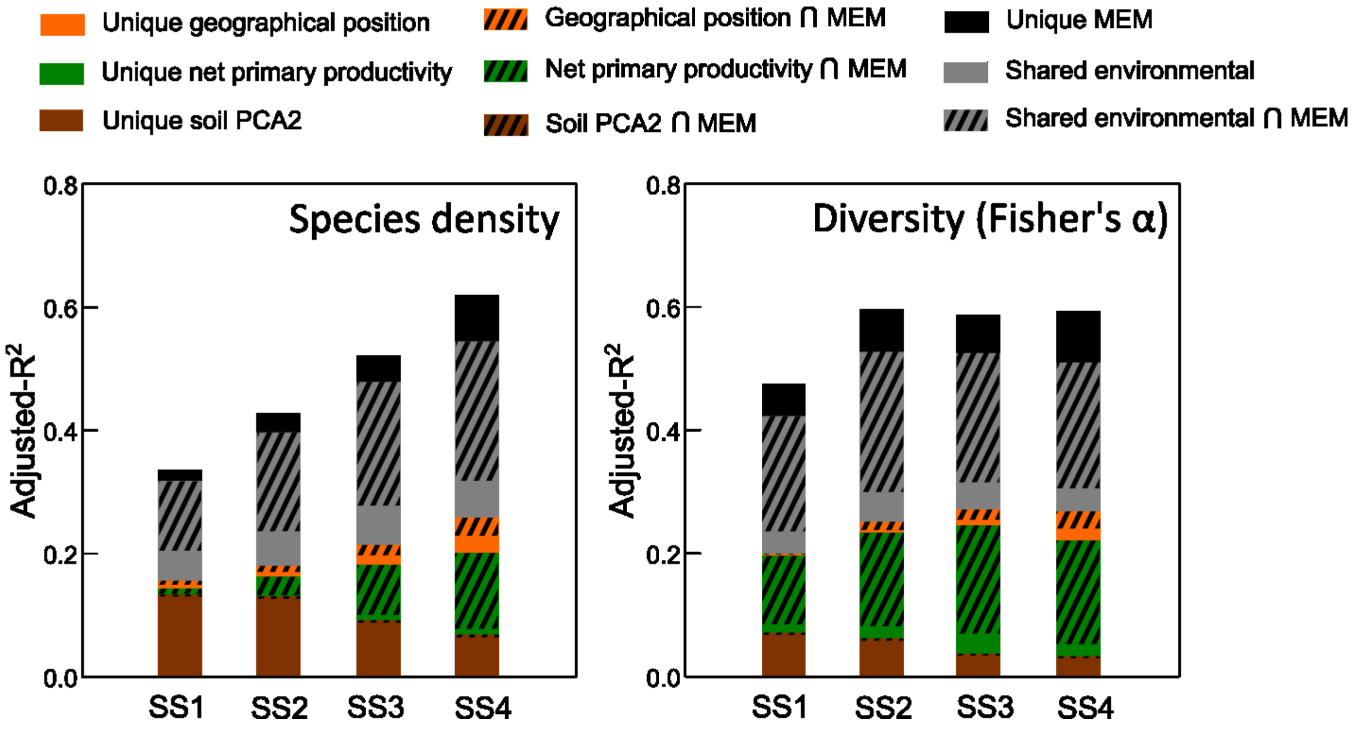

Figure 5. Result of the commonality analysis of ground-dwelling ant species density and diversity. The total variation in the response variable explained by the full model is partitioned into fractions of variation explained uniquely by Moran's Eigenvector Map (MEM), geographical position, net primary productivity, soil PCA2, and the environmental correlates (sum of the variation shared between geographical position, net primary productivity and soil PCA2, with each pairwise shared variation); Striped colors correspond to spatially structured variation (i.e., shared with MEM) explained by each environmental correlate, and the shared environmental variation explained.

SS4 for species density, but was scale-independent for diversity. In all cases, the variation explained by MEM was higher that the variation explained uniquely by NPP or geographical position, but it was usually comparable to the variation explained uniquely by soil PCA2. Finally, overall model performance showed clear scale-dependency for species density (with increasing explained variation with increasing scale), while for ant diversity, only at SS1 there was a somewhat lower proportion of explained variation. From SS2 to SS4, the total variation explained by our models did not vary, with values being very similar to those found for species density at SS4 (Fig. 5).

Discussion

In the present study we aimed to disentangle the relative roles of ecological and evolutionary factors that structure biodiversity patterns at multiple spatial scales. In short, we found a positive relationship between net primary productivity and species density, an effect that became stronger as spatial scale increased. This result agrees with the scaling rule of the species-energy hypothesis, which predicts increased climatic control on diversity at coarser spatial scales (Chase & Leibold, 2002; Evans *et al.*, 2005; Field *et al.*, 2009). We also found that this scale-dependent effect was related to abundance patterns, since ant diversity – which was corrected for abundance differences – was strongly related to net primary productivity irrespective of scale. This finding indicates that the effect of productivity on ant biodiversity is not the result of a sampling effect, but of reduced extinctions in high productivity localities. While climatic gradients limited large-scale patterns of species density, we found an increased importance of local edaphic conditions as scales became finer. The amount of sand and coarser particles in the soil (PCA2) negatively affected ant species density and, to a lesser extent, also reduced ant diversity. This indicates that sampling effects underlie the relationship between soil and ant species richness, i.e., more species are sampled from the species pool when soil conditions allow higher densities of ant colonies. Finally, our results indicate that geographical/historical factors also play a role in determining patterns of ant diversity, particularly at larger spatial scales. As a whole, our study conforms to the hierarchical theory of biodiversity (Levin, 1992; Whittaker *et al.*, 2001; Vellend, 2010), since we found higher importance of local environmental factors at small scales, while at larger scales climate was the major driver of diversity patterns. We further detected a minor contribution of geographical/historical factors, which are expected to drive biodiversity patterns at large scales.

The patterns of ground-dwelling ant biodiversity within the Cerrado savannas were mainly determined by climatic factors, since net primary productivity (NPP) was the best predictor of diversity patterns when abundance differences were controlled for. This conforms to a previous analysis of macroscale drivers of ant species richness within the Cerrado savanna localities analyzed here, in which Vasconcelos *et al.*(2018) found a reversed latitudinal gradient in ant diversity. The authors related this pattern to higher climatic favorability in central and southern regions, compared to the dryer conditions of northern regions; and also to the evolutionary association between Neotropical ant taxa and moist forests (Vasconcelos *et al.*, 2018). In the present study, NPP was also an important driver of species density, but mainly at large spatial scales. In fact, the variation in species density explained by NPP (sum of adjusted R^2 of the unique and spatially structured variation explained by NPP) showed a fourteen fold increase from SS1 to SS4. This finding is in accordance with the scaling rule of the species-energy hypothesis, which predicts a reduced climatic control on diversity when observations are made at very fine spatial scales (Chase & Leibold, 2002; Evans *et al.*, 2005; Field *et al.*, 2009).

Although climate is regarded as a major driver of macroscale patterns of diversity, the mechanism underlying this relationship is a matter of intense debate (Evans *et al.*, 2005; Fine, 2015). The results of the present study indicate that the influence of NPP in ant biodiversity is not a sampling artifact, since this factor explained a larger proportion of the variation in ant diversity than the variation in species density. Instead, it is likely that NPP affects ant diversity by the abundance-extinction mechanism, i.e., larger population sizes in high productivity regions prevent local extinctions, leading to higher regional species pools. It is possible that higher plant productivity result in increased energy flow in the food web of ant species, which in turn result in higher population sizes (e.g., Kaspari *et al.*, 2000). Plant productivity is known to drive the abundance and diversity of arthropods (e.g., Siemann, 1998; Hooper *et al.*, 2000). Increased arthropod abundance, in turn, would cascade up the food chain, having a positive effect on predator, scavenger and generalist species, which are among the most common ant functional guilds (Brandão *et al.*, 2012). It is thus reasonable to assume that increased plant productivity result in increased energy flow within ant food webs, buffering local extinctions. The importance of the abundance-extinction mechanism is expected to be higher at large scales; as grains increase, the proportional increase in energy generates a higher total resource availability, increasing the probability that a population will be large enough to avoid local extinction (Evans *et al.*, 2005). In the present study, however, the influence of NPP on ant diversity was only slightly smaller at SS1, and did not vary from SS2 to SS4, which is an unexpected result. It is possible that NPP enhances the coexistence of ant diversity at fine grains via, for instance, reduced niche breadths or smaller consumer pressure, which are mechanisms more likely to operate at small scales (Evans *et al.*, 2005). Alternatively, productivity may increase species evenness, resulting in higher number of species for a given number of individuals in high productivity sites (Hurlbert, 2004).

Climate thus limits species pool sizes, but it is impossible for all species of the regional pool to be found at the fine scale in which individuals coexist. Therefore, regional diversity patterns are filtered by processes which operate at smaller spatial scales, such as metacommunity dynamics within landscapes (Leibold *et al.*, 2004; Andersen, 2008), or biotic and abiotic interactions within localities (Huston, 1999; Whittaker *et al.*, 2001; Vellend, 2010; Baldeck *et al.*, 2012). We found that ant biodiversity was also driven by local factors, since the amount of sand and coarse fragments in the soil (soil PCA2) was negatively related to both species density and diversity of ground-dwelling ants. Moreover, soil PCA1, which is positively correlated to silt and coarse fragments and negatively correlated to sand content, also had a negative influence in species density, albeit much smaller than that of PCA2. As expected, the effect of soil conditions was stronger at the smallest spatial scale. For instance, the variation in species density and diversity explained by soil PCA2 (sum of adjusted R^2, as described above) showed approximately a two-fold decrease from scales SS1 to SS4. Soil texture is known to determine the coexistence of ant species (Johnson, 2000) as well as local patterns of ant diversity (Peck *et al.*, 1998; Bestelmeyer & Wiens, 2001; Solar *et al.*, 2016; but see Delsinne *et al.*, 2010; Jacquemin *et al.*, 2012). In the present study, two soil variables were the most important driver of ant biodiversity. Sand content measures the proportion of particles with diameter between 0.05 mm and 2 mm, while coarse fragments are particles with diameter > 2 mm. While texture (clay, silt and sand particles) are classic measures of soil characteristics, the quantification of coarse fragments is a much neglected measure of soil condition (Poesen & Lavee, 1994). Sandier soils (or, conversely, with less clay content) have been associated with higher ant diversity in grassland (Boulton *et al.*, 2005; Campbell & Crist, 2017) and savanna ecosystems (Andersen *et al.*, 2015). In contrast, we found an opposite result in the Cerrado savannas analyzed here, i.e., reduced biodiversity in sandier soils, which indicate that the effect of sand content in ant diversity patterns is likely to be idiosyncratic. The percentage of coarse fragments in the soil was also negatively related to ant species density and diversity. It is possible to reason that rock fragments in the soil hinder the growth of ant colonies, since these fragments occupy space that could otherwise be used by ants to expand their nests. Alternatively, these large fragments may pose a difficulty in the excavation of nests, considering that there is a limit to the size of soil pellets that an ant can carry (Monaenkova *et al.*, 2015).

While making inference from correlative results, one cannot rule out the possibility that some unmeasured factor underlie the observed relationship, confounding the analysis. Therefore, it is possible that the edaphic conditions measured in this study are correlated to unknown factors that, in turn, affect ant biodiversity patterns. For instance, physico-chemical soil parameters had a weak influence on small-scale patterns of hypogeic ant diversity (Jacquemin *et al.*, 2012), which is surprising, given that this guild of subterranean ants directly interact with the soil environment. Moreover, ground-dwelling ants in eastern Amazonia showed lower species density and diversity in sandier soils, but these results could not be unequivocally attributed to a direct effect of soil conditions on ant communities due to the presence of confounding factors such as topography and water drainage (Vasconcelos *et al.*, 2003). In a temperate grassland, on the other hand, vegetation structure showed little influence on ant community, while sand increased the abundance (and diversity) of all ant species and that of three dominant species individually (Boulton *et al.*, 2005). These results point to a direct effect of soil texture on ant species, possibly related to limitations that soils with low sand (or high clay) content may pose to ant nest excavation (Boulton *et al.*, 2005). Although the present results show an opposite (negative) effect of sand on ant biodiversity, we also found little influence of measures of vegetation structure on species density and diversity. In addition, the influence of soil on ant biodiversity was reduced when abundance differences were accounted for. For instance, at the smallest spatial scale, the variation explained by soil PCA2 showed a nearly twofold increase from species density to diversity. Therefore, at small scales, the patterns of species density may be driven by a sampling mechanism that is unrelated to productivity, but to soil characteristics that allow higher ant abundances. Studies of ant assemblages within large geographical extents should focus on factors that enhance colony abundance, such as plant productivity or warm temperatures (Kaspari *et al.*, 2000). Moreover, ant species coexistence are likely to be driven by processes operating at the establishment phase, when ant propagules (queens) colonize new areas and compete for nesting resources (Andersen, 2008). Experimental tests within the Cerrado savannas could assess if soils with a lower proportion of coarse fragments and sand sustain higher densities of ant colonies and, consequently, more species at small spatial scales.

The interaction between abundance-driven effects of local edaphic conditions and abundance-independent effects of climatic favorability within the Cerrado region determined most of the patterns of ant biodiversity found across spatial scales. In fact, of the total variation explained by the full model, the contribution solely attributed to NPP and soil PCA2 (sum of unique, shared and spatially structured adjusted R^2) was of 71% for species density and 78% for diversity (mean across scales). Nevertheless, the relative contribution of NPP and soil PCA2 to the total explained variation decreased from the smallest to the largest spatial scale for both biodiversity metrics. This decreased importance of climatic and edaphic factors at larger scales was matched by an increase in the effect of geographical/historical factors. Although the variation explained by geographical position (sum of unique and spatially structured adjusted R^2) did not exceed five percent for both species density and diversity, more ant species were found in localities at the core than at the periphery of the Cerrado distribution. In addition, the variation explained by this factor was 2.7-fold smaller when analyzing diversity than species density, indicating that this effect may be related to increased density of species at core Cerrado regions.

Irrespective of the diversity measure considered, the effect of geographical position was more important at largest spatial scales, which conforms to the hierarchical theory of diversity (Whittaker *et al.*, 2001; Hortal *et al.*, 2010; Vellend, 2010). History and geographical location often play important roles in determining the patterns of biotic diversity at large scales, conditioning the relationship between water-energy budgets and species richness (Latham & Ricklefs, 1993; Fine, 2015), a patterns that has also been observed for ants (Dunn *et al.*, 2009; Jenkins *et al.*, 2011). It is not within the scope of the present study to disentangle the underlying factors that resulted in higher ant biodiversity in the core than in the periphery of the Cerrado region. Among the possible explanations for this pattern, is the centre-periphery hypothesis, which predicts that the population occupancy of a given species is higher at the centre compared to the periphery of the species' geographical range (Pironon *et al.*, 2017). Alternatively, the core of the Cerrado region appear to have suffered less climatic and environmental changes across the Quaternary climatic fluctuations, and have been considered as refugial areas within the Cerrado (Werneck *et al.*, 2012; Bueno *et al.*, 2017). This historical stability, coupled with a larger relative area (of Cerrado vs. non-Cerrado vegetation) in the core region may be related to the hypothesis that higher diversity in tropical compared to temperate regions is the result of high climatic favorableness over long time periods within large extents in the tropics (the energy-time-area hypothesis; Jetz & Fine, 2012; Fine, 2015). Finally, the mid-domain effect (Colwell *et al.*, 2004) predicts a peak in diversity at mid domains due to the geometrical constraints in the distributions of species ranges. In fact, ant species associated to savanna habitats in the Cerrado had a peak in diversity at mid latitudes (Vasconcelos *et al.*, 2018) and future studies could assess if this is due to the random arrangement of species ranges within the Cerrado region.

The ability of our models to predict biodiversity patterns of ground-dwelling ants in the Cerrado was increased at larger spatial scales, especially regarding species density. For instance, the percentage of variation which was not explained by the models (residual variation) decreased from 66.8% at SS1 to 38.4% at SS4 for species density. This means that unmeasured factors within our study region are driving abundance-driven patterns of ant biodiversity, particularly at finer spatial scales. One of the factors that may contribute to the residual variation in ant biodiversity present in this analysis is the size of the patches of vegetation. Despite the standardization of the area sampled in each locality (as recommended by Whittaker *et al.*, 2001), the effective size of the habitat was not the same across the study region, since the spatial arrangement of transects within localities resulted in very different areas. By analyzing the size of remnants of natural vegetation, the relationship between area and species richness was inversed, since Cerrado savannas are better preserved at northern areas, while the more ant species-rich savannas at the central and southern regions are much more fragmented (Sano *et al.*, 2010). While differences in area may influence the patterns of diversity at larger spatial scales, biotic interactions likely drive fine-scale patterns of species occurrences. Even though interspecific competition are important factors in the assembly of local ant communities in the Cerrado (e.g. Camarota *et al.*, 2016), the outcome of ant species interactions is idiosyncratic (Andersen, 2008; Parr & Gibb, 2010) and, thus, hard to predict at macroecological scales. Moreover, fine-scale assembly of ant species may also depend on neutral factors, such as lottery or priority effects that occur at the establishment phase of colonies (Andersen, 2008). In this context, variations in habitat conditions would be expected to affect the patterns of ant biodiversity. Heterogeneity was found to be a multiscale driver of ant diversity in sandhill savanna habitats (Spiesman & Cumming, 2008) as well as in the Cerrado savannas (Pacheco & Vasconcelos, 2012; Maravalhas & Vasconcelos, 2014). Therefore, it is a surprising result that, regardless of scale, the metrics of environmental heterogeneity analyzed here showed a negligible influence on ant biodiversity patterns. This is likely due to the sampling design, which prioritized the sampling of the ant fauna in well-preserved areas of cerrado savanna vegetation, i.e., habitat heterogeneity was in fact minimized within sampling locations.

The findings of the present study indicate that the relative importance of ecological and evolutionary processes that drive biodiversity depend on the spatial scale in which observations are made. While local edaphic conditions largely affected the density of ground-dwelling ant species at fine spatial scales, net primary productivity, was a most important determinant of ant species density at coarser scales. The importance of productivity was even greater after abundance differences were accounted for, indicating that high productivity does not increase ant biodiversity by a random sampling effect. Rather, our results support that the abundance-extinction mechanism underlie the relationship between productivity and biodiversity. In this sense, we can infer that climatically favorable localities within the Cerrado region experienced reduced local extinctions compared to less favorable localities, which led to differences in regional pool sizes. Productivity thus exerts a hierarchically superior effect on ant biodiversity, since the number of species occurring locally is ultimately limited by the number of potentially occurring species in the regional pool. On the other hand, factors such as edaphic characteristics were shown to be important filters of local assembly of ant species. We found that soils with less sand and rock content supported higher species density and diversity at small scales. However, opposite to what we found for productivity, soil was a better determinant of species density than diversity patterns. Soil conditions may limit the number of ant colonies coexisting within a given area, thus driving small-scale variations in ant biodiversity by a sampling mechanism. Therefore, soil conditions have a hierarchically inferior control on ant communities, which interacts with productivity-limited species pool sizes.

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Supporting information

Table S1. Results of multi-model inference analysis based on Akaike's Information Criterion (AICc weights). Shown are the relative variable importance and model-averaged coefficients of ten correlates (related to four hypotheses) that may explain patterns of species density (mean and total species richness) and diversity (Fisher's α) of ground-dwelling ants in the Cerrado savannas.

Diversity metric	**SS1**		**SS2**		**SS3**		**SS4**	
Hypothesis/correlates	Import.	Coeff.	Import.	Coeff.	Import.	Coeff.	Import.	Coeff.
Species density								
Species-energy								
Mean anual rainfall	0.13	-0.037	0.13	0.001	0.15	0.101	0.14	0.018
Net primary productivity	0.18	0.146	0.26	0.220	0.6	0.380	0.86	0.414
Heterogeneity								
Diversity land cover classes	0.2	-0.154	0.17	-0.090	0.15	-0.019	0.15	0.018
Heterogeneity in greenness	0.13	0.023	0.15	0.076	0.15	0.099	0.25	0.053
Closed habitat (% cover)	0.2	0.159	0.18	0.109	0.14	0.043	0.12	-0.009
Geographical/historical								
Geographical position	0.16	-0.200	0.18	-0.239	0.27	-0.414	0.52	-0.310
Historical dfference in rainfall	0.19	0.149	0.22	0.169	0.2	0.136	0.18	-0.030
Local environment								
Soil PCA1	0.66	-0.354	0.53	-0.299	0.39	-0.246	0.34	-0.080
Soil PCA2	0.96	-0.556	0.98	-0.578	0.86	-0.516	0.6	-0.246
Greenness index	0.14	-0.007	0.14	0.018	0.13	0.037	0.11	-0.001
Diversity (Fisher's α)								
Species-energy								
Mean anual rainfall	0.15	-0.112	0.16	0.110	0.31	0.201	0.21	0.173
Net primary productivity	0.7	0.452	0.93	0.508	1	0.579	0.97	0.557
Heterogeneity								
Diversity land cover classes	0.14	-0.032	0.23	0.211	0.24	0.205	0.19	0.189
Heterogeneity in greenness	0.19	0.163	0.23	0.178	0.19	0.146	0.43	0.276
Closed habitat (% cover)	0.24	0.250	0.13	0.013	0.13	-0.033	0.13	-0.099
Geographical/historical								
Geographical position	0.16	-0.214	0.32	-0.433	0.37	-0.457	0.47	-0.546
Historical dfference in rainfall	0.17	0.008	0.18	-0.102	0.24	-0.178	0.45	-0.286
Local environment								
Soil PCA1	0.24	-0.219	0.13	-0.057	0.13	-0.060	0.12	-0.087
Soil PCA2	0.65	-0.417	0.55	-0.360	0.33	-0.263	0.23	-0.248
Greenness index	0.33	0.252	0.18	0.134	0.15	0.097	0.11	-0.003

Table S2. Results of commonality analysis of a set of correlates of species density and diversity (Fisher's α) of ground-dwelling ants in the Cerrado savannas, which partition the total variation in the response variable in shared and unique variation explained by each correlate. Shown are the (unique and shared) fractions of the environmental correlates: net primary productivity (NPP), geographic position (GEO) and soil conditions (PCA2); as well as one spatial correlate, Moran's Eigenvector Map (MEM).

	Species density				**Diversity (Fisher's α)**			
Variables	SS1	SS2	SS3	SS4	SS1	SS2	SS3	SS4
NPP	0.000	0.000	0.008	0.009	0.013	0.019	0.032	0.018
GEO	0.006	0.007	0.015	0.027	0.001	0.004	0.009	0.019
PCA2	0.129	0.124	0.086	0.062	0.066	0.056	0.033	0.028
MEMs	0.017	0.030	0.042	0.075	0.052	0.069	0.061	0.084
NPP,GEO	0.001	0.000	-0.005	-0.006	0.004	-0.003	-0.007	-0.009
NPP,PCA2	0.017	0.025	0.037	0.031	0.038	0.040	0.038	0.027
GEO,PCA2	0.040	0.041	0.042	0.045	0.002	0.020	0.019	0.025
NPP,MEMs	0.009	0.031	0.082	0.124	0.111	0.152	0.176	0.169
GEO,MEMs	0.007	0.010	0.017	0.030	-0.001	0.013	0.017	0.028
PCA2,MEMs	0.003	0.004	0.004	0.005	0.004	0.004	0.003	0.003
NPP,GEO,PCA2	-0.010	-0.011	-0.012	-0.011	-0.007	-0.008	-0.007	-0.006
NPP,GEO,MEMs	-0.004	-0.007	-0.011	-0.020	-0.003	-0.011	-0.013	-0.019
NPP,PCA2,MEMs	0.086	0.125	0.158	0.178	0.169	0.193	0.176	0.165
GEO,PCA2,MEMs	0.017	0.021	0.023	0.028	0.014	0.020	0.016	0.020
NPP,GEO,PCA2,MEMs	0.015	0.021	0.031	0.042	0.007	0.026	0.030	0.037
Total variation explained	0.332	0.423	0.517	0.616	0.471	0.594	0.584	0.591
Residual variation	0.668	0.577	0.483	0.384	0.529	0.406	0.416	0.409

Capítulo 2 - Ground-dwelling ant beta diversity: factors driving turnover and nestedness patterns in a spatial scaling framework

Jonas Brochado Maravalhas & Heraldo Luís de Vasconcelos

Introduction

To appropriately protect biodiversity it is fundamental to understand what factors determine the spatial and temporal variations in species coexistence. The concept of beta diversity – the variation in species composition – is thus central for this purpose, given its ability to shed light into the mechanisms of species assembly in natural communities (Myers & LaManna, 2016; Socolar *et al.*, 2016). Species richness patterns are the result of interactions between large-scale factors that limit the size of regional species pools, and of small-scale factors that filter the pool into local assemblages of coexisting species (Ricklefs, 1987; Wiens, 1989; Whittaker *et al.*, 2001; Vellend, 2010). Beta diversity represents a scalar that links the hierarchy of factors driving biotic diversity at different spatial and temporal scales (Myers & LaManna, 2016). It essentially measures how much bigger the regional (gamma) diversity is from mean local (alpha) diversity and, therefore, it is bound to the scale in which the alpha and gamma components are estimated.

In the analysis of geographical patterns of beta diversity, the alpha and beta components that generate them are related to the spatial scale concepts of grain and extent (Whittaker *et al.*, 2001). Grain measures the spatial resolution of the lowest level of analysis, or the alpha component, while extent represents the geographical range of these inventories, or the gamma component. By systematically varying the grain and extent of analysis, i.e., a sliding window framework (Barton *et al.*, 2013), one can make predictions regarding the response of beta diversity values across a range of hierarchical spatial scales. Beta diversity is expected to be highest at the local scale, since factors such as microhabitat environmental sorting (Leibold *et al.*, 2004; Hortal *et al.*, 2010), the outcome of biotic interactions (Huston, 1999), and/or stochastic occupancy factors (Chase, 2010) will result in high variability in species composition across fine-scale local samples. Lower values of beta diversity are expected within samples taken at the landscape and regional scales, since larger sampling units capture a larger fraction of the regional pool and, therefore, the similarity between samples increase (Wiens, 1989; Nekola & White, 1999; Ricklefs, 2004; Barton *et al.*, 2013). Beta diversity increases again at continental and global scales, since historical factors and dispersal barriers result in highly dissimilar communities across regions (Ricklefs, 2004; Soininen *et al.*, 2007; Barton *et al.*, 2013).

An important aspect to consider in the analysis of beta diversity patterns is that compositional dissimilarities are generated by distinct ecological processes: nestedness and turnover (Baselga, 2010; Podani & Schmera, 2011; Legendre, 2014; Ulrich *et al.*, 2017). Nestedness occurs when richness differences among localities result in species-poor localities being a subset of species-rich localities; being thus, ultimately controlled by local patterns of colonization and extinctions (Ulrich *et al.*, 2009; Baselga, 2010; Dobrovolski *et al.*, 2012). A variety of factors may produce nestedness-driven dissimilarities, such as differences in habitat quality and disturbance history, species dispersal limitation or sampling effects (Svenning *et al.*, 2011; Matthews *et al.*, 2015). Turnover, on the other hand, is produced when localities have a distinct species composition that is not the result of richness differences, but of species replacement. Turnover may be driven by a variety of non-exclusive mechanisms (Hortal *et al.*, 2010; Myers *et al.*, 2013), such as the distance decay in dissimilarity(Nekola & White, 1999; König *et al.*, 2017), environmental species-sorting (Leibold *et al.*, 2004), neutral dynamics of species occupancy (Chase, 2010; Catano *et al.*, 2017), the legacy of historical events (Svenning *et al.*, 2011; Wen *et al.*, 2016) and differences in species pool sizes (Kraft *et al.*, 2011; Karger *et al.*, 2015).

Understanding how different factors affect the patterns of turnover and nestedness at different spatial scales is fundamental to design efficient networks of protected areas, to measure species losses, and to maintain processes that drive species diversity (Socolar *et al.*, 2016). If nestedness is the dominant component of beta diversity one should prioritize the conservation of species-rich localities, whereas high species turnover demands the creation of several protected areas within landscapes (Leprieur *et al.*, 2011; Gianuca *et al.*, 2017). Insect communities are ideal models to study the interaction of processes that drive species variations across hierarchical spatial scales (Hortal *et al.*, 2010). Despite the high abundance, richness and ecological importance of this group, macroecological and conservational studies of insects face many challenges, most notably shortfalls in taxonomic and biogeographic knowledge of insect species (Diniz-Filho *et al.*, 2010). To overcome these issues, one can apply standardized sampling of a given taxonomic group over large regions, thus providing fine-scale data of species occupancy within localities that are distributed along geographic and climatic gradients.

In a recent study, Vasconcelos *et al.* (2018) conducted intensive surveys of the ant fauna within the Cerrado savannas of central Brazil. The authors found a reversed latitudinal gradient in ant diversity that was driven by variations in rainfall within the region, and related this finding to evolutionary affinities of Neotropical ant faunas to moist forests (Vasconcelos *et al.*, 2018). Large-scale climatic gradients constrain the regional species pool of ground-dwelling Cerrado ants, while local factors such as edaphic properties limit ant abundance at fine spatial scales (Chapter 1 of thesis, Maravalhas, 2018). Understanding what drives spatial patterns of beta diversity is fundamental to elucidate how regional patterns and local processes interact to determine species richness across scales. Beta diversity measures the compositional dissimilarity between small-scale samples, informing us the extent to which this dissimilarity contributes to the large-scale diversity. On a different perspective, large-scale diversity patterns influence the extent to which small-scale samples may vary in composition. A multiscale assessment of beta diversity is thus essential in the attempt to disentangle the relative roles of different ecological and evolutionary processes in driving diversity patterns.

In this study we aimed at answering the following questions: i) What factors drive spatial patterns of ant beta diversity? ii) What is the relative contribution of turnover and nestedness to total beta diversity? iii) Does the relative importance of these factors or the contribution of turnover and nestedness vary with the spatial scale in which beta diversity was calculated? To answer these questions, we used standardized sampling of the ground-dwelling ant fauna of the Cerrado savanna (preliminary results of this dataset may be seen at Vasconcelos et al. 2018) to calculate beta diversity at five hierarchical spatial scales. These scales simultaneously vary in terms of grain (size of sampling units) and extent (spatial dispersion of samples), i.e., a sliding window framework (Barton *et al.*, 2013). Given that the spatial scales analyzed here range from the site to the landscape scale domain, according to Pearson & Dawson's (2003) classification, we expect a monotonic decline in beta diversity from the smaller to the largest spatial scales (Barton *et al.*, 2013). We further partitioned beta diversity into its additive components of species turnover and nestedness (Baselga, 2010) to test if the relative contribution of these components also vary with scale. We then related turnover and nestedness patterns to a set of environmental factors that are expected to influence beta diversity, assessing the scale-dependency of the relative importance of these factors. Since turnover and nestedness are considered to be antithetic drivers of beta diversity, being the result of different ecological processes (Ulrich *et al.*, 2009; Baselga, 2010; Matthews *et al.*, 2015). The factors analyzed were: i) the size of species pools; two measures of environmental heterogeneity, ii) heterogeneity in greeness and iii) elevational variation; and two descriptors of local environmental conditions, iv) sand content in the soil and v) percentage cover of closed-habitat vegetation. Fourth, the total variation in turnover and nestedness that was explained by our models was then partitioned into the proportion of variation explained uniquely by the set of environmental factors, the proportion explained uniquely by space and the proportion or variation explained simultaneously by the environment and space.

Material and methods

Study region and sampling

We conducted this study in the Brazilian *Cerrado* savannas, an ecoregion that originally extended for over 2.5 million square kilometers of the Neotropics. Although the region is characterized by a mixture of vegetation types that range from open grasslands to closed woodlands and forests, the dominant formation is a type of savanna vegetation characterized by a continuous herbaceous layer and a discontinuous canopy of scattered trees (Ratter *et al.*, 1997). The Cerrado harbors high levels of species richness and endemism, being considered a biodiversity *hotspot* (Myers *et al.*, 2000); despite this, continued agribusiness expansion and ineffective legal protection pose a serious threat to the conservation of this ecosystem (Strassburg *et al.*, 2017).

In a total of 29 localities distributed within the Cerrado domain (Fig. 1), we selected well preserved areas of typical savanna vegetation and conducted standardized sampling of

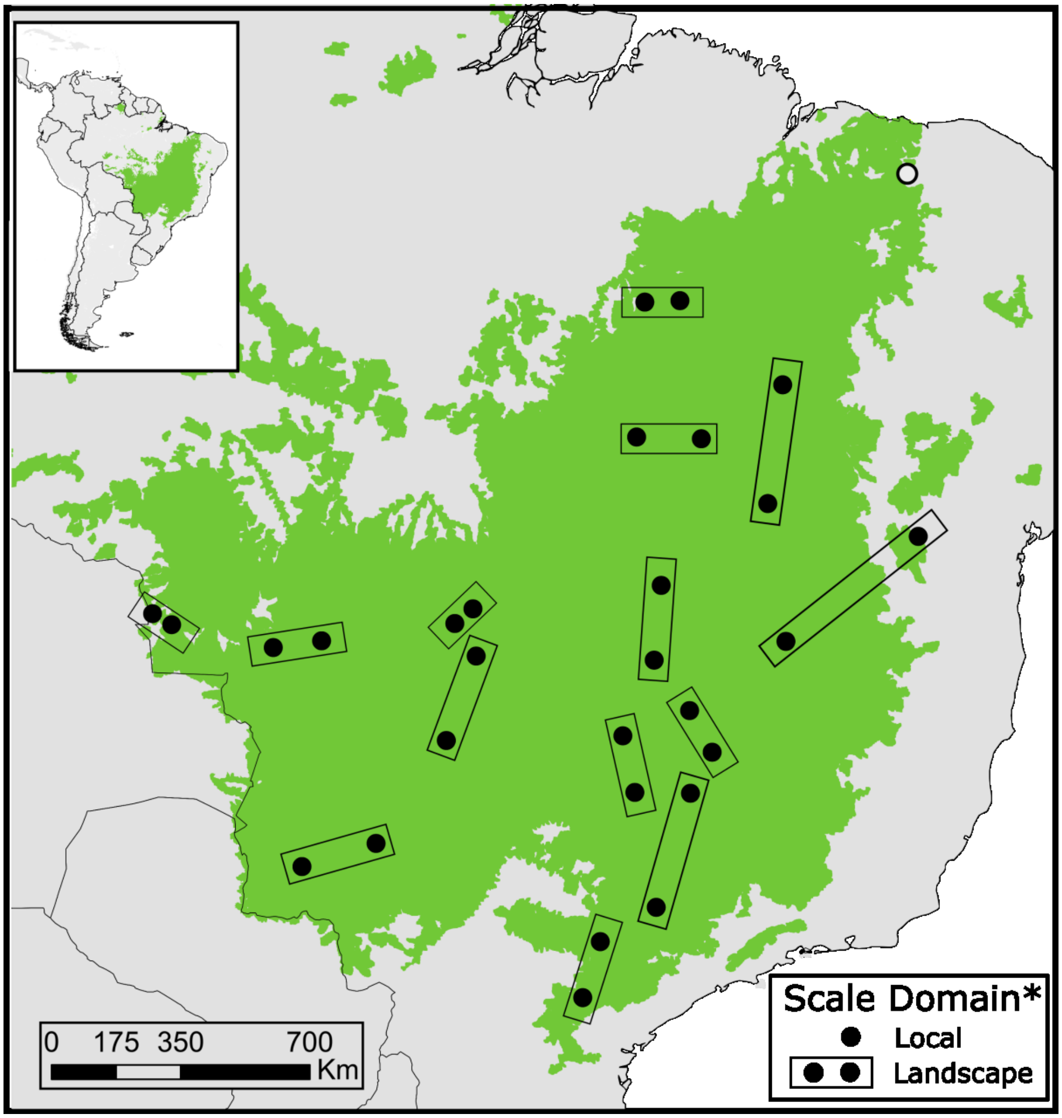

Figure 1. Map of the study region where the ground-dwelling ant fauna was surveyed. The green area represents the domain of the Cerrado savannas. The shape of Cerrado domain was generated by overlapping distribution maps of 1,454 typical Cerrado plant species. These maps represent the limits of the watersheds in which any given plant species was recorded, based on knowledge of various specialists (WWF-Brasil, 2015). Full black circles represent each of 28 localities were standardized sampling was conducted, while the empty circle is a locality that was not considered in this study. Localities were further grouped into 14 landscapes (rectangles).

*Scale domain classification as in Pearson & Dawson (2003).

the ground-dwelling ant community by the use of pitfall traps. Between 2010 and 2015 we surveyed the ground-dwelling ant fauna once in each locality. Within each locality, three transects were established with about 1 km of distance between them. Each transect consisted of 10 sampling points with 40 m distance between them, where four pitfall-traps were buried at ground level in a grid of 2.5 x 2.5 m (Fig 2). Traps remained active for 48 hours, after which the contents of the four traps were combined into one sample and fixated in 96% ethanol. Samples were then sorted with the aid of a stereomicroscope and one specimen of each ant species in each sample was mounted and compared to a reference collection, identified to genera and species or assigned to a morphospecies code. For the analyses presented here, we excluded one locality since pooling pairs of localities at the largest scale of analysis required an even number of localities. We excluded the northernmost locality (Fig. 1) since it was the most distant from the remaining ones. Moreover, arboreal ants were commonly collected in ground-level pitfall traps, but, for the purpose of the this study, we excluded the records of ant species that nest/feeds in trees, following the classification of Vasconcelos *et al.* (2018).

Sliding window framework

We followed the sliding window framework proposed by Barton *et al.* (2013) to measure beta diversity of the ground-dwelling ant fauna across spatial scales (from local to landscape scales) that vary simultaneously in terms of grain and extent. The grain, also known as focus, is related to the spatial resolution of sampling, i.e., the size of the smaller sampling unit. The extent is the total spatial coverage of samples, i.e., the geographical area that they encompass (Fig. 2). Therefore, in each locality (N = 28), the smallest spatial scale (SS1) consisted of a pair of consecutive sampling points, i.e., grain of roughly 2 m (distance between traps within points) and an extent of 40 m (distance between points). In the next scale (SS2), the pair of points that constitute SS1 are pooled and compared to a consecutive pooled pair of points within one transect. SS3 constitutes two sets of four samples within one transect; and SS4 a pair of transects (eight samples) within each locality. The largest spatial scale (SS5) consisted of pairs of localities (16 sampling points each) that were combined in a way that the overall pairwise geographic distances were minimized, and thus considered two independent samples from landscapes (N = 14) within the Cerrado savannas (Fig. 1 and 2). Finally, we used the whole dataset (30 samples per locality, 60 samples per landscape) to measure the size of the regional species pool within each locality/landscape, which were further used to model ant beta diversity together with other environmental correlates. It is worth mentioning that the five spatial scales analyzed here may be classified into one of three scale domains proposed by Pearson & Dawson (2003): scales SS1 to SS3 are within the site domain, SS4 corresponds to the local domain and SS5 to the landscape domain (Fig. 2).

One of the first formulations of beta diversity considered it to be the ratio between gamma and alpha diversities ($\beta = \gamma / \bar{\alpha}$, Whittaker's multiplicative beta diversity) which can be viewed as the degree of community differentiation (Whittaker, 1960). Alternatively, beta diversity can be measured as the difference in richness between the gamma and alpha components ($\beta = \gamma - \bar{\alpha}$, additive beta diversity; Crist & Veech, 2006). The classic multiplicative and additive beta diversities contrast with multivariate beta diversity (Anderson *et al.*, 2011). This metric is based on pairwise dissimilarity among sampling units and is commonly analyzed by multiple regression of distance matrices or ordinations (Legendre *et al.*, 2005; Tuomisto & Ruokolainen, 2008; Anderson *et al.*, 2011). In the present study, at each spatial scale, 'grain' defines the alpha diversity component, or the mean number of species found at each sampling unit, while 'extent' defines the gamma component, or the total number of species found within sampling units. Thus, multiplicative beta diversity could be calculated, but this metric fails to distinguish between beta diversity due to turnover (species replacement) and nestedness (richness differences)(Baselga, 2010; Legendre, 2014). Therefore, we calculated the pairwise dissimilarity (of sampling units) in each locality/landscape at each spatial scale. We used the Sørensen index of dissimilarity ($\beta_{sør}$), which is equivalent to Whittaker's beta diversity, but that can be additively partitioned into the components of turnover (the richness independent Simpson's index, β_{sim}) and the nestedness-resultant dissimilarity ($\beta_{nes} = \beta_{sør} - \beta_{sim}$) (Baselga, 2010), hereafter referred simply as nestedness. Furthermore, we calculated the proportional contribution of the turnover component by calculating the ratio between turnover and beta diversity ($\beta_{ratio} = \beta_{sim}/\beta_{sør}$). One-way ANOVAs were used to test if $\beta_{sør}$, β_{sim}, β_{nes} and β_{ratio} were affected by spatial scale and, if differences were significant, the significance of pairwise differences was assessed using Tukey's honestly significant difference test.

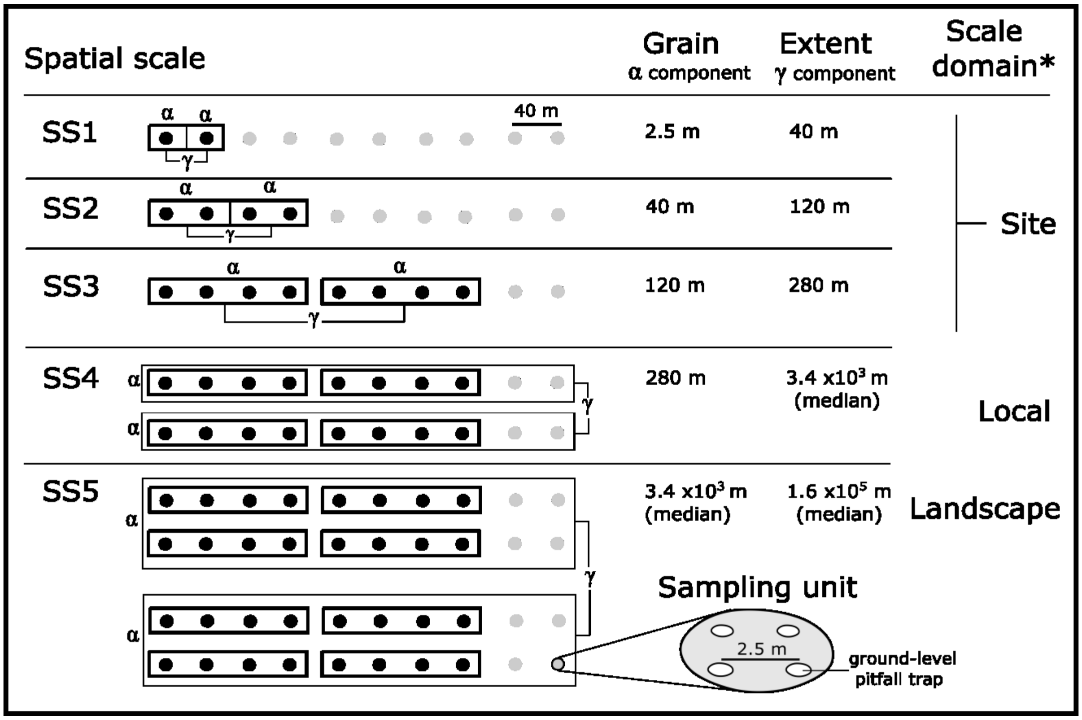

Figure 2. Schematic representation of the spatial scales considered in this study and the corresponding scale domain. Spatial scales were defined by systematically changing the grain (the resolution of the smallest unit of analysis) ant the extent (the geographical extension of sampling units), i.e., a sliding window framework, as proposed by Barton *et al.* (2013). Beta diversity values were calculated in each scale by defining the grain as the alpha diversity component and the extent as the gamma diversity component. The sampling unit consists of a composite sample of four ground-level pitfall traps in which ground-dwelling ants were collected. In each corresponding scale, black circles represent sampling units that were used to calculate beta diversity values, while gray circles are units that were not considered. *Scale domain classification following Pearson & Dawson (2003).

We used a set of five candidate correlates that may influence the patterns of beta diversity at the spatial scales analyzed here, which were: the size of the species pool; one measure of environmental heterogeneity based on differences in vegetation greenness; one measure of environmental heterogeneity based on elevational variability; one local environmental descriptor based on the content of sand in the soil and one local environmental descriptor based on the proportion of area covered by closed-habitat vegetation (woodlands and forests). Species pool sizes affect beta diversity by either promoting higher turnover in species-rich regions (Kraft *et al.*, 2011; Karger *et al.*, 2015) or higher nestedness in species-poor regions (Boyero *et al.*, 2015). Spatial heterogeneity is regarded as a major driver of compositional dissimilarities (Tews *et al.*, 2004) and may act at different spatial scales (Pickett & Cadenasso, 1995; Stein *et al.*, 2014). Finally, local environmental factors such as edaphic conditions or type of vegetation cover are likely to drive patterns of beta diversity through environmental sorting (Leibold *et al.*, 2004; Hill *et al.*, 2017), while the presence of different vegetation physiognomies may further affect ant beta diversity by processes such as mass-effect (Shmida & Wilson, 1985; Andersen, 2008).

To estimate the size of the regional pool of species within each locality (SS1 to SS4) or within each landscape (SS5), we used the whole dataset (30 samples per locality, 60 samples per landscape) which consists of nearly a twofold increase in the sampling size in comparison to the sampling size used to calculate beta diversity. We computed the estimated species richness (rarefied to N = 28 for localities and N = 56 for landscapes) since two samples were lost in one locality. Regarding the remaining correlates, we created buffers of 400 m radius around the first sampling point of each transect in each locality. Within this buffer we created spatially balanced points from which we extracted the variables of interest using the software ArcGis (ESRI, 2012). Variable extraction depended on the scale of analysis, and for SS1 to SS3 was based on ca. 40 points within the transect being analyzed, for SS4 we combined the points of each transect within each locality (ca. 80 points) and for SS5 we combined the points of each locality within landscapes combined the points of each locality within landscapes (ca. 160 points). For elevational variability (one of the twot measure of environmental heterogeneity) we downloaded digital elevation maps (SRTMGL3 at 90 m resolution, Farr *et al.*, 2007) and calculated the standard deviation in elevation between points within each buffer. For the second measure of heterogeneity (heterogeneity in greenness) a map of environmental homogeneity at a spatial resolution of 1 km was used to extract mean values within buffers. This variable represents the complement of the similarity in EVI (enhanced vegetation index) between any pixel and its adjacent pixels, and was the best-performing metric of spatial heterogeneity based on satellite imagery in a Global-scale analysis (homogeneity metric; Tuanmu & Jetz, 2015). To characterize the local soil conditions of each locality we extracted the mean content (part per ton) of sand particles in the soil (Hengl *et al.*, 2017) within buffers. Although sampling was conducted at the dominant savanna vegetation, there was some variability regarding the presence of other physiognomies within each sampling locality, most notably closed woodlands. Therefore, as a local environmental descriptor, we further calculated the proportion of points (in each buffer) classified as forest or woodland, hereafter referred to as closed habitats (IGBP classes 2 to 8, MCD12Q1, Friedl *et al.*, 2010).

Data analysis

To evaluate the relative importance of environmental correlates of beta diversity across scales, we used multimodel inference based on the Akaike's Information Criterion (AICc, corrected for small samples, see Brewer *et al.*, 2016). AICc estimate how well a model predicts the variation of a response variable, penalizing overparametrized models (Jørgensen, 2004). Based on a global model using all five predictor variables (species pool size, elevational variability, heterogeneity in greenness, percentage cover of closed habitat and the percentage of sand in the soil) we constructed models containing all possible combinations of variables (including single variable models). This procedure, known as *all subsets* regression analysis, averages AICc weights – which is a measure of the probability that a given model is indeed the best model – for each variable contained in the set of models being considered (in this case all models with a cumulative sum of weights higher than 0.95). We used Moran's eigenvector maps (MEMs, Dray *et al.*, 2006) to account for possible spatial structures present within our study localities, selecting MEMs that removed significant residual spatial autocorrelation within our study sites ($\beta_{sør}$). Finally, we used variation partitioning (Borcard, 1992; Peres-Neto & Legendre, 2010) to determine how much of the variability in turnover and nestedness was explained uniquely by the set of environmental correlates, uniquely by space (MEMs) and the explained variation shared by the environmental and spatial variables.

We assessed the influence of geographical distance in driving the variability in ant beta diversity, but did not include this factor within the multimodel inference analysis, since the distance between pairs of samples at SS1, SS2 and SS3 was the same for all localities. Therefore, the possible effect of distance in beta diversity (and its components) was analyzed in two ways: i) at SS1, SS2 and SS3 (site scale domain) we used paired *t*-tests to assess the one-tailed hypothesis that sample pairs with larger extent will have higher beta diversity than sample pairs with small extent (Fig. 3). Therefore, $\beta_{sør}$, β_{sim} and β_{nes} were calculated between spatially aggregated sample pairs and spatially segregated sample pairs i.e., maintaining grain constant and varying extent from 40 m (aggregated) to 120 m (segregated) at SS1; 120 m to 280 m at SS2; and 280 m to approximately 1,500 m at SS3. ii) at SS4 (local domain) and SS5 (landscape domain) we used linear regression to determine the proportion of variation (adjusted-R^2) in $\beta_{sør}$, β_{sim} and β_{nes} that was explained by distance. At these scales, the distance between pairs of samples – sites within localities for SS4 and localities within landscapes for SS5 – varied randomly among the surveyed localities/landscapes and thus could be directly correlated to beta diversity values.

The response variables and correlates used in the modelling were transformed to z-scores, i.e., were centered (mean = 0) and scaled (standard deviation = 1). Analysis were performed in R (R Core Team, 2015) using packages 'betapart' (pairwise values of $\beta_{sør}$, β_{sim} and β_{nes}), 'MuMIn' (multimodel inference analysis), and 'stats' (ANOVA and paired *t*-test); and SAM software (Rangel *et al.*, 2010) was used to generate and select MEMs.

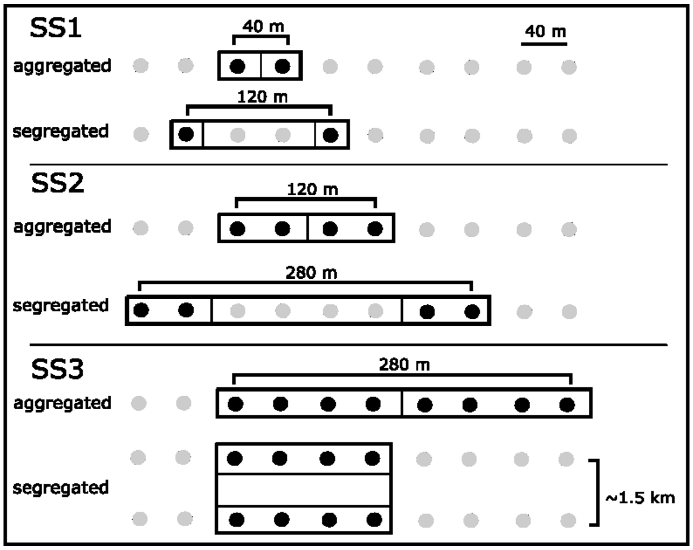

Figure 3.Sampling scheme of paired *t*-tests designed to assess if increased distance between samples (extent) resulted in increased values of ant beta diversity in the Cerrado savannas. In each of the 28 localities beta diversity was calculated for a pair of spatially aggregated samples (minimum extent) and a pair of spatially segregated samples (increased extent). In each scale, black circles represent sampling units that were used to calculate beta diversity values, while gray circles are units that were not considered.

Results

Beta diversity ($\beta_{sør}$) of ground-dwelling ants in the Cerrado was driven mainly by turnover (β_{sim}) rather than by nestedness (β_{sim}). The mean percentage of contribution of β_{sim} to $\beta_{sør}$, within all localities and scales, was 88.5%, ranging from 49.2% to 100%.

Variation in $\beta_{sør}$ was affected by spatial scale ($F_{4,121} = 12.0$, $p < 0.0001$; Fig. 4), and this was true for both the β_{sim} and β_{nes} components ($F_{4,121} = 6.1$, $p = 0.0002$ and $F_{4,121} = 4.7$, $p = 0.0015$, respectively). $\beta_{sør}$ was highest among samples at the smallest scale (SS1: mean ± SD = 0.484 ± 0.143) compared to larger scales (SS2:0.421 ± 0.087; SS3: 0.367 ±0.09; and SS4: 0.366 ± 0.108). However, $\beta_{sør}$ at the largest spatial scale (SS5: 0.451± 0.105) was higher than at SS3 and was not significantly different from $\beta_{sør}$ at SS2 or SS4. The scaling pattern observed for $\beta_{sør}$ was mirrored on β_{sim} and β_{nes} components (Fig. 4) and, therefore, the relative contribution of the beta diversity components (β_{ratio}) did not vary with scale ($F_{4,121} = 1.7$, $p = 0.144$).

The effect of distance on ant beta diversity varied with scale. Paired *t*-tests within localities showed that, at SS3, segregated pairs of samples had higher beta diversity than aggregated pairs, and this was true for $\beta_{sør}$ ($t_{27} = -3.79$, $p = 0.0004$), β_{sim} ($t_{27} = -1.75$, $p = 0.045$) and β_{nes} ($t_{27} = -2.25$, $p = 0.016$). At SS2 there was also higher values of $\beta_{sør}$ in segregated compared to aggregated samples ($t_{27} = -1.81$, $p = 0.04$), but not for β_{sim} and β_{nes} at SS2, or for any diversity metric at SS1. Furthermore, the percentage of variation in $\beta_{sør}$, β_{sim} and β_{nes} explained by distance was negligible within localities (SS4, adjusted $R^2 = 0.00$, 0.02 and 0.08, respectively) and within landscapes (SS5, 0.07, 0.10 and 0.07, respectively).

The relative importance of environmental drivers was assessed only for the β_{sim} and β_{nes} components of beta diversity (Fig. 5; Table 1 of Supporting Information). The size of the species pool had a positive influence on β_{sim} from SS1 to SS4, and was the most important predictor of β_{sim} at SS3. In contrast, the species pool negatively influenced β_{nes}, being the best predictor from SS1 to SS4. Measures of environmental variability had an overall low influence over β_{sim}, although heterogeneity in greenness was the most important predictor at SS4 (positive effect). On the other hand, β_{nes} was positively related to elevational variability (mainly at SS4) and negatively related to heterogeneity in greenness (SS3 and SS4), except in SS1, SS2 and SS5.

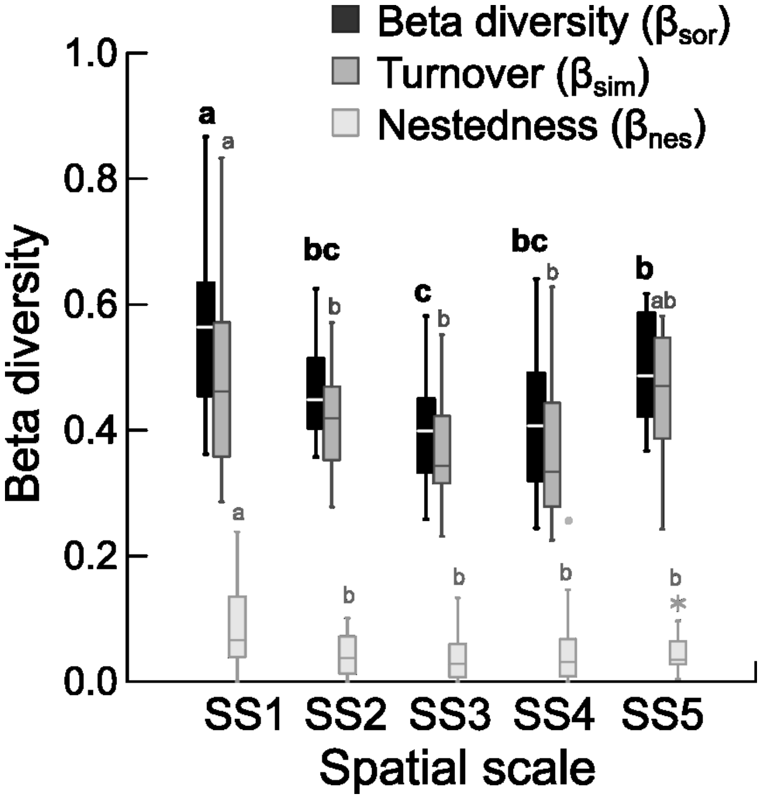

Figure 4. Box plot (median, 1st and 3rd quartiles) of ground-dwelling ant total beta diversity ($\beta_{sør}$) and its additive components of turnover (β_{sim}) and nestedness-resultant dissimilarity (β_{nes}). Beta diversity values were calculated at five spatial scales that represent a sliding window of increasing grain and extent. Different letters above boxes indicate significant pairwise difference between scales (Tukey's honestly significant difference test), which was assessed for each metric of beta diversity separately.

The proportion of sand in the soil was negatively related to β_{sim} and had a peak in importance at SS2. This variable was also positively related to β_{nes} (except in SS3), but its importance was low across scales. The proportion of closed habitats had a positive influence on β_{sim} (except at SS2 and SS4) and was the most important predictor at both the smallest (SS1) and largest (SS5) spatial scales. This variable negatively affected β_{nes}, but had an overall weak relative importance, even when it was the best ranked correlate (at SS5) (Fig. 5). The proportion of variation explained by the models showed similar scale-dependency for both β_{sim} and β_{nes} components, being lower at the intermediate scale (SS3) compared to smaller (SS1 and SS2) and larger (SS4 and SS5) scales (Fig. 6). The full model (environment plus space) was able to predict from 40% to 50% of the variability in β_{sim} and from 21% to 39% in β_{nes}. Moreover, a large proportion of the variation in β_{sim} that was explained by environmental factors was spatially structured, with the exception of SS4. There was high unique contribution of environment for β_{nes}, but some spatially structured effect was present at SS2 and SS4. Finally, for both beta diversity components, the proportion of variation explained purely by space was below 10% across scales (Fig. 6).

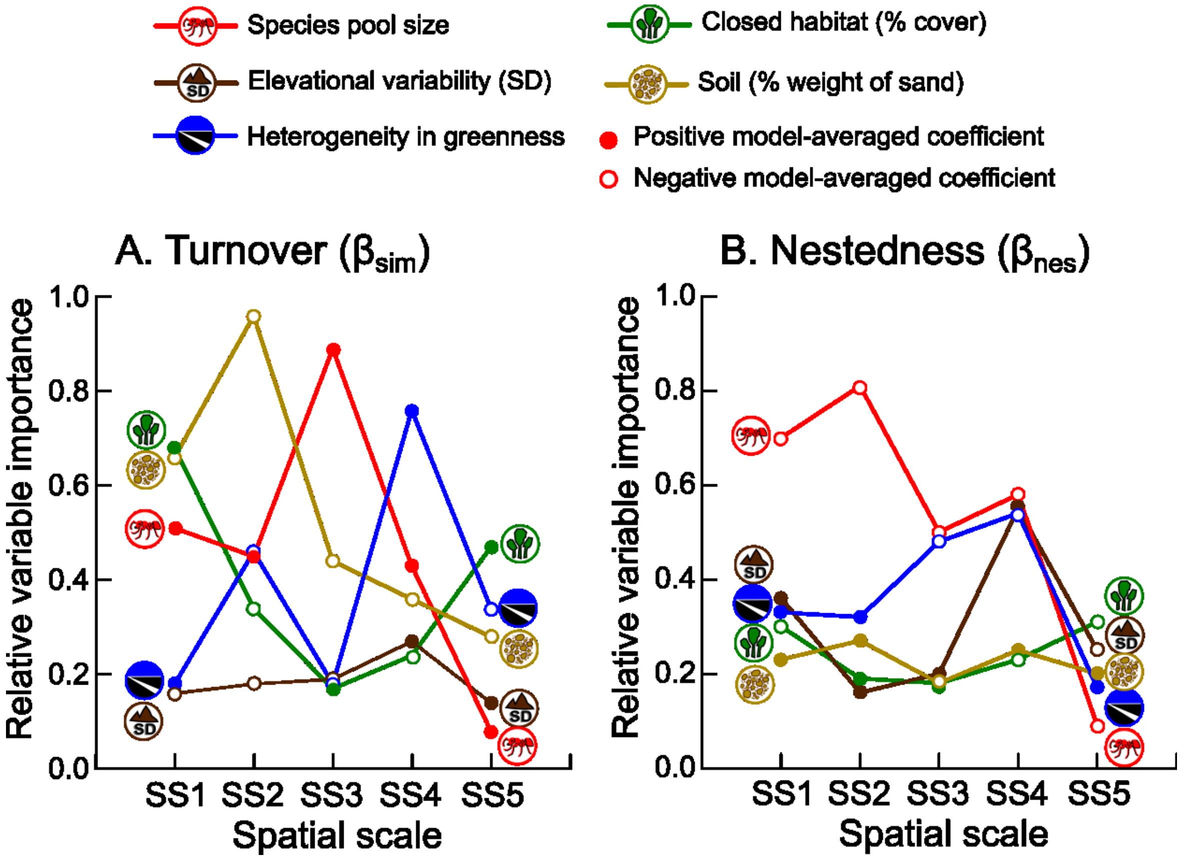

Figure 5. Relative variable importance (and direction of the effect) of five environmental correlates in driving patterns of A) turnover (β_{sim}) and B) nestedness-resultant dissimilarity (β_{nes}) of ground-dwelling ants in the Cerrado savannas. Five spatial scales represent a sliding window of increasing grain and extent. Correlates were: i) species pool size, estimated richness for N = 28 samples (SS1 - SS4) and N = 56 samples (SS5); ii) Elevational variability: standard deviation of elevation (digital elevation maps) within sampling area; iii) Homogeneity: differences in EVI (enhanced vegetation index).; iv) Closed habitat: proportion of the sampling area that was covered with closed habitat vegetation (woodlands and forests); and v) proportion of sand content in the soil. Values of relative variable importance were obtained by a multimodel inference procedure. We further used the model-averaged coefficients to determine the direction of the effect, i.e., if any given variable had a positive (full circle) or negative (empty circle) correlation with β_{sim} or β_{nes}.

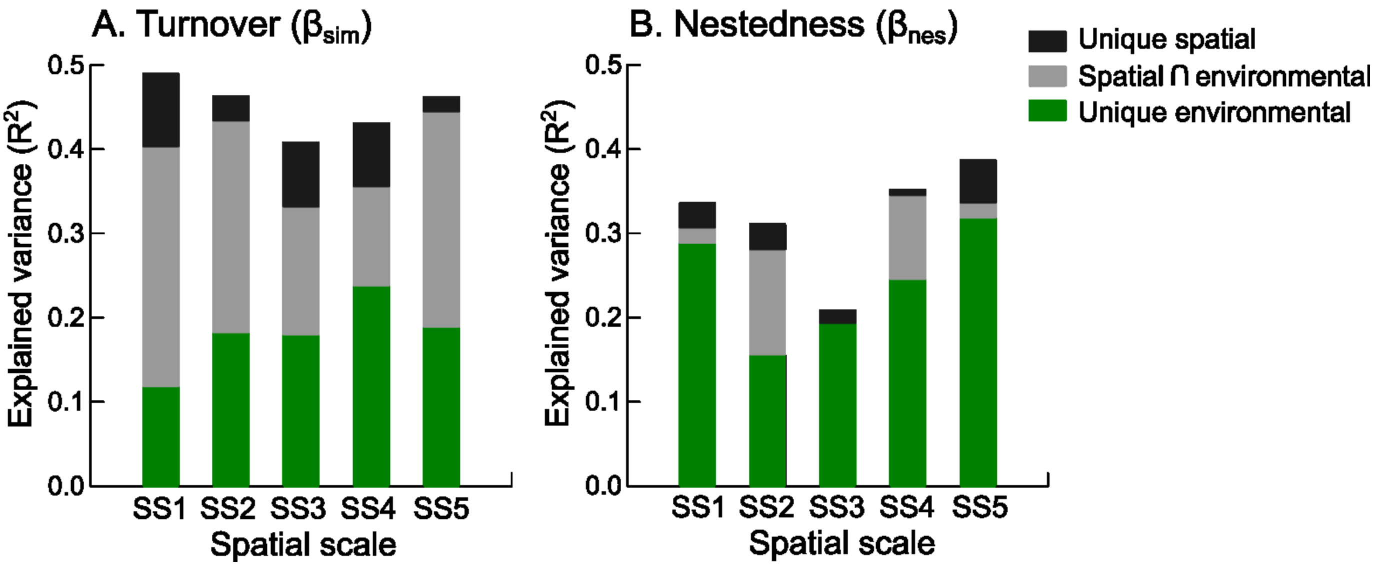

Figure 6. Variation partitioning of A) turnover (β_{sim}) and B) nestedness-resultant dissimilarity (β_{nes}) in Cerrado savanna ground-dwelling ants. Across the five spatial scales of increasing grain and extent, the total variation (adjusted R^2) explained by our models was partitioned into three additive components: i) proportion of variation explained uniquely by space (Moran's eigenvector maps); ii) proportion of variation explained uniquely by a set of five environmental correlates; and iii) proportion of variation shared by the spatial and environmental predictors.

Discussion

Our results demonstrate that spatial scale affects the patterns of ground-dwelling ant beta diversity within the Cerrado region. However, the relative contribution of beta diversity components did not change with scale, with turnover being the major driver of beta diversity overall. The variation in turnover and nestedness was related to similar environmental factors, albeit the direction of the effect was opposite between these diversity components. At small and intermediate scales, sites with a larger species pool showed increased turnover and reduced nestedness. At intermediate to larger scales, spatial heterogeneity in vegetation greenness played an important role, but while it caused an increase in turnover, it had a negative effect over nestedness. Moreover, at very small scales, the variation in turnover was mainly determined by local environmental factors, such as the amount of sand in the soil and the proportion of closed habitats. Surprisingly, we found a small overall contribution of spatial processes, since geographical distance was weakly related to beta diversity and the proportion of variability in nestedness and turnover explained purely by space was low irrespective of scale.

As expected by the sliding window framework (Barton *et al.*, 2013) and by predictions regarding the scale-dependency of beta diversity (Nekola & White, 1999; Whittaker *et al.*, 2001; Mac Nally *et al.*, 2004; Hortal *et al.*, 2010), our results show that the highest values of pairwise dissimilarity were found at the smallest spatial scale. Samples drawn at very fine grains and at small spatial extents are likely to be compositionally dissimilar from each other, resulting in high beta diversity among small-scale samples. As spatial grain and extent increases, a larger proportion of gamma diversity is comprised within the alpha components and, therefore, beta diversity decreases (Nekola & White, 1999; Mac Nally *et al.*, 2004; Barton *et al.*, 2013). Compared to the smallest spatial scale, we found lower values of beta diversity at intermediate to large scales; however, contrary to the expected, beta diversity increased again at the largest spatial scale, i.e., within landscapes. The variability in beta diversity at this scale, however, was not related to the geographical distance between pairs of localities within landscapes. Communities tend to decrease in similarity with increasing distance, a phenomenon known as the distance-decay of similarity. However, the detection of this effect is scale-dependent, and is expected to be strongest when both grain and extent are maximized (Nekola & White, 1999; Steinbauer *et al.*, 2012).Therefore, the failure to detect distance effects at the largest scale may stem from the small scale of analysis in regard to the dispersal limitations of ant species; or that local conditions are more important determinants of differences in ant composition within the Cerrado region, thus obscuring the signal of distance. However, we did find an effect of distance when comparing aggregated and segregated pairs of samples at SS3, i.e., at the site scale. As expected, when a set of four sampling points were compared to a set of four samples in another transect (extent of approximately 1.5 km), dissimilarity was higher than comparing two sets of four samples within one transect (extent of 280 m). This is in accordance with a previous analysis of five of the sampling localities that were considered here, which an increased dissimilarity was found is spatially segregated samples compared to spatially clumped samples (Vasconcelos *et al.*, 2014). Nevertheless, it is important to stress that the effect-sizes found in the paired tests were not high, indicating that distance is not a major determinant of patterns of beta diversity.

Although spatial scale was a major determinant of beta diversity patterns, it did not affect the relative contribution of its components of turnover and nestedness, being turnover the major contributor of beta diversity across scales. While the highest contribution of nestedness was found at the smallest scale, the mean percentage of total beta diversity attributed to nestedness was lower than 16%, at this scale, and was below 12% at the remaining scales. Many studies have reported similar results regarding the dominance of the turnover component over beta diversity patterns of different organisms (Matthews *et al.*, 2015; Solar *et al.*, 2015), including ants (Bishop *et al.*, 2015; Silva *et al.*, 2017; Liu *et al.*, 2018); fewer studies, however, have addressed if the relative contribution of turnover and nestedness components changes across hierarchical spatial scales. In agreement with the findings of the present study, amphibian beta diversity in the Brazilian Atlantic Forest is mainly driven by turnover at various spatial scales, although the contribution of nestedness was somewhat higher at the smaller scales (Melchior *et al.*, 2017). Furthermore, ants from forests and savannas in Indonesia and Brazil showed consistently low contribution of nestedness across scales, regions and vegetation types, although savanna sites tended to have higher relative contribution of nestedness than forests (Schmidt *et al.*, 2017). Also, within the Brazilian savanna sites, Schmidt *et al.* (2017) found that values of nestedness at the biome scale (between sites, roughly equivalent to SS5 in the present study) were very similar to those at the landscape scale (between transects, equivalent to SS4), both of which are very close to the values found here at each respective scale.

A long-standing issue in the analysis of macroecological patterns of diversity is to disentangle the relative roles of stochastic spatial processes and deterministic environmental sorting of species, since environmental factors are themselves spatially structured. In the present study we found a relatively small contribution of purely spatial processes in driving the variation in ant turnover and nestedness, and this result was constant across the spatial scales analyzed. However, a large proportion of the variation in turnover explained by environmental variables was spatially structured, while nestedness patterns showed a larger proportion of variation explained uniquely by the set of environmental factors. Interestingly, at the smallest and largest spatial scales, this spatially structured environmental effect was highest than at intermediate scales for turnover, but lower than at intermediate scales for nestedness. Turnover and nestedness represent two distinct processes that generate compositional dissimilarities and, thus, different mechanisms have been proposed to explain the variation in these beta diversity components (Ulrich *et al.*, 2009; Baselga, 2010; Svenning *et al.*, 2011; Matthews *et al.*, 2015). However, we found some interesting convergences in relation to which environmental driver best explained the variation in turnover and nestedness components across spatial scales. For both turnover and nestedness, we found a peak in the importance of heterogeneity in greenness at intermediate scales; and a decrease in importance of the species pool with increasing scale. On the other hand, environmental characteristics such as soil and percentage cover of closed habitats had a greater relative importance for the turnover than the nestedness component, and the effect on turnover was strongest at small scales. Furthermore, as a general rule, a given factor that was positively related to turnover had a negative effect on nestedness, the opposite being true. This finding reinforces the idea that turnover and nestedness are antithetic drivers of beta diversity, and although they certainly are the result of different mechanisms, similar environmental conditions may give rise to these mirrored patterns.

Overall, the correlate that best explained the variation in nestedness was the size of the species pool, and as expected, smaller pool sizes resulted in increased levels of nestedness. Patterns of nestedness arise when sites experience ordered extinctions and colonization (Ulrich *et al.*, 2009) and can be the result of variations in habitat area and quality, dispersal limitations, history of disturbances and differences in the regional pool of species (Ulrich *et al.*, 2009; Matthews *et al.*, 2015). Higher levels of nestedness have been found in environments with lower species richness (Solar *et al.*, 2015), and in sites that experienced higher extinction rates due to past glaciation events (Dobrovolski *et al.*, 2012). In central Brazil, ant beta diversity showed a higher contribution of nestedness in dry forests near the Caatinga than near the Cerrado biome, which was attributed to a less predictable weather in the xeric Caatinga (Silva *et al.*, 2017). In fact, patterns of aridity in the Caatinga biome played an important role in driving local patterns of ant diversity (Leal *et al.*, 2017). Moreover, ant species composition in this biome was shown to be an impoverished subset of the Cerrado ant species composition. This is further reinforced by the present study, since we found that species-poor sites had higher contribution of nestedness compared to species-rich sites. The reversed latitudinal gradient in ant species richness of the savanna localities analyzed here are mainly driven by a gradient in increasing rainfall from lower to higher latitudes (Vasconcelos *et al.* 2018). This climatic favorability in central and southern regions of the Cerrado enhances plant productivity, which in turn likely buffered ant species from local extinctions (Chapter 1 of thesis, Maravalhas, 2018). But while productivity exerts a hierarchically superior effect on ant species richness, being less important at smaller scales (Chapter 1 of thesis, Maravalhas, 2018), richness patterns showed a greater influence over nestedness at smaller rather than larger spatial scales. We found that differences in the size of the species pool had high importance at SS1 and SS2, than decreased in importance at SS3 and SS4, but it remained among the best performing variables. Finally, at SS5, the species pool showed the lowest importance among the variables analyzed, meaning that similar levels of nestedness were found in species-rich and species-poor landscapes.

We predicted an increase in species turnover with increasing size of the species pools, given that in regions with a larger species pools, a higher proportion of species will be excluded from the local assemblage simply due to niche space limitations, causing high turnover among samples in species-rich regions (Kraft *et al.*, 2011; Karger *et al.*, 2015). The present results show that, indeed, higher species pool sizes resulted in increased turnover of ant species. However, turnover patterns were more strongly related to the species pool at site and local scale, while at the landscape scale, turnover showed no relationship with pool sizes. This indicates that the sampling effect of pool sizes on species turnover is only observable at small spatial scales. This is an expected result, since at larger spatial scales, the alpha component approaches gamma, and thus most species of the regional pool will be found at the local assemblage. On the other hand, at small spatial scales, species-rich locations showed higher rates of turnover simply due to ecological constrains that limit the number of species coexisting within a certain area. Indeed, Harrison *et al.* (2006) suggested that productivity exerts a top-down influence on patterns of beta diversity by increasing the regional species pools and thus increasing the discrepancy between the alpha and gamma diversity components, i.e., beta diversity. Similarly, Chase (2010) attributed the higher beta diversity found in high compared to low productivity ponds to stochastic assembly of species at small spatial scales. Local assembly of ant communities depend, to a large extent, on propagule arrival, and thus is determined by regional patterns in species richness (Andersen, 2008). Within our study region, productivity was found to drive variations in ground-dwelling ant diversity (Chapter 1 of thesis, Maravalhas, 2018), which, in turn, may affect ant turnover and nestedness at small spatial scales.

Although stochastic processes likely play a role in driving ant turnover at the site and local scales, our results also point to the importance of deterministic factors at these spatial scales. We found a greater influence of local environmental characteristics over turnover patterns, and the importance of these factors decreased with increasing scale. This conforms to the hierarchical theory of diversity, which postulate that large-scale factors (driven mainly by area, history and climate) limits the size of the species pools that are then filtered by local environmental factors and biotic interactions at finer spatial scales (Ricklefs, 1987; Whittaker *et al.*, 2001; Hortal *et al.*, 2010). We found that ant turnover between pairs of adjacent samples (SS1) was best predicted by the proportion of closed habitats and by the proportion of sand in the soil within sampling localities. At the next scale, species turnover between two pairs of samples (SS2) were driven mainly by the proportion of sand in the soil. The importance of this factor then decreased monotonically with increasing scale, but still had a considerable effect on turnover patterns at the remaining scales (SS3-SS5). Edaphic characteristics have been regarded as major drivers of local patterns of plant diversity in temperate grasslands (Zemunik *et al.*, 2016; Conradi *et al.*, 2017), and the inclusion of soil variables increases the performance of models predicting plant diversity in tropical forest (Baldeck *et al.*, 2012). Moreover, soil properties have long been recognized as important factors structuring ant communities (Peck *et al.*, 1998; Bestelmeyer & Wiens, 2001), although some studies found no relationship between ant diversity and edaphic conditions (Delsinne *et al.*, 2010; Jacquemin *et al.*, 2012). For instance, studies conducted in grassland and savanna ecosystems found higher ant diversity in soils with higher sand and lower clay content (Boulton *et al.*, 2005; Andersen *et al.*, 2015; Campbell & Crist, 2017), while the results shown here point to a negative relationship between ant turnover and the proportion of sand in the soil. Taken together, these findings indicate that the effect of soil on ant assembly is likely to be idiosyncratic even within structurally similar ecosystems. Moreover, edaphic characteristics were found to be major drivers of small-scale patterns of ant species richness in the Cerrado region, likely by a influencing the abundance of ant colonies, an effect that cascaded up the spatial hierarchy (Chapter 1 of thesis, Maravalhas, 2018). Thus, soil-driven differences in abundance likely interact with differences in the size of the species pools, determining the degree of ant species replacement at very fine spatial scales.

Ant beta diversity at the site domain (SS1 to SS3) was found to be mostly driven by soil conditions and by the size of the species pools; however, at the local scale, turnover and nestedness patterns were better predicted by heterogeneity in greenness. This variable measures the difference in EVI between a pixel (~1 km resolution) and its adjacent pixels (Tuanmu & Jetz, 2015), an extent that roughly corresponds to the distance between pairs of transects within localities (SS4). At this scale, heterogeneity in greenness showed a positive relationship with turnover and a negative relationship with nestedness. Although the link between habitat variability and turnover is long recognized, heterogeneity is not regarded as a major driver of nestedness (Matthews *et al.*, 2015) and in fact few studies have addressed this relationship. Higher levels of environmental heterogeneity may produce an increase in nestedness of bird in an Australian landscape (Fischer & Lindenmayer, 2005) and in mesocosm experimental zooplankton communities from Belgium (Gianuca *et al.*, 2017). On the other hand, Solar *et al.* (2015) found that land-use classes with higher heterogeneity in an Amazonian rainforest landscape (i.e., less intense human modification) had increased contribution of turnover and reduced contribution of nestedness, a result that agrees with the present findings. This indicates that the relationship between heterogeneity and nestedness is not as simple as the relationship between heterogeneity and turnover.

Habitat heterogeneity is regarded as a major driver of species turnover between biotic communities (Stein *et al.*, 2014), affecting the patterns of species coexistence across multiple spatial scales (Shmida & Wilson, 1985; Pickett & Cadenasso, 1995; Leibold *et al.*, 2004; Stein *et al.*, 2014). We found increased species turnover between transects in localities with higher variability in greenness. Since transects were established at similar vegetation physiognomies both within and between localities, these results indicate that subtle variations in vegetation greenness may still produce turnover of ant species. The Cerrado region is environmentally heterogeneous even at relatively small spatial scales (Silva *et al.*, 2006), which may lead to high levels of species replacement across localities (Ratter *et al.*, 1996; Vasconcelos *et al.*, 2018). Ant species are known to be highly sensitive to changes in habitat type (Andersen & Majer, 2004; Crist, 2009) and environmental sorting of species was shown to be an important mechanism of ant assembly at multiple spatial scales (Spiesman & Cumming, 2008). This is also true for ants of the Cerrado region, where habitat variability is considered to be a major driver of species turnover at different scales (Pacheco & Vasconcelos, 2012; Maravalhas & Vasconcelos, 2014). Furthermore, high functional packing of the species-rich *Pheidole* ant genus in the Cerrado savannas point to the important role of environmental sorting in the assembly of ant communities (Neves *et al.*, 2018). Together, the results of these studies and ours indicate that environmental sorting may be an important mechanism of ant assembly even at local spatial scales, since we found higher species turnover between transects within sites with more varying levels of greenness. Moreover, we also found evidence of an increased importance of environmental sorting at larger spatial scales. Ant turnover between localities within landscapes was best explained by the proportion of closed habitats (mainly woodlands). To analyze ant beta diversity at the landscape scale we grouped pairs of localities so to minimize the distance between localities. In our data set, the proportion of closed habitat (mean value between localities) was correlated to the range (of the proportion of closed habitats) between the two localities that constitute each landscape. Therefore, at the landscape scale turnover was highest when comparing localities with distinct proportions of habitat types other than typical savanna.

Variation in beta diversity of ground-dwelling ants within Cerrado savanna sites was constrained by the spatial scale in which the alpha and gamma diversity components are measured. Beta diversity was highest at the smallest spatial scale and decreased with increasing scale, but further showed an increase at the largest spatial scale. Although spatial scale determined the magnitude and variability of ant beta diversity, the relative contribution of the turnover and nestedness components did not change across scales. In fact, species turnover was the major driver of beta diversity in all spatial scales and at nearly all localities analyzed. Even though the distance between pairs of samples showed a limited effect on ant beta diversity, patterns of variability in the turnover and nestedness components could be related to different environmental drivers. Generally these factors had opposite effects on each beta diversity component, i.e.: a factor that was positively related to turnover was negatively related to nestedness, and vice versa. Moreover, there was a marked scale-dependency of the relative importance of these drivers, which were somewhat consistent between the beta diversity components. For instance, the species pool size had higher relative importance at smaller scales for both turnover and nestedness. On the other hand, measures of habitat heterogeneity where more important drivers of turnover and nestedness at larger scales, particularly at transects within localities (SS4). Other factors, however, affected only the species turnover component, such as the proportion of closed habitats and the proportion of sand in the soil, both of which had a reduction in importance with an increase in scale. Taken together, the results of the present study reiterate the importance of spatial scale in shaping the patterns of beta diversity. However, scale did not affect the relative contribution of the species turnover and nestedness components of beta diversity. Moreover, we show that different environmental factors control turnover patterns of ground-dwelling ant within the Cerrado savannas. We found a shift from abundance-driven passive sample of species from the regional pool – which is manifested at fine spatial scales, to environmental sorting of species – which is stronger at coarser scales.

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Supporting information

Table S1. Results of multi-model inference analysis based on Akaike's Information Criterion (AICc weights). Shown are the relative variable importance and model-averaged coefficients of five environmental correlates that may explain patterns of turnover (β_{sim}) and nestedness-resultant dissimilarity of ground-dwelling ants in the Cerrado savannas. Coefficients in bold indicate values that do not overlap with the 95% confidence interval.

Beta diversity component	**SS1**		**SS2**		**SS3**		**SS4**		**SS4**	
Correlates	Import.	Coeff.	Import.	Coeff.	Import.	Coeff.	Import.	Coeff.	Import.	Coeff.
Turnover										
Species pool sizes	0.51	0.31	0.45	0.31	0.89	**0.48**	0.43	0.29	0.08	0.08
Elevational variability	0.16	-0.02	0.18	-0.11	0.19	-0.07	0.27	0.19	0.14	0.25
Heterogeneity in greenness	0.18	0.07	0.46	-0.31	0.18	-0.05	0.76	**0.43**	0.34	-0.43
Closed habitat (% cover)	0.68	0.39	0.34	-0.25	0.17	0.01	0.24	-0.17	0.47	0.52
Sand (% wieght of soil)	0.66	-0.42	0.96	**-0.55**	0.44	-0.29	0.36	-0.27	0.28	-0.44
Nestedness										
Species pool sizes	0.70	-0.41	0.81	**-0.45**	0.50	-0.33	0.58	-0.36	0.09	-0.09
Elevational variability	0.36	0.25	0.16	0.01	0.20	0.11	0.55	0.32	0.25	-0.36
Heterogeneity in greenness	0.33	0.29	0.32	0.26	0.48	-0.32	0.54	-0.35	0.17	0.28
Closed habitat (% cover)	0.30	-0.23	0.19	0.06	0.18	0.09	0.23	-0.19	0.31	-0.42
Sand (% wieght of soil)	0.23	0.16	0.27	0.20	0.18	-0.08	0.25	0.20	0.20	0.33

Discussão

Os estudos apresentados nesta tese mostram como diferentes fatores ecológicos e evolutivos variam em importância relativa entre escalas espaciais e assim determinam os padrões de diversidade de formigas no Cerrado. Em concordância com a teoria hierárquica da diversidade (Ricklefs, 1987; Levin, 1992; Whittaker *et al.*, 2001; Vellend, 2010), foi possível demonstrar que os padrões de riqueza (diversidade alfa) de espécies de formigas do Cerrado são organizados por uma hierarquia de fatores espacialmente estruturados. Em largas escalas, fatores geográficos, históricos e – principalmente – climáticos determinam variações regionais no banco de espécies, que por sua vez limita a riqueza em escalas espaciais inferiores. Nestas escalas mais finas, entretanto, características do solo exercem uma forte influência sobre os padrões de diversidade, principalmente por influenciar a abundância de indivíduos. Já os padrões de dissimilaridade composicional (diversidade beta) seguiram parcialmente as previsões do quadro teórico de escalonamento espacial (Barton *et al.*, 2013). Conforme esperado, os valores de diversidade beta foram maiores na menor escala e diminuíram com o aumento da escala; porém na maior escala os valores foram superiores que em escalas intermediárias, um resultado não esperado para a escala da paisagem. O componente de troca foi o principal determinante da beta diversidade de formigas no Cerrado, e a contribuição relativa dos componentes de troca e aninhamento não variou com a escala. Porém a importância relativa dos diferentes fatores ambientais relacionados à variação na troca e no aninhamento mostrou uma marcada dependência de escala. O banco de espécies teve maior influência em escalas menores, enquanto medidas de heterogeneidade foram mais importantes nas maiores escalas. Além disso, os padrões de troca foram influenciados por fatores edáficos em pequenas escalas.

O primeiro capítulo desta tese demonstra que a diversidade alfa (densidade e diversidade de espécies) foi determinada por fatores hierárquicos, já que a produtividade primária líquida (PPL) foi o principal preditor tanto da densidade (em maiores escalas) como da diversidade (independente da escala) de formigas de solo. Este resultado está em acordo com os resultados de uma análise prévia deste mesmo banco de dados, em que uma maior diversidade de formigas foi encontrada em regiões com menores déficits hídricos, indicando a forte associação da fauna de formigas Neotropicais com florestas úmidas (Vasconcelos *et al.*, 2018). No presente estudo, foi possível demonstrar qual mecanismo determina a relação entre PPL e diversidade alfa de formigas. O mecanismo de amostragem prevê que maiores produtividades podem acarretar em maiores abundâncias, o que por sua vez acarretaria numa amostragem aleatória de mais espécies do banco regional, aumentando a riqueza local (Kaspari *et al.*, 2003; Evans *et al.*, 2005). No presente estudo, no entanto, o efeito de PPL foi maior quando diferenças na abundância foram controladas, o que indica que esta relação não se deve a um efeito de amostragem, e sim ao mecanismo de abundância-extinção. Assim, maiores fluxos energéticos na cadeia alimentar (maior produtividade) resultam em populações mais estáveis, reduzindo assim taxas de extinção local e ocasionando num maior banco de espécies (Kaspari *et al.*, 2000; Evans *et al.*, 2005). Além do controle climático, a diversidade alfa de formigas no Cerrado provavelmente também é influenciada por processos geográficos e históricos, particularmente em escalas espaciais maiores. No presente estudo, a diversidade alfa de formigas foi moderadamente afetada pela posição geográfica de cada localidade em relação à região de estudo. Maior densidade e diversidade de espécies foram encontradas em localidades da região central comparado com localidades de regiões periféricas do Cerrado. Embora não seja do escopo deste estudo discernir entre os possíveis fatores relacionados a esse padrão geográfico, é possível listar: o efeito centro-periferia na abundância de espécies (Pironon *et al.*, 2017); a presença, notavelmente na região Central, de áreas de refúgio durante flutuações climáticas do Quaternário (Werneck *et al.*, 2012; Bueno *et al.*, 2017), que pode estar relacionada com a medida de tempo-área-favorabilidade climática (Fine, 2015); além do efeito do domínio médio, que prevê um pico de diversidade em regiões centrais (montanhas, ecorregiões) devido ao arranjo geométrico das distribuições de espécies (Colwell *et al.*, 2004).

Padrões de diversidade alfa de formigas no Cerrado, portanto, são hierarquicamente limitados pelas condições climáticas que afetam o tamanho dos bancos de espécies, além de possíveis efeitos geográficos e históricos. Diferenças no banco de espécies, por sua vez, podem ser importantes determinantes dos padrões de diversidade beta, por afetarem tanto os componentes de aninhamento (Matthews *et al.*, 2015) como de troca (Kraft *et al.*, 2011). Conforme o esperado, foi encontrada uma relação negativa entre o tamanho do banco de espécies e o aninhamento; este efeito, no entanto, foi mais importante nas escalas menores. Padrões de aninhamento resultam de extinções ordenadas em diferentes escalas espaciais (Ulrich *et al.*, 2009) e, conforme apresentado anteriormente, extinções locais em regiões climaticamente desfavoráveis do Cerrado são importantes determinantes dos padrões de diversidade de formigas. Em regiões mais áridas, próximas à ecorregião da Caatinga, houve maiores níveis de aninhamento do que regiões climaticamente favoráveis. Em suporte a este achado, diversos estudos demonstraram a importância dos padrões de aridez na limitação das espécies de formigas da Caatinga, bem como do aninhamento da comunidade de formigas dessa ecorregião em relação à do Cerrado (Leal *et al.*, 2017). Entretanto, a importância relativa do banco de espécies em determinar os padrões de aninhamento foi maior em menores escalas, sendo praticamente inexistente na escala da paisagem. De forma semelhante, a troca de espécies foi afetada pelo banco de espécies de maneira mais marcada em escalas menores, porém, neste caso, a troca estava positivamente relacionada ao banco regional de espécies. Diferenças regionais de diversidade podem exercer forte influência sobre os padrões geográficos de troca (e.g. Karger *et al.*, 2015). Esta relação se deve a um efeito neutro, já que, em regiões com maiores bancos de espécies, uma maior proporção destas espécies estará ausente de uma determinada unidade amostral simplesmente devido a limitações físicas da área. Portanto, espera-se uma elevada troca entre amostras de regiões com alta riqueza regional do que entre amostras de regiões empobrecidas de espécies (Kraft *et al.*, 2011).

Além do efeito do banco regional, os padrões de troca de espécies de formigas foram determinados por fatores edáficos em escalas espaciais pequenas. Foi encontrada uma reduzida taxa de troca em locais com maior quantidade de areia no solo e este efeito provavelmente está relacionado com a relação entre características do solo e a densidade de espécies de formigas. Embora a produtividade determine os padrões de diversidade alfa em larga escala, o efeito desta variável na densidade de espécies reduziu marcadamente da maior para a menor escala de análise, um padrão previsto pela regra de escalonamento da hipótese de espécies-energia (Chase & Leibold, 2002; Evans *et al.*, 2005; Field *et al.*, 2009). Este efeito se deve provavelmente pela ação de fatores locais, nomeadamente medidas granulométricas do solo, que afetam os padrões de ocupação de formigas por meio de diferenças na abundância. A textura do solo pode afetar a coexistência de diferentes espécies de formigas (Johnson, 2000) assim como pode determinar padrões locais de diversidade desses insetos (Peck *et al.*, 1998; Bestelmeyer & Wiens, 2001; ver porém Delsinne *et al.*, 2010; Jacquemin *et al.*, 2012). No presente estudo foi encontrada uma relação negativa entre a densidade de espécies de formigas e duas variáveis de solo: a proporção de areia (partículas com diâmetro entre 0.05 e 2 mm) e de fragmentos grosseiros (> 2 mm), representados pelo eixo do PCA2 do solo. Estes resultados contrastam com estudos anteriores, em que uma maior riqueza de espécies de formigas foi encontrada em locais com maior proporção de areia (Boulton *et al.*, 2005; Andersen *et al.*, 2015; Campbell & Crist, 2017), indicando que o efeito da presença de areia no solo sobre as comunidades de formigas talvez seja idiossincrático. No presente estudo, PCA2 do solo afetou tanto a diversidade (independente da abundância) como a densidade de espécies (dependente da abundância). Entretanto, a variância explicada pelo solo foi significativamente maior para a densidade do que para a diversidade de formigas, indicando que o efeito de solo PCA2 na diversidade alfa de formigas se dá por meio de um mecanismo de amostragem, i.e., mais indivíduos (e espécies) são amostrados quando condições edáficas favoráveis (menos areia e menos fragmentos grosseiros) permitem uma maior abundância de espécies de formigas. Portanto, é possível inferir que esse efeito de cima para baixo do solo na abundância de formigas interage com as diferenças no banco de espécies, determinando os padrões de troca de espécies de formigas em escalas espaciais pequenas.

Padrões de diversidade biológica são comumente associados à heterogeneidade ambiental (Willig *et al.*, 2003; Tews *et al.*, 2004) e embora este fator tenha afetado os padrões de diversidade beta, a diversidade alfa não foi afetada pela heterogeneidade ambiental. Esses padrões foram analisados em diferentes escalas espaciais e relacionados a diferentes medidas de heterogeneidade e em todos os casos a relação diversidade-heterogeneidade foi baixa. Este resultado é surpreendente, considerando que a heterogeneidade é um importante determinante de padrões locais de riqueza de espécies de diversos grupos taxonômicos e em múltiplas escalas espaciais (Shmida & Wilson, 1985; Pickett & Cadenasso, 1995; Stein *et al.*, 2014). Por outro lado, ao avaliar os padrões de diversidade beta, e especialmente o componente dominante de troca, foi possível detectar a influência da heterogeneidade. Formigas são extremamente sensíveis a mudanças no habitat (Andersen & Majer, 2004; Crist, 2009) e, nas savanas do Cerrado, a heterogeneidade ambiental pode afetar a riqueza e composição de formigas em diferentes escalas espaciais (Pacheco & Vasconcelos, 2012; Maravalhas & Vasconcelos, 2014). Níveis maiores de empacotamento funcional também foram encontrados em escalas maiores comparadas com escalas menores para o gênero *Pheidole*, um dos mais especiosos dentre as formigas (Neves *et al.*, 2018). No presente estudo, os padrões de troca em escalas espaciais maiores foram em grande parte determinados pela heterogeneidade na vegetação, sendo que esta variável foi a melhor preditora da troca de espécies entre transectos dentro de localidades. De modo semelhante, na escala da paisagem, valores de troca foram maiores quando pares de localidades tinham maiores diferenças na estrutura da vegetação do que em pares de localidades mais homogêneos. Em suma, os resultados apresentados evidenciam a importância de processos de alocação de espécies (Leibold *et al.*, 2004; Spiesman & Cumming, 2008) na montagem de assembleias de formigas do Cerrado.

Conclusão

Os resultados da presente tese indicam que padrões geográficos de biodiversidade são determinados pela interação de fatores ecológicos e evolutivos que operam em diferentes escalas espaciais. Foi possível demonstrar que tanto a diversidade alfa (densidade e diversidade de espécies) quanto a diversidade beta (troca e aninhamento de espécies) seguiram padrões previstos de escalonamento espacial. No primeiro capítulo a diversidade alfa de formigas de solo do Cerrado foi determinada por uma hierarquia de fatores cuja importância relativa depende da escala de análise. Os resultados mostram que a diversidade de formigas foi, em grande medida, determinada por fatores climáticos que limitam a produtividade primária na região, que, por sua vez, controla os padrões regionais de diversidade de formigas. Como este efeito foi ainda mais marcado depois de controlar por possíveis diferenças na abundância, é possível concluir que uma maior favorabilidade climática reduz as taxas de extinção local, resultando num maior acúmulo de espécies no banco regional. A densidade de espécies (sem controlar pela abundância) também foi afetada pela produtividade, e este efeito foi mais importante em escalas maiores; ademais, esta redução na importância do clima foi acompanhada por um aumento na importância de fatores locais. Em pequenas escalas, características do solo como a quantidade de areia e de pedras, explicaram grande parte da variação na densidade de espécies, provavelmente por meio de um mecanismo de amostragem (mais indivíduos significam mais espécies sendo amostradas do banco). Acima da escala regional, fatores geográficos e históricos também foram importantes, já que mais espécies de formigas foram encontradas em regiões centrais em comparação a regiões periféricas do Cerrado, porém o desenho amostral deste estudo possibilitou apenas uma detecção moderada desse efeito. É possível inferir, portanto, que a diversidade alfa de formigas é limitada pelo tamanho do banco regional de espécies, que varia em função da produtividade primária. Por outro lado, condições do solo limitam a abundância local de formigas, e, portanto determinam o número de espécies que podem ser recrutadas do banco regional de espécies. Já os resultados do segundo capítulo indicam que a diversidade beta de formigas também é limitada pelo banco de espécies, porém, ao contrário do encontrado para a diversidade alfa, esse efeito é maior em menores escalas. Maiores bancos regionais resultaram em um aumento na troca e uma redução no aninhamento, entretanto este efeito foi praticamente nulo na maior escala espacial. Isto se deve, em parte, a um aumento na importância da heterogeneidade ambiental na determinação dos padrões de troca e de aninhamento em maiores escalas. Este resultado indica uma maior importância de processos de alocação de espécies em determinar os padrões de diversidade na escala da paisagem. Por outro lado, fatores edáficos também afetaram de forma marcante os padrões de troca de espécies, visto que esta era menor em locais com maior quantidade de areia. Estes fatores locais limitam a abundância de espécies, e, com mais indivíduos, é possível que mais espécies sejam recrutadas do banco regional, aumentando a troca de espécies em pequenas escalas espaciais. Em suma, fatores operando em diferentes escalas espaciais determinam a diversidade de formigas de solo no Cerrado: características do solo afetam os padrões de abundância de indivíduos em escalas pequenas, controlando os padrões de diversidade em escalas maiores. Por outro lado, fatores hierarquicamente superiores, como clima ou a produtividade, definem variações no tamanho do banco de espécies entre regiões. Estas diferenças tem um efeito hierarquicamente superior, limitando os padrões de biodiversidade em escalas menores. Os resultados apresentados nesta tese demonstram a importância de incorporar a escala em estudos macroecológicos, tendo em vista a marcada dependência da escala da importância relativa dos fatores ecológicos e evolutivos que determinam os padrões espaciais de biodiversidade. O número de espécies que ocorrem em um determinado local, por exemplo, é determinado por uma hierarquia de fatores, visto que a riqueza em maiores escalas limita a riqueza em menores escalas. Fatores que afetam o número de espécies que ocorrem no banco regional são mais importantes em escalas maiores, enquanto fatores que determinam a abundância de indivíduos afetam padrões de riqueza em escalas menores. Padrões de dissimilaridade também são inevitavelmente dependentes da escala em que os componentes alfa e gama são medidos, de modo que a beta diversidade segue um padrão previsível ao longo de escalas espaciais hierárquicas. De um modo geral, as conclusões destes estudos têm importantes implicações na teoria ecológica: i) padrões espaciais na abundância podem influenciar a habilidade em estimar a importância relativa de diferentes determinantes de biodiversidade; ii) considerar a escala espacial de observação é crucial para determinar de forma apropriada a importância relativa dos fatores que determinam a diversidade alfa e beta; iii) uma hierarquia de fatores ecológicos e evolutivos interagem através das escalas espaciais e determinam os padrões geográficos de biodiversidade.

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Anexo

Tabela 1. Lista de espécies de formigas de solo coletadas em 29 localidades de vegetação savânica na região do Cerrado. Valores na tabela representam a percentagem média de ocupação de cada espécie (número de registros da espécie no local/número de amostras*100) em cada Região hidrográfica do Cerrado. As regiões hidrográficas e localidades amostradas (códigos conforme mapa da Figura 1 e Tabela 1) são: Amazônica (localidades 18 e 19), Paraguai (16, 17, 20 e 21), Paraná (10, 11, 12, 25, 26, 27, 28 e 29), Parnaíba (1 e 2), São Francisco (7, 8, 22, 23 e 24) e Tocantins-Araguaia (3, 4, 5, 6, 9, 13, 14 e 15). Ao final da tabela estão sumarizados, por Região hidrográfica, o número de localidades amostradas, o número total de registros e o número de espécies encontradas.

	Região hidrográfica					
	Amazônica	Paraguai	Paraná	Parnaíba	São Francisco	Tocantins-Araguaia
Amblyoponinae						
Prionopelta antillana			0.5			
Dolichoderinae						
Dolichoderus ghilianii		3.1				
Dolichoderus imitator					0.8	0.5
Dorymyrmex brunneus	39.6	2.1	4.7	2.1	5.8	2.1
Dorymyrmex goeldii	4.2	6.3	1.6		8.3	6.3
Dorymyrmex sp.01 pr. paranensis		9.4	17.7	12.5	13.3	28.1
Dorymyrmex sp.02			2.1		0.8	1.0
Dorymyrmex sp.03	6.3		1.6	10.4		8.3
Dorymyrmex sp.05				29.2	3.3	4.2
Dorymyrmex sp.07				2.1		0.5
Dorymyrmex sp.09					4.2	
Dorymyrmex sp.10		7.3	6.8		5.0	0.5
Dorymyrmex sp.13			1.6			
Dorymyrmex sp.15 pr. bituber			1.0			
Dorymyrmex sp.17	29.2					1.0
Forelius sp.10		1.0	0.5			
Forelius sp.11			0.5			
Forelius sp.pr. albiventris	33.3	1.0	2.1	6.3	25.8	14.6
Forelius sp.pr. brasiliensis		4.2	1.6	43.8	5.0	37.0
Forelius sp.pr. maranhaoensis	31.3		0.5	37.5	15.8	17.2
Gracilidris pombero	18.8	7.3	4.7	2.1	8.3	12.5
Leptomyrmex relictus						1.0

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Tabela 1, continuação

	Região hidrográfica					
	Amazônica	Paraguai	Paraná	Parnaíba	São Francisco	Tocantins-Araguaia
Linepithema angulatum			0.5			0.5
Linepithema aztecoides		3.1	4.2		0.8	
Linepithema cerradense	16.7	15.6	76.0	37.5	30.8	33.9
Linepithema iniquum			0.5		0.8	
Linepithema micans			3.1			
Linepithema sp.01					1.7	
Linepithema sp.10						0.5
Tapinoma cf. melanocephalum		1.0			2.5	0.5
Tapinoma sp.01	2.1			6.3		1.6
Tapinoma sp.03					0.8	12.5
Tapinoma sp06		2.1	3.6			6.8
Dorylinae						
Eciton quadriglume					0.8	1.6
Eciton rapax			1.0			
Labidus coecus	2.1	1.0	5.7		5.0	2.1
Labidus praedator			2.1		1.7	1.6
Neivamyrmex dorbignii			0.5			
Neivamyrmex pseudops					4.2	0.5
Neivamyrmex sp.01						0.5
Neivamyrmex sp.02						0.5
Neivamyrmex sp.04		1.0			1.7	0.5
Neivamyrmex sp.06			1.0		1.7	0.5
Neivamyrmex sp.07		2.1	2.1		2.5	
Neivamyrmex sp.08			0.5		0.8	1.0
Neivamyrmex sp.09	2.1					0.5
Nomamyrmex esenbecki			0.5		0.8	1.6
Ectatomminae						
Ectatomma brunneum	18.8	3.1	3.6	8.3	17.5	17.2
Ectatomma edentatum	25.0	18.8	23.4	29.2	48.3	18.8
Ectatomma lugens	4.2	19.8	6.8		6.7	3.1
Ectatomma muticum				50.0	18.3	31.8
Ectatomma opaciventre	64.6	16.7	14.1		40.8	21.9
Ectatomma permagnum	54.2	20.8	31.3		7.5	20.3
Ectatomma planidens	12.5	19.8	1.0		9.2	5.2
Ectatomma tuberculatum	2.1	8.3	7.3		3.3	9.9
Gnamptogenys acuminata		1.0	2.6	2.1	2.5	2.1
Gnamptogenys hartmani			0.5			
Gnamptogenys nana						1.0
Gnamptogenys striatula	27.1	7.3	12.5	2.1	0.8	24.0
Gnamptogenys sulcata	4.2	1.0	1.6			1.0

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Tabela 1, continuação

	Região hidrográfica					
	Amazônica	Paraguai	Paraná	Parnaíba	São Francisco	Tocantins-Araguaia
Formicinae						
Acropyga fuhrmanni					0.8	
Acropyga goeldii			0.5		2.5	
Acropyga sp.01						0.5
Brachymyrmex coactus	4.2	6.3	1.0		6.7	4.2
Brachymyrmex pilipes	12.5		0.5			1.0
Brachymyrmex sp.01			5.2		13.3	6.3
Brachymyrmex sp.02			15.1	16.7	41.7	20.8
Brachymyrmex sp.03			1.6		4.2	0.5
Brachymyrmex sp.04						1.0
Brachymyrmex sp.05	6.3	13.5	31.3	2.1	12.5	15.1
Brachymyrmex sp.11			1.6			0.5
Brachymyrmex sp.12	41.7	34.4	44.8	22.9	5.8	29.7
Brachymyrmex sp.14	2.1					
Brachymyrmex sp.20						0.5
Brachymyrmex sp.22						0.5
Camponotus blandus	60.4	36.5	14.1	8.3	47.5	56.3
Camponotus cingulatus	6.3	2.1	15.6		4.2	7.3
Camponotus leydigi	2.1	3.1	0.5	2.1	3.3	12.0
Camponotus melanoticus	25.0	29.2	9.9	16.7	18.3	23.4
Camponotus novogranadensis			20.3	2.1	4.2	6.8
Camponotus pr. Cingulatus			3.6	14.6	6.7	4.7
Camponotus renggeri	8.3	12.5	8.3		2.5	3.6
Camponotus rufipes		4.2	12.5		15.0	5.7
Camponotus senex	12.5	35.4	39.1	60.4	25.0	38.0
Camponotus sp.09	20.8	1.0	1.0	4.2	26.7	20.8
Camponotus sp.10		2.1	5.7		5.0	4.2
Camponotus sp.14	8.3	16.7	4.7	8.3	15.8	15.1
Camponotus sp.25						1.6
Camponotus sp.28					0.8	
Camponotus sp.29			0.5	2.1		
Camponotus sp.35	10.4	3.1	2.1			1.0
Camponotus sp.42		1.0	9.4			0.5
Camponotus sp.72		35.4	8.3	2.1	0.8	16.7
Camponotus sp.73						0.5
Gigantiops destructor	2.1					
Nylanderia sp.01	22.9	15.6	25.0	12.5	10.0	35.4
Nylanderia sp.02		10.4	4.7		4.2	0.5
Nylanderia sp.04	6.3	9.4	15.6		2.5	1.0
Paratrechina longicornis		3.1				

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Tabela 1, continuação

	Região hidrográfica					
	Amazônica	Paraguai	Paraná	Parnaíba	São Francisco	Tocantins-Araguaia
Myrmicinae						
Acromyrmex aspersus	4.2	2.1	4.7			1.0
Acromyrmex crassispinus		1.0			0.8	
Acromyrmex landolti	16.7	2.1	3.1	8.3	5.0	4.2
Acromyrmex sp.04 pr. niger				4.2		
Acromyrmex subterraneus		4.2				1.6
Apterostigma sp.01		1.0	11.5		2.5	1.6
Apterostigma sp.02		2.1	0.5		1.7	
Apterostigma sp.03			1.0			0.5
Atta laevigata	18.8	30.2	15.1	2.1	10.8	12.0
Atta sexdens		6.3	8.3	2.1	0.8	2.1
Blepharidatta conops		1.0	1.0	33.3	16.7	14.6
Cardiocondyla emeryi			0.5			0.5
Carebara anophtalma	6.3		1.0			
Carebara brevipilosa			1.0		0.8	1.6
Carebara sp.03						0.5
Carebara sp.04						0.5
Carebara sp.05						0.5
Carebara sp.pr. paya			1.6			
Carebara urichi			1.0			
Crematogaster (gr. acuta) sp.08				2.1		
Crematogaster (gr. acuta) sp.20	29.2					
Crematogaster cf. abstinens	6.3				3.3	9.9
Crematogaster distans			0.5			
Crematogaster evallans	4.2	13.5	3.1			6.8
Crematogaster limata						0.5
Crematogaster sp.01						1.6
Crematogaster sp.11 cf. oxygenoides		1.0			0.8	
Crematogaster sp.18						1.6
Crematogaster sp.22		2.1	3.1		1.7	
Crematogaster sp.26			1.0	2.1		1.6
Crematogaster sp.pr. obscurata		2.1	18.8		8.3	2.1
Cyatta abscondita			1.6		0.8	
Cyphomyrmex gr. rimosus sp.26			0.5			0.5
Cyphomyrmex lectus	8.3	11.5	15.1		7.5	7.3
Cyphomyrmex olitor		2.1	0.5			1.0
Cyphomyrmex peltatus	16.7					1.6
Cyphomyrmex rimosus	16.7		5.7			5.7
Cyphomyrmex sp.07						1.0
Cyphomyrmex sp.20			1.6			5.7

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Tabela 1, continuação

	Região hidrográfica					
	Amazônica	Paraguai	Paraná	Parnaíba	São Francisco	Tocantins-Araguaia
Cyphomyrmex sp.33			13.0			
Cyphomyrmex sp.37						0.5
Cyphomyrmex transversus	25.0	9.4	17.2	20.8	10.8	30.7
Hylomyrma reitteri			1.6			
Kalathomyrmex emeryi					3.3	
Megalomyrmex silverstrii	8.3		1.0		0.8	0.5
Megalomyrmex sp.03					0.8	0.5
Megalomyrmex symmetochus		1.0				
Mycetagroicus cerradensis					3.3	0.5
Mycetarotes parallelus	8.3	3.1	0.5		0.8	
Mycetarotes senticosus		1.0				
Mycetosoritis explicata			0.5			
Mycocepurus goeldii	4.2	5.2	33.9		20.8	9.9
Mycocepurus smithii	14.6	11.5	15.1	2.1	18.3	9.9
Mycocepurus sp.03					2.5	
Mycocepurus sp.04					2.5	
Mycocepurus sp.09 pr. Smithii		1.0				
Mycocepurus sp.10					2.5	
Myrmicocrypta camargoi			0.5			
Myrmicocrypta sp.02			1.0			
Myrmicocrypta sp.03		2.1				
Myrmicocrypta squamosa	6.3		5.7		4.2	16.1
Nesomyrmex sp.06			1.6			
Ochetomyrmex semipolitus	4.2	3.1	4.7		5.8	7.3
Octostruma iheringi						0.5
Oxyepoecus browni		3.1	4.7		1.7	0.5
Oxyepoecus sp.03		1.0	3.6			1.0
Oxyepoecus vezenyii	2.1					
Pheidole aberrans			0.5			
Pheidole alpinensis			0.5			
Pheidole ambigua		1.0	11.5			0.5
Pheidole aper			1.0			
Pheidole cavifrons		3.1				
Pheidole cyrtostela	16.7	3.1	0.5		2.5	2.1
Pheidole fracticeps	31.3	40.6	51.6	50.0	46.7	63.0
Pheidole gertrudae		21.9	16.7			5.2
Pheidole jelskii		8.3	15.6		4.2	2.1
Pheidole obscurithorax	4.2		0.5			
Pheidole oxyops	39.6	34.4	70.3		24.2	5.7
Pheidole radoszkowskii	16.7	18.8	24.0	20.8	10.0	22.9

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Tabela 1, continuação

	Região hidrográfica					
	Amazônica	Paraguai	Paraná	Parnaíba	São Francisco	Tocantins-Araguaia
Pheidole rufipilis	22.9	4.2	6.8			
Pheidole schwarzmaieri		5.2	17.2		0.8	3.6
Pheidole scolioceps	2.1	1.0				0.5
Pheidole sp.01			1.6	2.1	0.8	1.0
Pheidole sp.03	2.1	5.2	19.8	2.1	5.8	3.6
Pheidole sp.07		4.2	2.6	6.3	6.7	6.3
Pheidole sp.08	6.3	11.5	15.1		13.3	8.3
Pheidole sp.09			4.2	4.2	5.0	7.8
Pheidole sp.10	2.1	1.0	8.3		2.5	4.2
Pheidole sp.102			0.5			
Pheidole sp.103			0.5			
Pheidole sp.104			1.0			
Pheidole sp.105			1.6			
Pheidole sp.106			0.5			
Pheidole sp.107			0.5			
Pheidole sp.108			1.6			
Pheidole sp.109			0.5			
Pheidole sp.110						0.5
Pheidole sp.113		1.0				
Pheidole sp.12	20.8	3.1	7.3	2.1	9.2	1.6
Pheidole sp.13	8.3		0.5		14.2	6.3
Pheidole sp.14		2.1	1.6		1.7	3.6
Pheidole sp.15	12.5	9.4	31.8	37.5	21.7	40.1
Pheidole sp.25					1.7	0.5
Pheidole sp.26		1.0	1.0		9.2	1.6
Pheidole sp.27			2.6			3.1
Pheidole sp.28					0.8	
Pheidole sp.29					0.8	
Pheidole sp.30					0.8	
Pheidole sp.37		4.2	3.6		0.8	0.5
Pheidole sp.40			6.3	2.1	1.7	4.7
Pheidole sp.41					4.2	
Pheidole sp.43			0.5		1.7	
Pheidole sp.44					8.3	
Pheidole sp.45	6.3	1.0	12.5	2.1	0.8	0.5
Pheidole sp.47		1.0	0.5			
Pheidole sp.50		1.0				3.1

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Tabela 1, continuação

	Região hidrográfica					
	Amazônica	Paraguai	Paraná	Parnaíba	São Francisco	Tocantins-Araguaia
Pheidole sp.51			0.5			3.1
Pheidole sp.52	10.4		1.0		3.3	1.0
Pheidole sp.53		8.3	0.5		0.8	
Pheidole sp.55	2.1		8.9			2.1
Pheidole sp.65			4.7		2.5	
Pheidole sp.66						2.6
Pheidole sp.72		1.0	2.1	2.1		1.0
Pheidole sp.79	2.1					
Pheidole sp.84			1.0			
Pheidole sp.88	2.1		2.1		1.7	1.0
Pheidole sp.90		3.1	7.3		5.0	
Pheidole sp.91			3.6			
Pheidole sp.92			2.1			
Pheidole sp.93			3.1			
Pheidole sp.94			1.0			
Pheidole sp.95			0.5			
Pheidole sp.97			1.6			
Pheidole sp.98		1.0	0.5			
Pheidole sp.pr. tetrica	2.1			25.0	0.8	22.9
Pheidole subarmata	39.6	6.3	12.0		0.8	7.3
Pheidole susannae			7.8			
Pheidole synarmata		3.1	7.3		4.2	2.6
Pheidole triconstricta	87.5	15.6	54.7	62.5	76.7	52.6
Pheidole vafra	22.9	9.4	27.1		9.2	9.9
Pogonomyrmex naegelli	41.7	7.3	5.7		16.7	5.2
Rogeria sp.01	2.1	2.1	2.1	4.2		6.3
Rogeria sp.02			4.7		1.7	0.5
Rogeria sp.04	4.2					3.6
Sericomyrmex maravalhas		1.0				1.6
Sericomyrmex scrobifer				2.1	5.8	0.5
Sericomyrmex sp.05		1.0	0.5		2.5	1.0
Solenopsis globularia	4.2	1.0	5.7	20.8	1.7	5.7
Solenopsis iheringi		2.1	2.6		1.7	
Solenopsis loretana	2.1	7.3	17.7			4.2
Solenopsis sp.04	12.5		3.1	14.6	26.7	14.6
Solenopsis sp.06		17.7	29.7	10.4	28.3	17.2
Solenopsis sp.07			0.5			1.0
Solenopsis sp.08					2.5	
Solenopsis sp.10					10.0	2.1
Solenopsis sp.11	2.1					6.8

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Tabela 1, continuação

	Região hidrográfica					
	Amazônica	Paraguai	Paraná	Parnaíba	São Francisco	Tocantins-Araguaia
Solenopsis sp.12	6.3		1.0	18.8	15.0	10.9
Solenopsis sp.14	2.1	25.0	26.6	8.3	4.2	10.9
Solenopsis sp.15			4.2		5.8	4.7
Solenopsis sp.17	70.8	4.2	4.2	6.3		13.5
Solenopsis sp.21		2.1	4.7		2.5	4.7
Solenopsis sp.23			4.7		1.7	0.5
Solenopsis sp.24			0.5			
Solenopsis sp.25			0.5			
Solenopsis sp.26			2.1			2.1
Solenopsis sp.27			0.5			
Solenopsis sp.28			0.5			
Solenopsis substituta	47.9	12.5	17.7	10.4	24.2	45.3
Solenopsis tridens			0.5	8.3	8.3	4.2
Strumigenys conspersa			0.5			
Strumigenys eggersi	6.3	1.0	2.6		0.8	1.6
Strumigenys elongata		1.0				
Strumigenys grytava	10.4		0.5		2.5	2.6
Strumigenys infidelis			3.6			1.0
Strumigenys lanuginosa			1.0			
Strumigenys sp.04	8.3					3.1
Strumigenys sp.06		2.1			0.8	
Strumigenys sp.07			0.5			0.5
Strumigenys sp.09			1.6		0.8	1.0
Strumigenys sp.1 nov					0.8	
Strumigenys sp.15			0.5			
Strumigenys xenochelyna						0.5
Trachymyrmex bugnioni	2.1	2.1	1.0	4.2	5.0	13.0
Trachymyrmex dichrous			1.6		1.7	
Trachymyrmex gr. urichi sp.02			0.5			
Trachymyrmex holmgreni		3.1	1.0		0.8	0.5
Trachymyrmex relictus					0.8	
Trachymyrmex sp.01			3.6			1.0
Trachymyrmex sp.03	20.8	14.6	2.6		12.5	4.2
Trachymyrmex sp.05		1.0	3.6		2.5	0.5
Trachymyrmex sp.08			0.5			
Trachymyrmex sp.09				14.6	10.8	1.0
Trachymyrmex sp.11				12.5	3.3	
Trachymyrmex sp.15			9.4		0.8	0.5
Trachymyrmex sp.21		1.0			0.8	1.6
Trachymyrmex sp.26			2.6		1.7	

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Tabela 1, continuação

	Região hidrográfica					
	Amazônica	Paraguai	Paraná	Parnaíba	São Francisco	Tocantins-Araguaia
Trachymyrmex sp.31			0.5			
Trachymyrmex sp.36			1.6			
Trachymyrmex sp.39						0.5
Trachymyrmex urichi						0.5
Tranopelta gilva	4.2	3.1	3.1		0.8	1.0
Wasmannia auropunctata	25.0	18.8	45.3	16.7	36.7	27.6
Wasmannia sigmoidea			1.6			
Wasmannia sp.04			0.5			0.5
Ponerinae						
Acanthostichus brevicornis			0.5			0.5
Acanthostichus femoralis	4.2					
Anochetus gr. inermis sp.04						1.0
Anochetus inermis	4.2	2.1	1.0		0.8	2.1
Anochetus vexator		2.1		2.1		2.6
Centromyrmex brachycola		1.0			3.3	1.0
Dinoponera australis			11.5			20.8
Dinoponera gigantea						9.9
Dinoponera mutica	20.8					
Dinoponera quadriceps			2.1	14.6	1.7	7.3
Hypoponera foreli		1.0	1.0		1.7	
Hypoponera sp.01		3.1	4.2		2.5	1.6
Hypoponera sp.02			2.1			
Hypoponera sp.03			2.6			
Hypoponera sp.04	2.1					
Hypoponera sp.06		1.0	3.6		1.7	
Hypoponera sp.08		1.0				
Hypoponera sp.09			0.5			
Hypoponera sp.10			0.5			
Hypoponera sp.11			1.6			
Hypoponera sp.12		1.0				
Hypoponera sp.16						0.5
Hypoponera sp.17						0.5
Hypoponera sp.18						0.5
Leptanilloides sp.02 nov	2.1					
Mayaponera constricta		2.1				
Neoponera commutata	4.2					1.0
Neoponera cooki						0.5
Neoponera laevigata					2.5	0.5
Neoponera marginata			2.6			
Neoponera verenae		1.0	21.4		3.3	1.6

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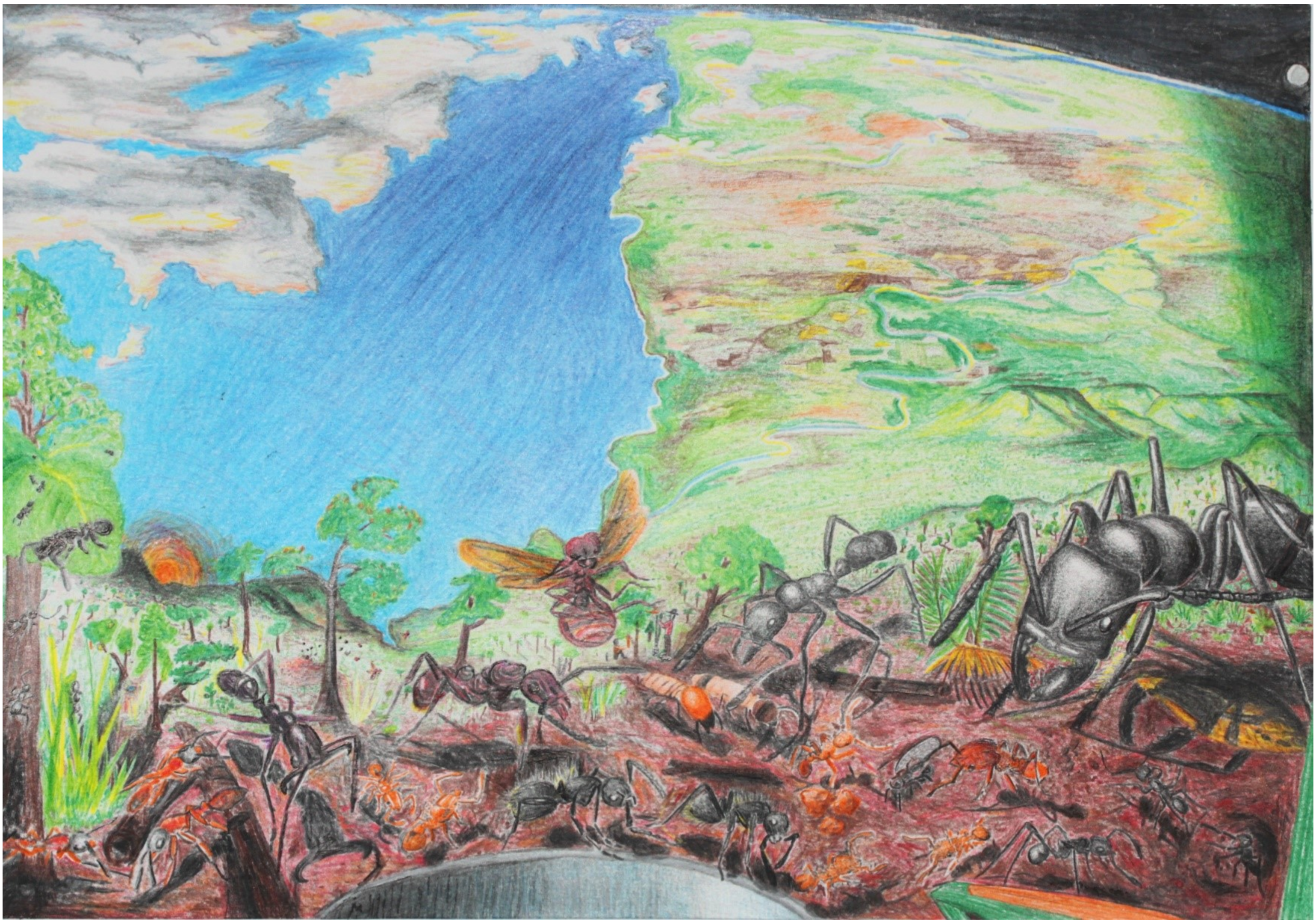
Tabela 1, final

	Região hidrográfica					
	Amazônica	Paraguai	Paraná	Parnaíba	São Francisco	Tocantins-Araguaia
Odontomachus bauri	18.8	11.5		16.7	10.8	6.8
Odontomachus chelifer		1.0	13.5		1.7	
Odontomachus meinerti	18.8	8.3	7.3			4.2
Odontomachus sp05					0.8	
Pachycondyla crassinoda	16.7	6.3				6.3
Pachycondyla harpax	2.1	12.5	28.6		7.5	6.8
Pachycondyla striata			18.8		5.8	
Platythyrea sinuata		1.0				
Pseudoponera stigma		1.0	2.6		0.8	1.0
Simopelta jeckylli	2.1					
Thaumatomyrmex mutilatus		1.0	0.5	2.1	0.8	
Pseudomyrmecinae						
Pseudomyrmex pallidus	4.2	5.2	11.5	4.2	0.8	3.1
Pseudomyrmex simplex			0.5	2.1	2.5	3.1
Pseudomyrmex sp.pr. lizeri			1.0			
Pseudomyrmex tenuis	2.1	8.3	2.6	2.1	5.0	4.2
Pseudomyrmex termitarius	45.8	32.3	5.2	43.8	17.5	20.8
Número de locais amostrados	2	4	8	2	5	8
Número de ocorrências	783	1012	3136	476	1618	2896
Número de espécies	109	147	238	74	181	222



Formigas do Cerrado através das escalas – ilustração por Jonas Maravalhas