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TESE DE DOUTORADO

Gradientes de diversidade de vespas e abelhas (Hymenoptera: Aculeata) em campos rupestres da Cadeia do Espinhaço

LUCAS NEVES PERILLO

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Tese apresentada ao Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre da Universidade Federal de Minas Gerais, como requisito parcial para obtenção do titulo de Doutor em Ecologia, Conservação e Manejo da Vida Silvestre.

Orientador: Dr. Frederico de Siqueira Neves

Co-orientadores: Dr. Ricardo Ribeiro de Castro Solar & Dr. Felipe Sá Fortes Leite

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As montanhas me chamam e tenho que atendê-las.

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Sumário

Resumo Geral

Entender quais são os padrões espaço-temporais e os mecanismos que determinam a distribuição da fauna de vespas e abelhas (Aculeata) associada ao campo rupestre da Cadeia do Espinhaço, importante cordilheira montanhosa brasileira, foi o principal objetivo desta tese, utilizando diferentes escalas e abordagens. No primeiro capítulo, mostramos que a distância geográfica ocasionada pela variação altitudinal é importante para a estrutura da comunidade ao longo do gradiente, sobretudo considerando a substituição de espécies (turnover) como mecanismo fundamental para a manutenção da diversidade beta. No segundo capítulo, questionamos a existência de sazonalidade na comunidade de vespas e abelhas associadas à fragmentos naturais de mata atlântica, e se métricas da paisagem influenciam nessa dinâmica temporal das espécies. Encontramos um efeito da sazonalidade na riqueza de espécies e mostramos que a substituição de espécies ao longo do tempo (turnover temporal) aumenta com a distância da mata contínua (única métrica que teve influência na riqueza, abundância ou composição de espécies). No último capítulo, definimos um ponto de coleta na base (em torno de 1100m de altitude) e outro nas proximidades do topo da montanha (variando entre 1400 e 2000m) em doze localidades ao longo da Cadeia do Espinhaço, com objetivo de entender os padrões de distribuição de vespas e abelhas ao longo do seu gradiente latitudinal e altitudinal. E ainda como as variáveis climáticas exercem influência nas suas diferentes escalas de diversidade. Nesse contexto, descobrimos que a altitude é mais importante do que a latitude em determinar as diversidades α e γ, tendo a temperatura como principal mecanismo climático para explicar esses padrões.

Palavras-chave: Hymenoptera, campo rupestre, Cadeia do Espinhaço, padrões espaço-temporais, estrutura de comunidades, diversidade β, latitude, altitude.

Abstract

Understanding spatial-temporal patterns and mechanisms that determine the distribution of wasps and bees fauna (Aculeata) associated with the *campo rupestre* of *Cadeia do Espinhaço*, an important Brazilian mountain range, was the main objective of this thesis, using different scales and approaches. In the first chapter, we shown that the geographic distance caused by the altitudinal variation is important for community structure, especially considering species turnover as a fundamental mechanism for the maintenance of beta diversity. In the second chapter, we questioned the existence of seasonality in wasps and bees communities associated with natural fragments of Atlantic forest, and whether landscape metrics influence this temporal species dynamic. We found an effect of seasonality on species richness and showed that temporal species turnover increases with continuous forest distance (the only metric that influenced species richness, abundance or composition). In the last chapter, we defined sample points at the base (around 1100m.a.s.l.) and near mountain summit (ranging from 1400 to 2000m.a.s.l.) in twelve locations along *Cadeia do Espinhaço*, in order to understand distribution patterns of wasps and bees along their latitudinal and altitudinal gradient and how climate variables influences it at different diversity scales. In this context, we found that altitude is more important than latitude in determining α and γ diversities, with temperature being the main climate mechanism to explain these patterns.

Key words: Hymenoptera, *campo rupestre*, *Cadeia do Espinhaço, spatio-temporal patterns, community structure*, β-diversity, latitude, elevation.

Apresentação

Contexto geral

Encontramos na atualidade inúmeros desafios para a conservação da diversidade biológica. Alterações globais, extensas intervenções nas paisagens e extinção de ambientes naturais estão ocorrendo em taxas cada vez mais aceleradas, sobretudo em áreas montanhosas tropicais. As alterações nos ambientes naturais são tão evidentes, que alguns defendem que estamos vivendo uma nova era geológica, o Antropoceno (veja Smith & Zeder 2013). Para agravar a situação, dados consistentes sobre os mecanismos ecológicos e até mesmo dados básicos de distribuição e diversidade de espécies apresentam deficiências e lacunas de coleta (Oliveira *et al.* 2016), dificultando a elaboração de metas de conservação e manejo que deverão ser aplicadas neste cenário de mudanças estimadas para um futuro próximo (Barry 1994; Parmesan 2006; Tylianakis *et al.* 2008). Em regiões montanhosas, mudanças climáticas podem causar malefícios ainda maiores, já que espécies restritas à ambientes elevados, condicionados aos ambientes extremos dos picos de montanha, não terão para onde migrar (Hoffmann 2011). Estas mudanças irão afetar diretamente o funcionamento destes ecossistemas (Hughes 2000; McCarty 2001; Parmesan & Yohe 2003) e cabe aos ecólogos tentar entender os padrões e mecanismos que regem a estrutura dessas comunidades biológicas.

A ecologia de comunidades é uma bagunça! Essa famosa frase escrita por John H. Lawton (1999) expressa a dificuldade de encontrarmos generalizações úteis no meio de tanta contingência. Apesar do elevado número de variáveis e mecanismos que emanam destas comunidades, todos estes podem ser enquadrados em apenas quatro categorias de processos: seleção, deriva, especiação e dispersão (Vellend 2010). Com essa organização, temos um conjunto logicamente completo de processos, dentro dos quais todos os outros mais específicos, como sucessão e relações ecológicas por exemplo, podem ser inseridos. Em meio aos inúmeros desafios, tais como a necessidade de enxergarmos a real importância dos variados mecanismos para a manutenção da diversidade de espécies (Chesson 2000) ou criarmos um conjunto de suas hipóteses unificadas (Palmer 1994), o desenvolvimento teórico e analítico que permeia a ecologia de comunidades recebe constantes contribuições. Hoje podemos utilizar, por exemplo, informações climáticas extrapoladas para todas as regiões do planeta (variáveis WorldClim v2; 1970–2000) como variáveis explicativas, temos arcabouço estatístico para calcular propriedades complexas das comunidades biológicas (Baselga & Orme 2012) e resolver problemas de amostragem, como o de pseudo-replicação temporal (Crawley 2013).

Para estudar estas e outras diversas questões, ambientes montanhosos são verdadeiros laboratórios naturais, já que suas variações altitudinais criam diferentes cenários nos quais conseguimos avaliar variações de temperatura, umidade e condições edáficas em um espaço geográfico reduzido (Wolda 1987; Kumar *et al.* 2009; Fernandes *et al.* 2016). A altitude interfere em uma série de variáveis, tais como temperatura, umidade e velocidade do vento, e essas características influenciam na distribuição espacial das espécies em diferentes faixas altitudinais (Wolda 1987). A tendência é de que a riqueza e abundância de espécies diminua com o aumento da altitude em diferentes grupos (Wolda 1987; Kumar *et al.* 2009; Kraft *et al*. 2011; Peters *et al.* 2016). Variações de temperatura, umidade e condições edáficas também são encontradas em diferentes latitudes, que também molda a distribuição espacial das comunidades (Pianka 1966; Schemske & Mittelbach 2017), com espécies ordenadas em um gradiente, sendo que áreas de maior diversidade estão em regiões com baixas latitudes (Stevens 1989; Kraft *et al*. 2011; Cancello *et al.* 2014).

Variações sazonais também são comuns em ambientes tropicais, especialmente quando consideramos mudanças na composição das espécies (Tylianakis *et al.* 2005). Esta composição de espécies é influenciada na escala local pela diversidade presente na escala regional (Arellano *et al.* 2014), determinado por processos como os de especiação e dispersão. Também é importante tentarmos entender como a diversidade total em uma dada região (ou seja, a diversidade gama) é dividida, sendo particionada em diversidade alfa (α) (isto é, número de espécies na escala local) e a diversidade beta (β) (diferenças na composição das espécies entre localidades) (Whittaker 1960, 1972; Tuomisto 2010; Baselga 2010). A diversidade β é uma importante propriedade dessas comunidades e é influenciada por diferentes escalas espaciais (Barton *et al.* 2013) e pela relação espécie-área (Horner-Devine *et al.* 2004). Os dois aspectos espaciais apresentados (latitude e altitude), somados às variações temporais (Rosenzweig 1995) e partições de diversidade (Legendre *et al.* 2005), são importantes aspectos que devem ser considerados para encontrarmos possíveis padrões de diversidade nas comunidades biológicas.

Nos trópicos, o estudo de cadeias montanhosas é incipiente, sobretudo considerando variações altitudinais, latitudinais e ambientais (Rosling *et al.* 2017). Dentre as áreas montanhosas encontradas no Brasil se destaca a Cadeia do Espinhaço, cordilheira situada nos estados de Minas Gerais e Bahia, onde predomina como fitofisionomia o campo rupestre (Fernandes 2016; Silveira *et al.* 2016). Nesses ambientes montanhosos, podemos estar perdendo espécies, fitofisionomias e habitats em taxas nunca antes vistas (Fernandes *et al.* 2016). Suas variações altitudinais representam uma das grandes fronteiras biogeográficas a ser estudada e permite que sejam propostos estudos sobre às variações ambientais dos organismos (Knapp 2005). Nesse ecossistema existe um avanço no conhecimento da flora (Fernandes 2016), mas pouco se conhece a respeito dos padrões de distribuição e os mecanismos determinantes aos insetos, particularmente das vespas e abelhas (Aculeata:

Hymenoptera), que têm a maior parte dos trabalhos em ambientes montanos do Brasil restritos a amostragens pontuais (p. ex.; Silveira & Cure 1993; Azevedo et al. 2008; Antonini 2005; Perillo *et al.* 2017). A complexidade dos sistemas montanos lança diversos desafios como, por exemplo, em que medida a variabilidade ambiental no tempo e espaço afeta a estrutura das comunidades e qual o papel dos gradientes ambientais nos padrões e mecanismos que determinam a biodiversidade.

O campo rupestre e a Cadeia do Espinhaço

Escolhemos como ambiente de estudo o campo rupestre, uma das formações rochosas mais singulares da paisagem brasileira e mundial (**Fig. 1A**). Para tal, selecionamos áreas ao longo da Cadeia do Espinhaço, conjunto de serras e montanhas que abriga grande parte deste ecossistema (Harley 1995; Vasconcelos 2009; 2011; Fernandes 2016), e possui diversas áreas insubstituíveis para a conservação da biodiversidade (Silva *et al.* 2008; Silveira *et al.* 2016) (**Fig. 1B**).

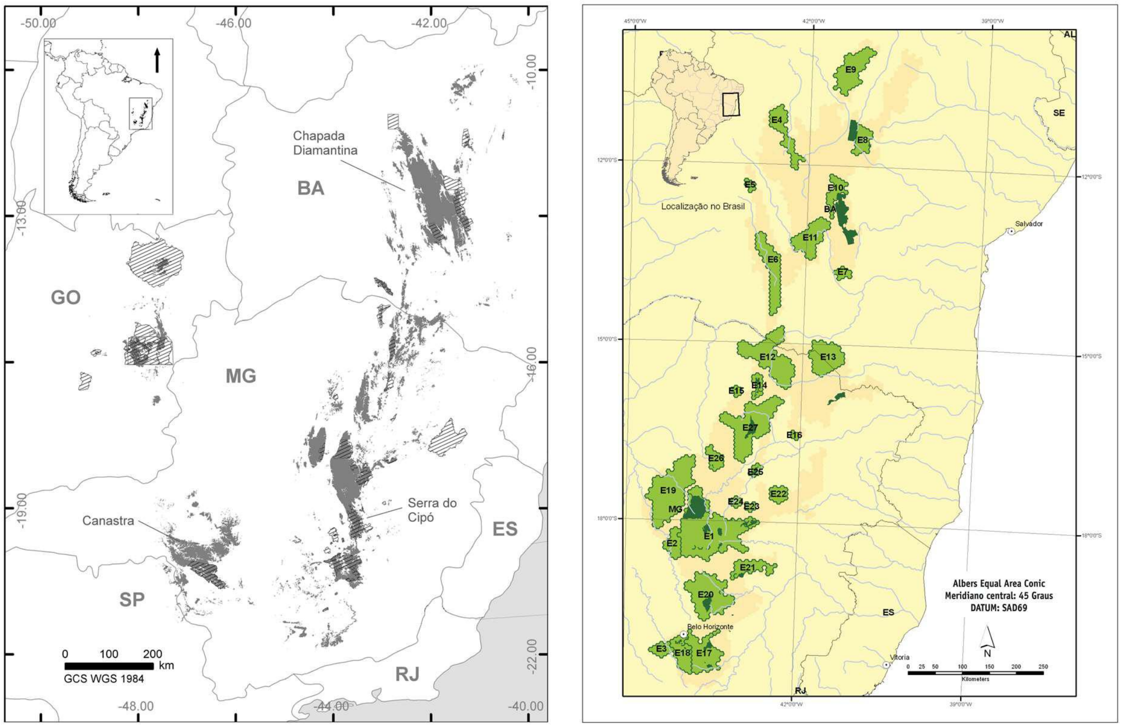

Figura 1. A- Mapa ilustrando a localização do campo rupestre no Brasil (adaptado de Silveira *et al.* 2016). **B-** Mapa Cadeia do Espinhaço. Em detalhe as áreas consideradas prioritárias para a conservação da biodiversidade (retirado de Silva *et al.* 2008).

O campo rupestre é um ambiente aberto e rochoso, com vegetação azonal (isto é, que tem características independentes do esperado para a região geográfica) (Alves *et al.* 2014; Silveira *et al*. 2016) e ocorre nos topos de montanhas do leste do Brasil (geralmente acima de 900 m de altitude) (Costa 2005). Sua formação rochosa é de origem pré-cambriana, remodeladas por movimentos tectônicos a partir do Paleógeno (Ab'Sáber 2000; Abreu 2005). Portanto, são consideradas paisagens antigas e inférteis, climaticamente tamponadas (*old climatically-buffered infertile landscapes* - OCBILs) (Hopper *et al.* 2016; Silveira *et al.* 2016), contendo provavelmente a mais antiga vegetação aberta do leste da América do Sul (Silveira *et al.* 2016). Têm litologia predominante composta por quartzitos e arenitos, com presença de neossolos litólicos e afloramentos ferruginosos, associados sobretudo ao domínio da caatinga e do cerrado (Giulietti *et al.* 1987, Ribeiro & Fernandes 2000; Benites *et al.* 2003, 2007; Jacobi & Carmo 2008).

Diversos estudos têm demonstrado que o campo rupestre apresentam uma grande biodiversidade, com elevada presença de elementos endêmicos, tanto na flora quanto na fauna (Giulietti *et al.* 1987, 1997; Silva & Bates 2002; Gonçalves *et al.* 2007; Vasconcelos & Neto 2007; Vasconcelos 2008; Oliveira 2010, Leite *et al.* 2012). O campo rupestre ocupa somente 0,78% da área do Brasil e abrigam mais de 15% da diversidade de plantas vasculares do país (mais de 5.000 espécies) (Silveira *et al.* 2016), recebendo o status de região mais rica em espécies no Brasil, país mais rico em número de espécies do mundo. A vegetação de campo rupestre e de altitude é ainda uma das mais ameaçadas (Costa *et al.* 1998; MMA 1999; Viana *et al.* 2005; Ribeiro & Freitas 2010). Muitos fatores contribuem para a grande diversidade biológica destas formações campestres, tais como a considerável variação altitudinal (Alves *et al*. 2014), que causa isolamento de populações nas diferentes serras (Costa 2005), a idade ancestral de suas formações geológicas, a variedade de microclimas (Barbosa *et al.* 2015) e a presença de um mosaico de fitofisionomias campestres e florestais (Rapini *et al.* 2008). Além do campo rupestre, encontramos formações florestais inseridas na vegetação campestre, como as matas de galeria e os capões de mata. Os capões de mata são ilhas de vegetação arbórea localizadas nessa matriz campestre dominante nos topos de montanha. Essas ilhas florestais são de formação edafoclimática, sendo dependentes de clima e solo específicos para o seu desenvolvimento (Coelho *et al*. 2017a; 2017b). Poucos trabalhos foram desenvolvidos nestes ambientes associados ao campo rupestre, com exemplos de estudos de flora (Rizzini 1979; Meguro *et al.* 1996; Coelho 2016) e entomofauna (Pereira *et al*. 2017). Todas estas características credenciam os campos rupestres como valiosa fonte de estudos de padrões evolutivos e de distribuição geográfica de espécies.

Grande parte do ecossistema campo rupestre é encontrado em uma das principais cadeias de montanha do Brasil, que recebe a alcunha de Cadeia do Espinhaço (*Rückenknochengebirge*), nome dado pelo Barão Wilhelm Ludwig von Eschwege, naturalista alemão que viveu no Brasil no início do século XIX (Eschwege 2005). A Cadeia do Espinhaço se estende por mais de 1.200 km (Norte-Sul), desde a Serra de Ouro Branco - MG (sul) até o norte da Chapada Diamantina - BA (Giulietti *et al.* 1987). Possui uma das mais relevantes variações altitudinais de todo território nacional, com altitudes variando entre 700 e 2.072 m, mas com largura leste-oeste poucas vezes ultrapassando os 100 km (Oliveira 2010). O Espinhaço ainda está inserido na interseção de três importantes biomas da América do Sul: a Caatinga, o Cerrado e a Mata Atlântica, sendo os dois últimos considerados *hotspots* da biodiversidade do Brasil (Myers *et al.* 2000), locais que abrigam grande biodiversidade, endemismo e sofrem grande pressão antrópica, incluídos entre os mais ameaçados do planeta (Mittermeier *et al.* 1999; Klink & Machado 2005). O campo rupestre aparece como refúgios biogeográficos em meio à esses três domínios (Giulietti *et al.* 1997; Gontigo 2008). Este contexto espacial, somado às variações de altitude, tipos de solo e microclima, garantem um vasto mosaico de fitofisionomias (Giulietti *et al.* 1997).

Um marco para os estudos na Cadeia do Espinhaço foi a publicação do quarto volume especial da revista Megadiversidade, compilada pela Conservação Internacional em 2008. Essa iniciativa fomentou discussões para a criação da Reserva da Biosfera na parte meridional da Cadeia (UNESCO 2009). Vários artigos foram publicados nos últimos anos e, recentemente, novos resultados de estudos no Espinhaço foram compilados em um livro sobre os campo rupestre (Fernandes 2016). No próximo ano (2018), um volume especial do periódico *Flora* ainda reunirá variados estudos sobre os campo rupestre (*Flora: Morphology, Distribution, Functional Ecology of Plants. Special Issue: Plant life on* campo rupestre).

Conhecimento sobre os insetos no Brasil

No Brasil, o início de um conhecimento sistematizado da fauna surge após a chegada dos naturalistas europeus, com os primeiros ainda no século XVII (Ihering 1914). Apesar de várias passagens de suas obras remeterem aos ambientes montanhosos, poucas menções aos insetos são encontradas nos livros durante o Brasil Colonial (p. ex., Taunay 1938; Gardner 1942). As citações são sobretudo sobre espécies de interesse médico e agrícola (p. ex., Wied-Neuwied 1942). Apesar dessa constante presença de naturalistas no Brasil, poucos tinham os insetos como foco principal de estudo. Mas vários coletaram espécimes e enviaram para coleções europeias e muitos tipos descritos se encontram em museus estrangeiros (Vulcano *et al.* 1980). Alguns merecem destaque: os entomólogos naturalistas Edouard Ménétries (criador da Sociedade de Entomologia Russa, 1824) e Pierre Emile Gounelle (1885) descreveram várias espécies de insetos; Frederich Sellow, apesar de botânico, coletou mais de 110.000 espécimes de insetos no Brasil (1818); o naturalista francês Louis Claude de Saulces de Freycinet (1817 e 1820) relatou a exuberância nas formas e cores dos insetos (Melo-Leitão 1934); o casal alemão Beske (década de 1840) colecionava e expedia insetos brasileiros para várias partes do mundo (Alves 2011). Papavero (1971) ainda lista 20 naturalistas que visitaram Minas Gerais no século XIX e coletaram invertebrados. O próprio Charles Darwin os cita em sua passagem pela mata atlântica, dizendo que: "... os insetos fazem um tal ruído que podem ser ouvidos do navio..." (Darwin 2006). Essas informações geradas por estes naturalistas ainda carece de um profundo resgate bibliográfico, facilitado com a recente digitalização do acervo brasiliana (http://www.brasiliana.com.br/).

Somente a partir da primeira metade do século XX que despontaram os primeiros grandes entomologistas e taxonomistas brasileiros, tais como: Ângelo Moreira da Costa Lima (Rio de Janeiro, autor de "Insetos do Brasil" de 1938); Cândido F. de Mello-Leitão (trabalhando com Arachnida, Museu Nacional do Rio de Janeiro); o casal Benedito A.M. Soares e Hélia H.M. Soares (ambos no Estado de São Paulo, com Arachnida); Cincinnato R. Gonçalves (Rio de Janeiro, Formicidae); a autora e entomóloga Maria Aparecida Vulcano (Coleoptera - desde a década de 1940); o Pe. Jesús S. Moure (1912–2010) (abelhas no Museu Paulista, Museu Paranaense e fundador do Departamento de Zoologia da UFPR). Recentemente, a entomofauna brasileira foi contemplada com a publicação do livro Insetos do Brasil: Diversidade e Taxonomia (Rafael *et al.* 2012). Várias espécies são descritas anualmente, sobretudo por institutos de pesquisa na UFMG, UFPR, INPA e USP, considerando centros de referência em grupos de himenópteros.

Mas o conhecimento sobre a fauna de insetos é ainda incipiente e deriva, em grande parte, de inventários realizados em áreas restritas, muitas vezes caracterizadas por baixo grau de conservação (Azevedo *et al.* 2008). Apesar da crescente exploração científica, existem lacunas inclusive no levantamento de espécies, sobretudo em áreas de difícil acesso como os topos de montanha (veja Silveira & Cure 1993; Perillo *et al.* 2017). Esse panorama nos incentivou a investigar a diversidade de vespas e abelhas em diferentes cenários dos campos rupestres brasileiros.

As vespas e abelhas: o grupo Aculeata (Hymenoptera)

Inserido na ordem de insetos Hymenoptera, o grupo monofilético Aculeata é composto por insetos que possuem o ovipositor modificado em forma de ferrão como vespas, formigas e abelhas (veja Rafael *et al.* 2012; Peters *et al.* 2017) (**Fig. 2**). No Brasil, baseado nas últimas revisões, temos espécies presentes em 23 das 26 famílias existentes de Aculeata (Silveira *et al.* 2002; Melo *et al.* 2012) e inúmeras espécies são descritas a cada ano.

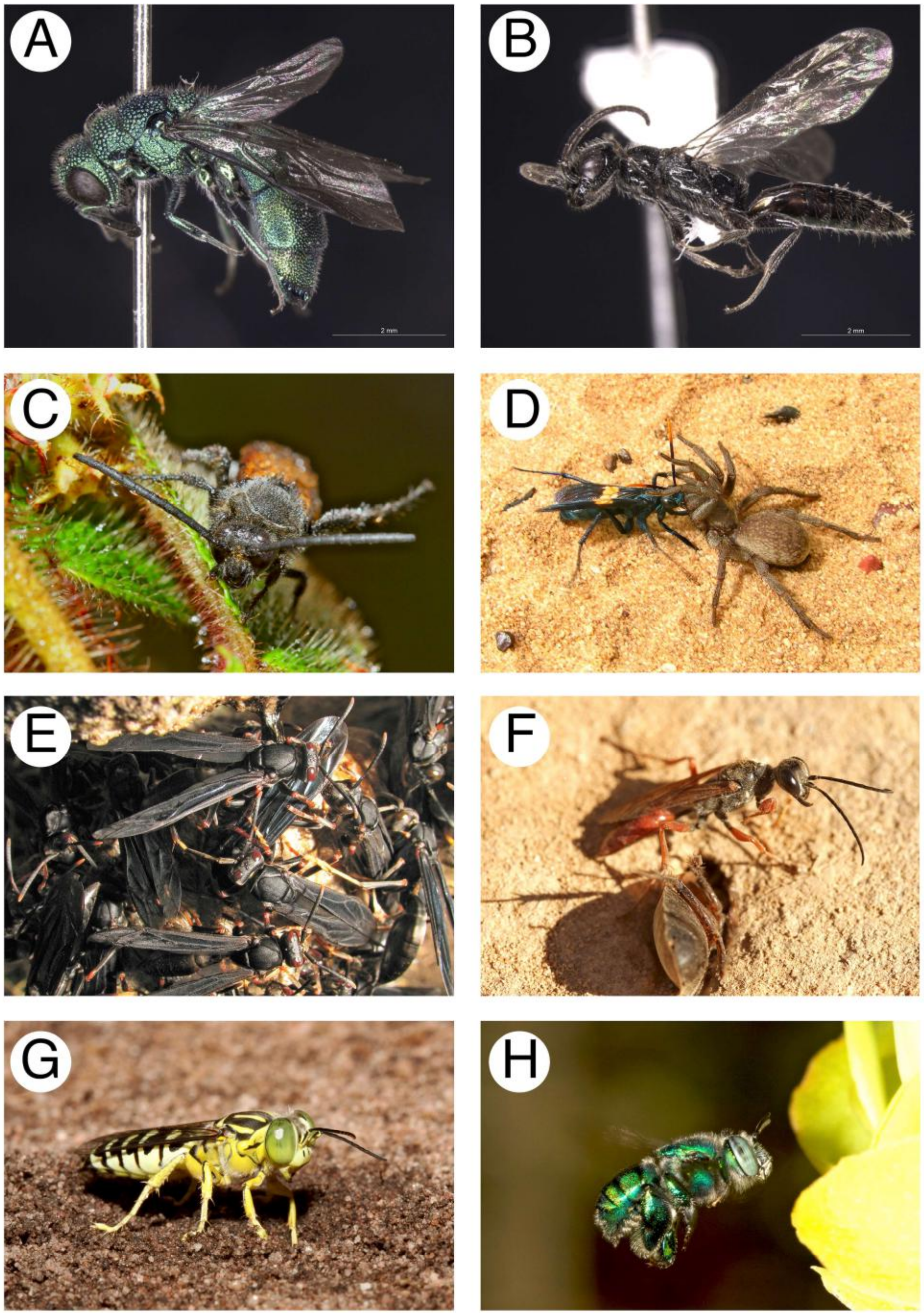

Figura 2. Alguns espécimes representantes das três superfamílias de Aculeata (Hymenoptera). Chrysidoidea – **A:** Chrysididae. **B:** Bethylidae. Vespoidea – **C:** Scoliidae. **D:** Pompilidae. **E:** Vespidae. Apoidea – **F:** Sphecidae. **G:** Crabronidae. **H:** Apidae. Fotos: Lucas Perillo.

Escolhemos esses insetos como objeto de estudo porque são interessantes organismos para se estudar, já que são mega abundantes, coletados facilmente, possuem um curto tempo de geração e respondem rapidamente às modificações do ambiente (Kremen *et al.* 1993; Missa *et al.* 2009). Ainda existe uma grande lacuna em levantamentos de espécies e ciência de base (Oliveira 2016) e em estudos ecológicos e sobre conservação (Lewis & Basset 2007). Como exemplo, nos trópicos, mais de 87% das plantas angiospermas dependem de polinizadores bióticos para reprodução (Ollerton *et al.* 2011; Novais *et al.* 2016) e neste grupo está inserido o maior número de espécies de polinizadores (Potts *et al.* 2010). Ainda prestam outros variados serviços ecossistêmicos, atuando no controle biológico de pragas agrícolas, na produção de mel e cera e têm um papel fundamental nas relações ecológicas (LaSalle & Gauld 1993).

Apesar da sua grande diversidade e importância para a humanidade, os invertebrados são frequentemente negligenciados nas políticas de conservação da biodiversidade (Cardoso *et al.* 2011), sobretudo em ambientes montanhosos (Pryke & Samways 2010). Investimento em estudos de taxonomia (Ely *et al.* 2017), estrutura das comunidades, distribuição geográfica, além da busca pela real diversidade dos insetos (Basset *et al.* 2012, 2015) são medidas importantes para delimitar áreas de interesse para conservação visando a manutenção dos serviços ambientais descritos acima.

Áreas estudadas, métodos empregados

Todas as áreas de estudo dessa tese foram distribuídas ao longo da Cadeia do Espinhaço. Para a escolha das áreas de coleta consideramos variados elementos (desde o status de conservação até amplitudes de altitude, sempre entre 1000 e 2072 m de altitude), mas sempre em localidades que mantinham a identidade do mosaico de ecossistemas presentes no campo rupestre (**Tabela 1; Fig. 3; Fig. 4**). No primeiro capítulo coletamos em um gradiente altitudinal na trilha para o Pico do Sol (ponto mais alto do Espinhaço – 2072m), na RPPN Santuário do Caraça (**Fig. 3 P-R**). No segundo capítulo, estudamos um arquipélago natural de ilhas florestais inserido numa matriz campestre, os capões de mata, inseridos na Área de Proteção Ambiental Morro da Pedreira e no Parque Nacional Serra do Cipó (**Fig. 3 M-O**). E para o terceiro capítulo, selecionamos 12 diferentes montanhas ao longo da Cadeia do Espinhaço (**Tabela 1; Fig. 3 A-L; Fig. 4**).

Tabela 1. Descrição das áreas de campo rupestre selecionadas para os capítulos da tese (Cap).

Cap.	**Localidade**	**Município**	**Estado**	**Latitude**	**Longitude**
1	RPPN Santuário do Caraça	Santa Bárbara	MG	20° 04' 37" S	43° 29' 37" O
2	P.N. Serra do Cipó	Santana do Riacho	MG	19 ° 14' 46" S	43° 33' 08" O
3	P.N. Chapada Diamantina	Mucugê	BA	12° 45' 48" S	41° 30' 40" O
3	Pico do Barbado	Abaíra	BA	13° 15' 43" S	41° 52' 37" O
3	Pico das Almas	Rio de Contas	BA	13° 30' 33" S	41° 53' 29" O
3	Pico da Formosa	Monte Azul	MG	15° 12' 25" S	42° 48' 04" O
3	P.E. Serra Nova	Rio Pardo de Minas	MG	15° 43' 11" S	42° 50' 10" O
3	Serra de Botumirim	Botumirim	MG	16° 50' 27" S	43° 04' 15" O
3	P.E. do Rio Preto	S. Gonçalo do Rio Preto	MG	18° 13' 05" S	43° 18' 56" O
3	P.E. Pico do Itambé	Sto. Antônio do Itambé	MG	18° 24' 00" S	43° 18' 05" O
3	Pico do Breu	Santana do Riacho	MG	19° 05' 46" S	43° 41' 14" O
3	RPPN Santuário do Caraça	Santa Bárbara	MG	20° 04' 37" S	43° 29' 37" O
3	P.E. Itacolomi	Ouro Preto	MG	20° 28' 53" S	43° 27' 48" O
3	P.E. Serra do Ouro Branco	Ouro Branco	MG	20° 30' 20" S	43° 37' 23" O

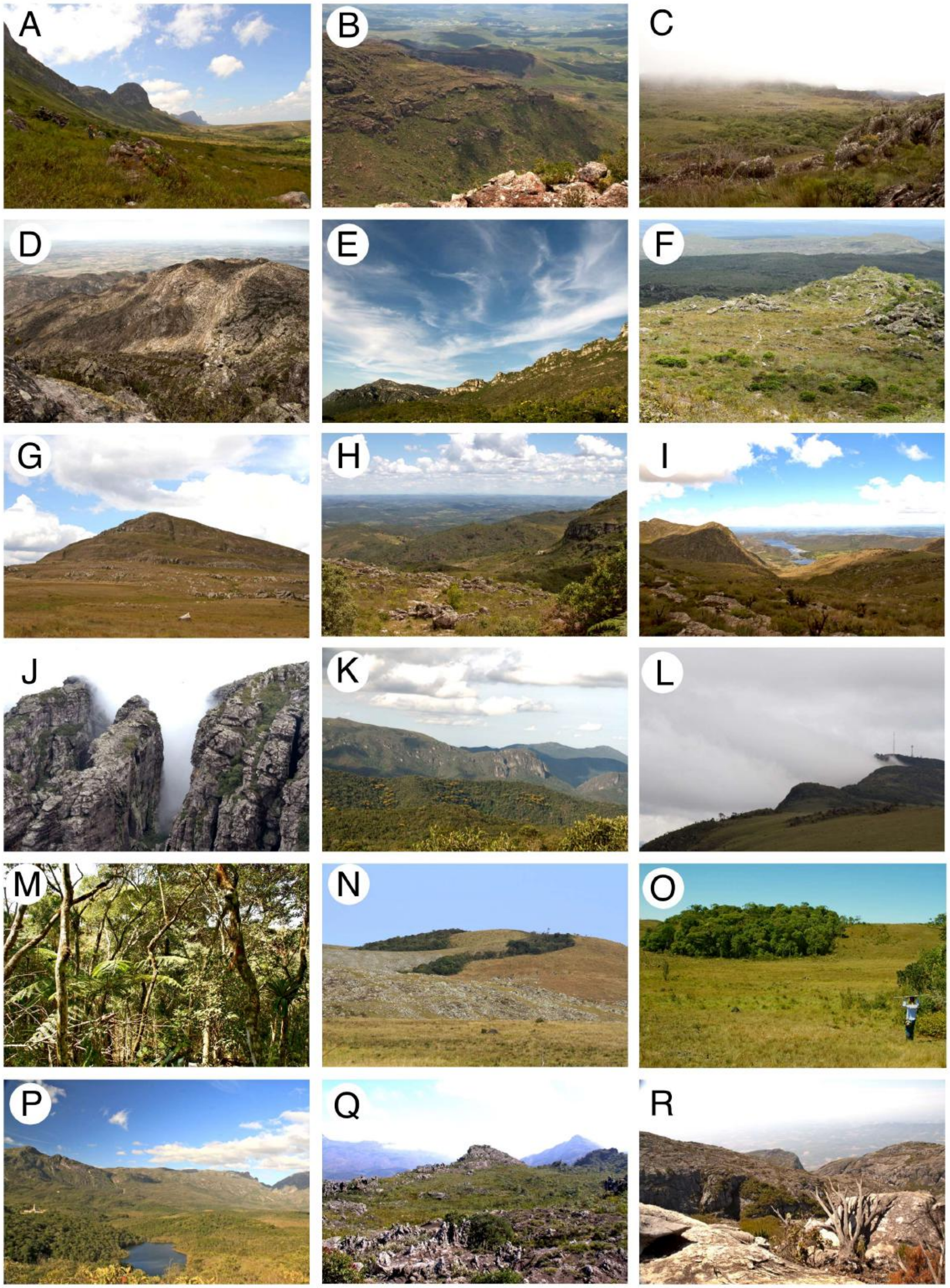

Figura 3. Localidades selecionadas para os estudos da tese. **A:** P.N. Chapada Diamantina. **B:** Pico do Barbado. **C:** Pico das Almas. **D:** Pico da Formosa. **E:** P.E. Serra Nova. **F:** Serra de Botumirim. **G:** P.E. do Rio Preto. **H:** P.E. Pico do Itambé. **I:** Pico do Breu. **J:** RPPN

Santuário do Caraça. **K:** P.E. Itacolomi. **L:** P.E. Serra do Ouro Branco. **M-O:** Capões de Mata, Serra do Cipó, MG. **P-R:** RPPN Santuário do Caraça. Fotos: Lucas Perillo.

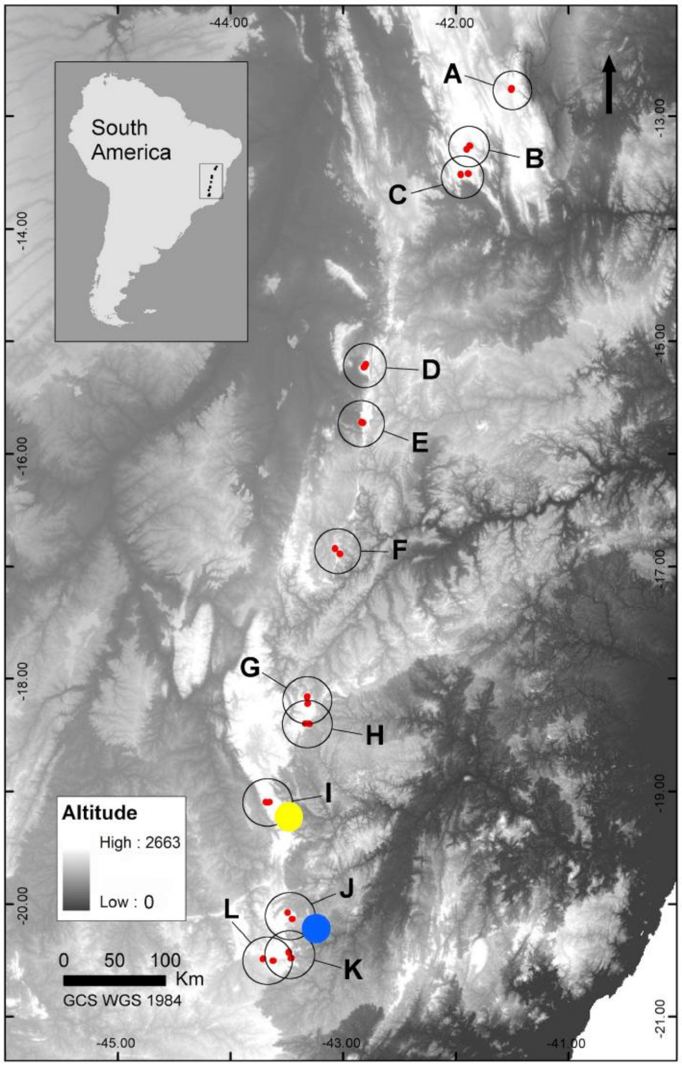

Figura 4. Localidades selecionadas para os diferentes capítulos da tese. **Capítulo 1** (círculo azul): RPPN Santuário do Caraça. **Capítulo 2** (Círculo amarelo): Capões de Mata, Serra do Cipó, MG. **Capítulo 3** (círculos vermelhos, buffers em preto): **A:** P.N. Chapada Diamantina. **B:** Pico do Barbado. **C:** Pico das Almas. **D:** Pico da Formosa. **E:** P.E. Serra Nova. **F:** Serra de Botumirim. **G:** P.E. do Rio Preto. **H:** P.E. Pico do Itambé. **I:** Pico do Breu. **J:** RPPN Santuário do Caraça. **K:** P.E. Itacolomi. **L:** P.E. Serra do Ouro Branco.

Para o levantamento das vespas e abelhas, utilizamos quatro tipos de armadilha. São elas: armadilha Malaise (de solo, **Fig. 5A** e arbórea, **Fig. 5B**), armadilha Moericke (*pan trap*; **Fig. 5C**), ninho-armadilha (**Fig. 5D**) e armadilha *pitfall* (de solo, **Fig. 5E** e arbórea, **Fig. 5F**). Estes são métodos complementares utilizados para coleta das diferentes famílias de vespas e abelhas (García 2003; Moreira *et al.* 2016).

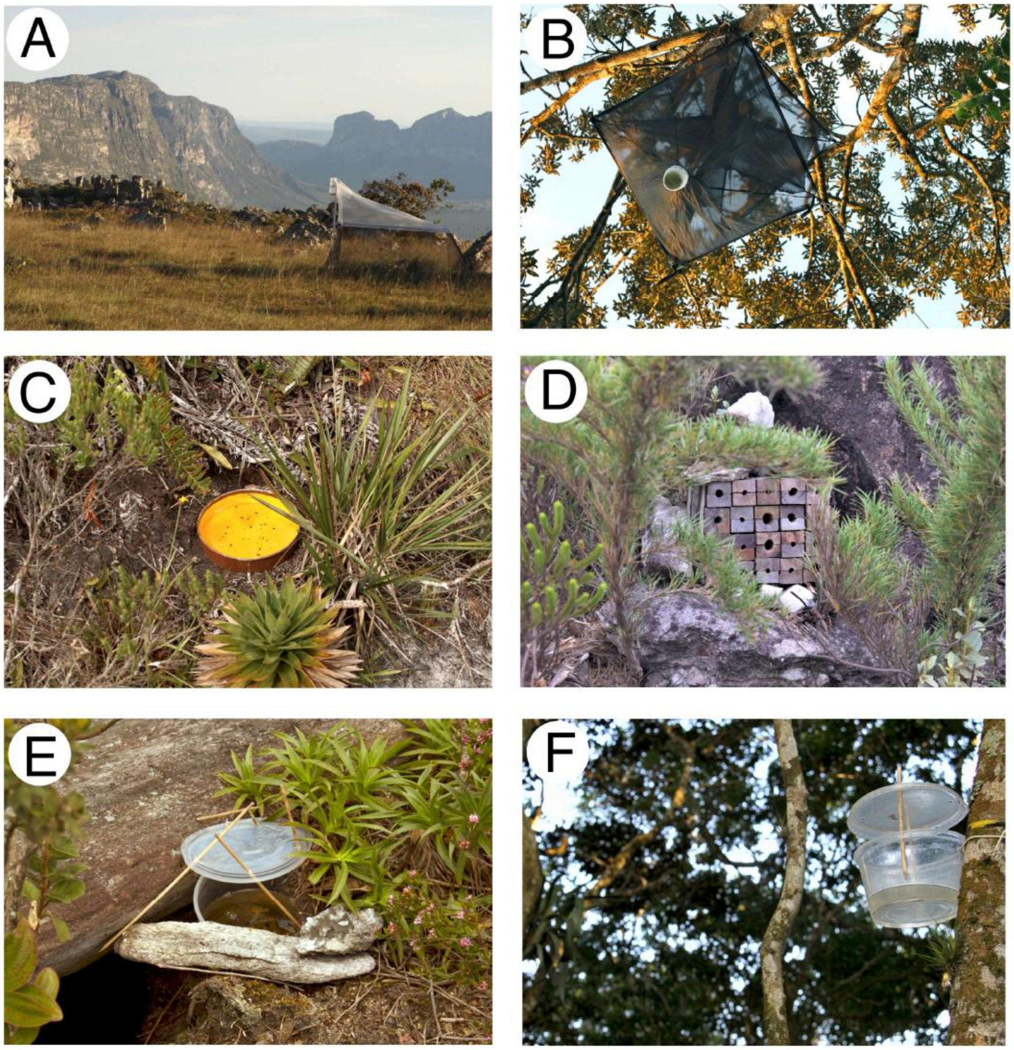

Figura 5. Métodos utilizados para o levantamento de vespas e abelhas (Aculeata: Hymenoptera) nos diferentes ambientes associados ao campo rupestre. Números correspondentes aos capítulos nos quais as armadilhas foram usadas. **A:** Armadilha Malaise (2 e 3). **B:** Armadilha Malaise de dossel (Malaise Window) (2). **C:** Armadilha Moericke (Pan

Trap) (1, 2 e 3). **D:** Ninho-armadilha (1). **E:** *Pitfall* de solo (2 e 3). **F:** *Pitfall* arbóreo (2). Fotos: Lucas Perillo.

Objetivos e apresentação dos capítulos

Esta tese tem como desafio aprofundar o conhecimento sobre a fauna de vespas e abelhas (Aculeata) associada ao campo rupestre à partir do levantamento de espécies sobretudo em áreas de difícil acesso, utilizando uma ampla variedade de metodologias de captura. Pretendemos entender quais são os padrões espaço-temporais e os mecanismos que determinam a distribuição dessa fauna utilizando os dados primários gerados. Para tal, dividimos a tese em três capítulos, utilizando diferentes escalas e abordagens.

Em um primeiro momento, objetivamos explorar padrões das comunidades de abelhas e vespas ao longo de um gradiente de altitude, com coletas quinzenais durante um ano. Esse levantamento ocorreu na RPPN Santuário do Caraça, que possui cerca de 10 mil ha e áreas as maiores amplitudes altitudinais da Cadeia do Espinhaço. O primeiro capítulo tem como principal pergunta: a variação altitudinal determina a composição de espécies de vespas e abelhas? Neste estudo, já publicado na revista PLOS ONE (Anexo I), mostramos que esta distância geográfica gerada pela elevação é importante para a estrutura da comunidade ao longo do gradiente, sobretudo considerando a substituição de espécies (turnover) como mecanismo fundamental para a manutenção da diversidade beta.

No segundo capítulo, em uma abordagem espaço-temporal, escolhemos um sistema composto por manchas naturais de floresta associados à uma matriz campestre na Serra do Cipó. Essas ilhas florestais, conhecidas como capões de mata, são um laboratório natural para estudos de metacomunidades (Coelho *et al.* 2017b). Questionamos a existência de sazonalidade na comunidade, e se métricas da paisagem influenciam nessa dinâmica temporal das espécies. Com dados de dois anos de coleta, mostramos que a substituição de espécies no tempo (turnover) aumenta com a distância da mata contínua, provável fonte de espécimes para os capões. Na escala estudada, nenhuma das outras métricas de paisagem utilizadas como variável explicativa teve influência na riqueza, abundância ou composição de espécies. Além disso, encontramos um efeito da sazonalidade na riqueza de espécies, e uma interação entre a cobertura do sub-bosque e a abundância de espécies nas diferentes estações. Pretendemos submeter o artigo para o periódico Biotropica.

Para o terceiro e último capítulo, definimos ao longo da Cadeia do Espinhaço doze localidades para coleta. Em cada localidade, selecionamos duas áreas de coleta em diferentes elevações: uma na base (em torno de 1100m de altitude) e outra nas proximidades do topo da montanha (variando entre 1400 e 2000m). O objetivo foi entender os padrões de distribuição de vespas e abelhas ao longo do gradiente latitudinal e altitudinal da Cadeia do Espinhaço e como as variáveis climáticas exercem influência nas diferentes escalas de diversidade das vespas e abelhas (Aculeata). Padrões gerais emergiram, com a altitude se mostrando mais importante do que a latitude em determinar as diversidades α e γ. A diversidade β não é determinada pela latitude nem pela altitude, apesar do turnover de espécies ser influenciado positivamente pela distância geográfica.

Apresentamos a seguir os três capítulos, escritos em inglês e atendendo à formatação exigida para cada periódico científico no qual o artigo foi publicado ou pretendido para submissão. Ainda incluímos como anexo a capa do primeiro capítulo já publicado (Anexo I) e mais dois produtos indiretos da tese. O Anexo II é um artigo publicado no volume especial de campo rupestre na revista FLORA, abordando o cenário atual de ameaças por intervenções humanas nos capões de mata da Serra do Cipó. O Anexo III é um texto em português publicado em uma revista de divulgação (MG BIOTA) sobre o mesmo ambiente.

Ainda, é válido salientar que outros produtos virão diretamente dos esforços de coleta realizados e da descrição taxonômica de espécies novas descobertas durante a tese. No laboratório, temos uma dissertação de mestrado e parte de uma tese de tese de doutorado em andamento utilizando os dados coletados por este projeto.

Então, boa leitura!

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Capítulo 1

Compositional changes in bee and wasp communities along Neotropical mountain altitudinal gradient

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Compositional changes in bee and wasp communities along Neotropical mountain altitudinal gradient

Short title: Bee and wasp diversity in a Neotropical mountain

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Abstract:

Climate conditions tend to differ along an altitudinal gradient, resulting in some species groups, patterns of lower species richness with increasing altitude. While this pattern is well understood for tropical mountains, studies investigating possible determinants of variation in beta-diversity at different altitudes are scarce. We sampled bee and wasp communities (Hymenoptera: Aculeata) along an altitudinal gradient (1,000 – 2,000 m.a.s.l.) in a tropical mountainous region of Brazil. Trap nests and Moericke traps were established at six sampling points, with 200 m difference in altitude between each point. We obtained average climate data (1970-2000) from Worldclim v2 for altitudes at each sampling site. Nest traps captured 17 bee and wasp species from six families, and Moericke traps captured 124 morphospecies from 13 families. We found a negative correlation between altitude and species richness and abundance. Temperature, precipitation, water vapor pressure, and wind speed influenced species richness and abundance, and were correlated with altitude. β-diversity was primarily determined by species turnover as opposed to nestedness, and Aculeate community similarity was higher for more similar altitudinal ranges. Moericke traps seem to be more efficient for altitudinal surveys compared to nest traps. We found high occurrence of singleton and doubleton species at all altitudes, highlighting the need for long-term studies to efficiently assess hymenopteran diversity in these environments.

Introduction

Beta-diversity (β) is a property of complex biological communities [1,2], and is inherently connected to large-scale measurements of species richness (i.e., gamma-diversity) through the species–area relationship found for nearly all organisms investigated thus far [3,4]. However, less attention has been paid to patterns of β-diversity [5–7], and the relative importance of environmental and geographic variables for beta diversity remains controversial. Although the importance of β-diversity to gamma-diversity has been investigated for several taxa and environments [5,8,9], it is much less understood than, for example, gradients in species richness or within-habitat diversity (i.e., alpha-diversity). Studies of tropical invertebrate β-diversity mostly emphasize habitat differences that influence species richness [10], and often fail to detect spatial effects at smaller spatial scales [11,12].

Beta-diversity can be decomposed into turnover (species replacement between sites) and nestedness (species loss or gain between sites) components [13]. Distinction between components is particularly important in threatened environments such as mountainous regions [14], where evaluation of the mechanisms involved in each may improve our descriptions of species spatial distributions [15]. Beta-diversity varies by altitude, and should be highest in heterogeneous habitats (e.g., tropical mountains) due to higher numbers of coexisting habitat specialists [16]. Studies of diversity patterns in tropical mountains mostly show a decline in plant and invertebrate species richness with increasing altitude [14,17–22]. This pattern may arise as a response to changes in weather conditions, such as wind speed, light intensity, humidity, and specially temperature [22]. Other factors such as reduction in habitat area, resource diversity, and primary productivity may also result in lower diversity at higher elevations [23–28]. Species richness does not always decline linearly with increasing altitude, as some studies indicate a hump-shaped pattern with peaks in diversity at intermediate altitudes (e.g., as caused by the mid-domain effect) (see [29] for more examples). Species richness may also increase with altitude, which has been documented for free-feeding herbivores in mesic habitats in Brazil [30,31] and parasitoid wasps (Hymenoptera: Ichneumonidae) in the Costa Rican low mountain ranges [32].

Bees and wasps are excellent model organisms for investigating how environmental variation along an altitudinal gradient influences insect beta-diversity. First, climatic variables and weather conditions are particularly important for insects [33,34], especially because thermoregulation capability is determined by ambient temperature [35,36]. Furthermore, bee and wasp diversity is strongly correlated with the availability of food and nesting resources [33,37,38], which are usually more scarce at high elevations (i.e., mountaintops) [38–41]. Bee and wasp diversity thus should decrease with increasing altitude (e.g., Hoiss et al. 2012). There are a few studies on hymenopteran distributions in old mountaintop ecosystems in Brazil, called '*campos rupestres*' and '*campos de altitude*' [14,31,43]. Among these studies the Aculeata clade is particularly well described (Hymenoptera: Apocrita) (see [44,45]for phylogeny) (e.g., [20,46–50]).

In this study we investigated bee and wasp species composition and richness along a tropical mountain altitudinal gradient. We specifically tested: 1. whether species richness decreases with increasing altitude along the gradient; 2. whether species composition changes with increasing altitude; and 3. whether the observed β-diversity patterns are primarily due to species turnover or nestedness.

Materials and Methods

Study sites

The study was developed in *Reserva Particular do Patrimônio Natural Santuário do Caraça* (hereafter the "Caraça Mountains") in Minas Gerais, Brazil (20°05'54" S, 43°29'17" W). The study area lies at the southern limit of the Espinhaço mountain range, which is the largest and one of the most important mountain formations (i.e., in terms of biodiversity) in Brazil. The Espinhaço range is large and extends almost continuously from northeastern to southeastern Brazil (over 1,200 km) [51], although altitudinal variation is milder than in other mountain ranges such as the Andes. The Espinhaço range has unique characteristics and geographically divides three of the main Brazilian biomes - *Cerrado*, Atlantic forest, and *Caatinga* – which together host a diverse array of endemic plant and animal species [52,53]. The Caraça Mountains host a protected area composed of heterogeneous habitat with different phytophysiognomies [54]. This area contains the highest peaks and has the greatest variation in altitude across the Espinhaço range (between 850 and 2,072 m.a.s.l.), where *campos rupestres* define a significant portion of the vegetation structure [55]. *Campos rupestres* are rocky mountaintop, neotropical, azonal vegetation complexes [56]. This region contains old, climate-buffered, and infertile landscapes (OCBILs), with probably the most ancient open vegetation in eastern South America [53].

Sampling Design

We collected Aculeate wasps and bees in the Caraça Mountains at six sampling plots with different elevations, with altitudes between 1,000 and 2,000 m.a.s.l. There was a 200 m difference in altitude between plots (Fig 1). We arranged packs containing twenty trap nests, consisting of 25 x 25 x 130 mm wood pieces with a central hole (11 cm depth) and diameters of 6, 9 and 12 mm (Fig 2a). Nine packs were placed at each plot with a distance of 50 m between packs, totaling 180 trap nests per sampling plot. Trap nests were inspected every two weeks for 12 months (17,820 trap-days). Traps colonized by Aculeata species were collected and replaced, then taken to the laboratory for monitoring until adult emergence. We also set nine Moericke traps at each plot (yellow, 25 cm diam. container filled with salty liquid, N=54) (Fig 2b), which were placed directly on the ground with a distance of 50 m between traps. Moericke traps were placed in the field during trap nest monitoring, where they remained for 48 hours per sampling period. There was a minimum of 15 days between sampling, which over 12 months resulted in 18 sampling events (46,656 trap-hours).

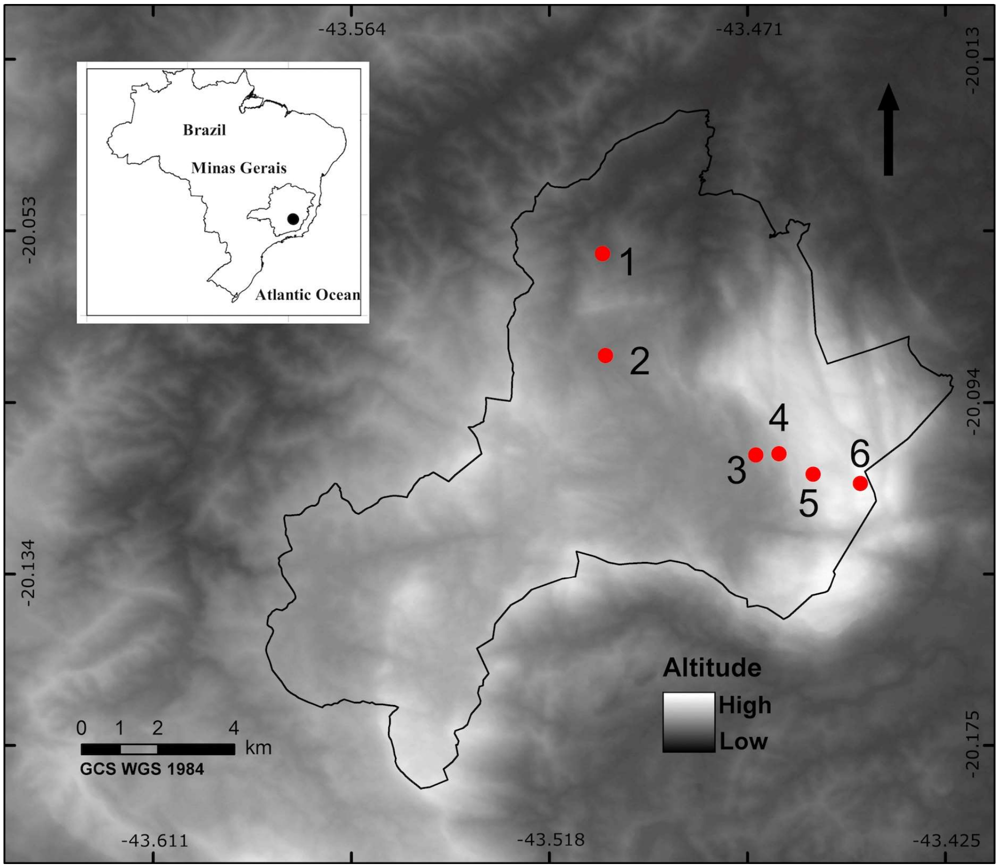

Fig 1. Location and distribution of sampling plots at RPPN *Santuário do Caraça*, Minas Gerais, Brazil. Numbers represent the six sampling plots. Plot altitude was as follows: 1=1,000; 2=1,200; 3=1,400; 4=1,600; 5=1,800; 6=2,000 m.a.s.l.

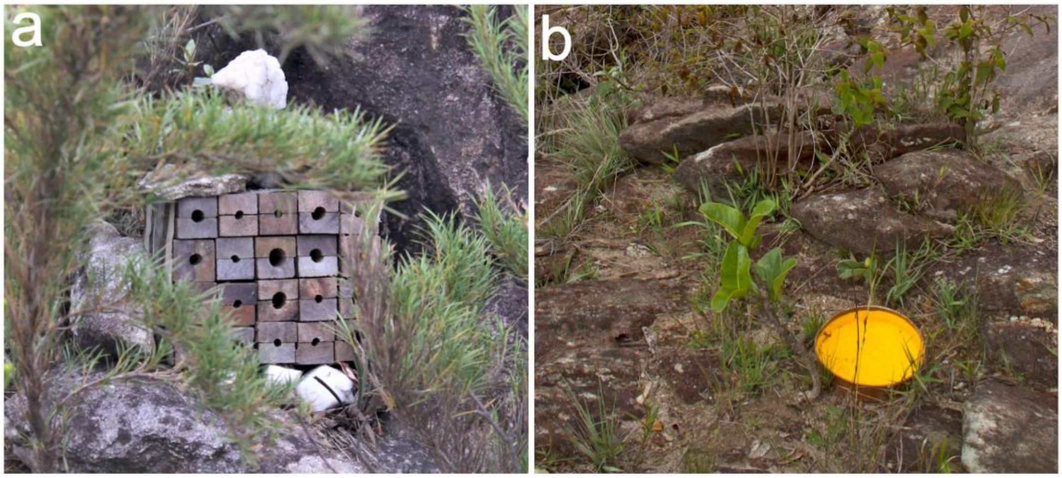

Fig 2. Trap nests (a) and Moericke traps (b). Nine trap nest packs containing twenty nests each, and nine Moericke traps were placed at each sampling plot.

All captured individuals belonging to Aculeate hymenopteran families were used in the study, with the exception of Formicidae (because our methodology was inappropriate for sampling these species) and Bethylidae (due to identification issues). Bees and wasps were identified to the lowest taxonomic level possible, based on Fernández & Sharkey keys [57] and also consulted specialists. Specimens were deposited in the *Coleção Entomológica da Universidade Federal de Minas Gerais* (CEUFMG) in Belo Horizonte, Minas Gerais, Brazil.

We obtained mean annual temperature (°C), precipitation (mm), solar radiation (kJ m^{-2} day^{-1}), wind speed (m s^{-1}) and water vapor pressure (kPa) at each site using Wordclim version 2 (1970-2000). We then tested for effects of these environmental variables on species richness and composition at each altitude.

Statistical analysis

Generalized linear models (GLMs) were used to determine the influence of altitude on Aculeata species richness and abundance. The residuals from the GLMs were assessed to determine the appropriateness of the error distribution [58] using the ‘rdiagnostic’ procedure in the RT4Bio package, and negative binomial regression models were used. We first ran correlation analyses to explore relationships between altitude and explanatory variables from Worldclim v2, and explanatory variables with high correlation values - Pearson's correlation coefficient (r) greater than 0.7 - were grouped into single variables for further analyses (S1 Fig) (see [59,60]). Non-correlated variables were included in GLM, and model simplification methods were used to identify relative importance. Sampling efficiency was analyzed using total species accumulation curves. A non-parametric estimator (Jackknife 1) was used to estimate total species richness for all sampling events at all altitudes.

We used a Mantel test to evaluate the distance decay of similarity (see Nekola and White 1999) among sample plot altitudes. We analyzed association patterns between distance matrices [61] using Jaccard dissimilarities for Aculeata species composition, and Euclidean distance matrices for altitudinal distance with 10,000 permutations.

To test the relative contributions of the two components of beta-diversity (species turnover and nestedness) across altitudes, we decomposed total β-diversity (represented by Sorensen dissimilarities: $\beta_{\text{SØR}}$) for multiple sites [13,62,63]. This approach allows us to calculate the relative contribution of each component - species replacement (Simpson dissimilarity: β_{SIM}) and nestedness ($\beta_{\text{SØR}} - \beta_{\text{SIM}} = \beta_{\text{SNE}}$) to total β-diversity [13] (in percentage).

We used R v.3.3.1 [64] to perform all statistical analyses. We used the 'Psych' package to calculate the correlation coefficient among WorldClim variables. Mantel tests and calculations of Euclidean distances between altitude pairs were carried out using 'vegan' and 'ecodist' packages, and the 'betapart v.1.3' package was used to partition beta diversity into turnover and nestedness components (see [65]).

Results

Community analyses

We collected 1,306 specimens distributed among 137 morphospecies and 14 families (S1 Table). The species accumulation curve did not reach an asymptote (Fig 3). According to the Jackknife 1 estimator, sampling adequacy was 69.92% (observed richness: 137; estimated richness: 195.94). We found a high number of rare species, with 58 singletons (42.34% of the total) and 17 doubletons (12.41% of the total).

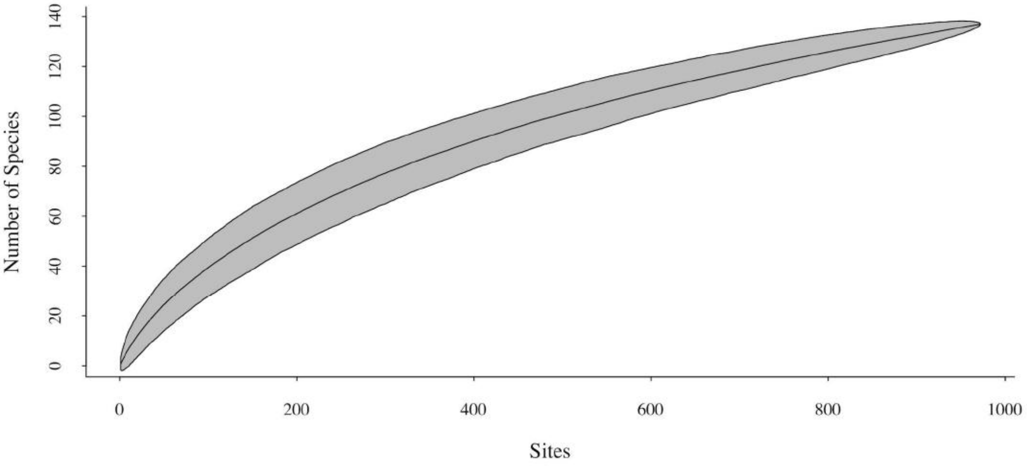

Fig 3. Species accumulation curve for Aculeate wasps and bees. Analyses using Jackknife 1 estimates. Specimens were collected at the RPPN Santuário do Caraça, Minas Gerais, Brazil.

Moericke traps captured 124 morphospecies belonging to 13 families. In 63 occupied trap nests (5.5% of the total), we captured 17 wasp and bee species belonging to six families (Table 1). Only four species - *Caenochrysis* sp.1 (Chrysididae), *Trypoxylon* sp.1, *Trypoxylon* sp.7 (Crabronidae), and *Penepodium* sp. (Sphecidae) – were captured using both collection methods. The Eumeninae *Stenonartonia mimica* (Kohl 1907) (Vespidae) was captured in a trap nest located at 1,000 m.a.s.l., representing the first such observation for the state of Minas Gerais as well as the northernmost latitude described for this species (20°03'31.8" S - 43°30'19.7" W) [66].

Table 1. List of Aculeata morphospecies found occupying trap nests at different altitudes in the Caraça Mountains, Brazil.

Morphospecies	Number of occupied nests	Emergence (Total)	Altitudes					
			1	2	3	4	5	6
VESPOIDEA								
Vespidae								
Eumeninae								
Monobia angulosa	9	30		30				
Ancistroceroides sp.	1	2			2			
Stenonartonia mimica	1	2	2					
APOIDEA								
Sphecidae **Sphecinae**								
Penepodium sp.	2	3			3			
Crabronidae **Crabroninae**								
Trypoxylon lactitarse	5	10		10				
Trypoxylon sp. 1	7	20		7		8	5	
Trypoxylon sp. 7	7	14	13	1				
Apidae **Apinae**								
*Centris (Heterocentris)*sp.	1	3	3					
Centris (Hemisiella) tarsata	14	53		45	8			
Mesocheira bicolor	1	5		5				
Tetrapedia sp.	1	1		1				
Megachilidae **Megachilinae**								
Megachile (Dactylomegachile) sp.	1	1				1		
Megachile (Austromegachile) sp.	4	13	13					
Megachile (Moureapis) sp.	1	6	6					
Megachile (M.) anthidioides	5	20		18	2			
CHRYSIDOIDEA								
Chrysididae **Chrysidinae**								

Caenochrysis sp.	2	3	1	2				
Ipsiura sp.	1	2	2					

Numbers represent the six sampling plots. Plot altitude was as follows: 1=1,000; 2=1,200; 3=1,400; 4=1,600; 5=1,800; 6=2,000 m.a.s.l.

All WorldClim variables were correlated with altitude except for solar radiation (S1 Fig), which had little importance in the GLM after model reduction. Therefore, altitude was used as the main explanatory variable for further analyses.

Influence of altitude on species richness and abundance

Aculeate hymenopteran richness and abundance were negatively correlated with altitude regardless of trap method used (P <0.001 for all tests) (Fig 4). At higher altitudes, fewer trap nests were occupied (four nests at 1,600 m, two at 1,800 m and none at 2,000 m; Fig 4a, Fig 4b and Table 1). The same pattern was found for Moericke traps (Fig 4c, Fig 4d).

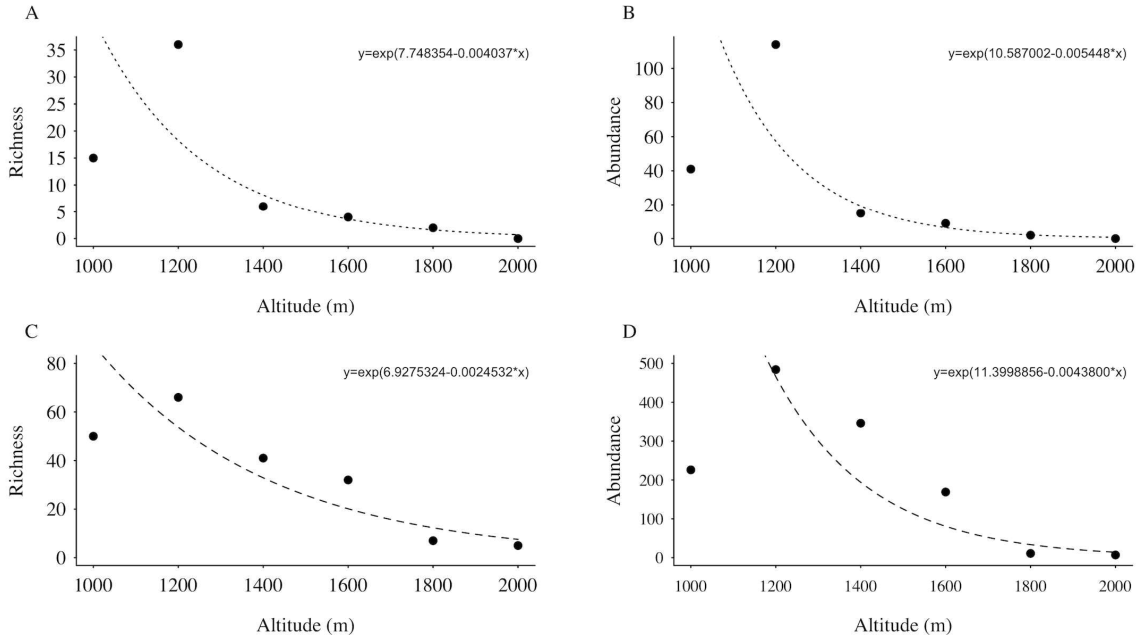

Fig 4. Relation of species richness and abundance with altitude. Species richness (a) and

abundance (b) in trap nests, and species richness (c) and abundance (d) in Moericke traps along an altitudinal gradient in the Caraça Mountains, Minas Gerais, Brazil.

Analysis of β-diversity patterns revealed a significant positive correlation between Aculeata pairwise community dissimilarity (β_{SOR}) and the Euclidean distance of altitude among sites (Mantel r = 0.85, $P < 0.01$, Fig 5). β-diversity partitioning showed that effects were mainly due to species turnover, which accounted for 81% of total variation (compared to 19% for nestedness). The only species collected at all altitudes was *Trypoxylon* sp. 3 (Crabronidae).

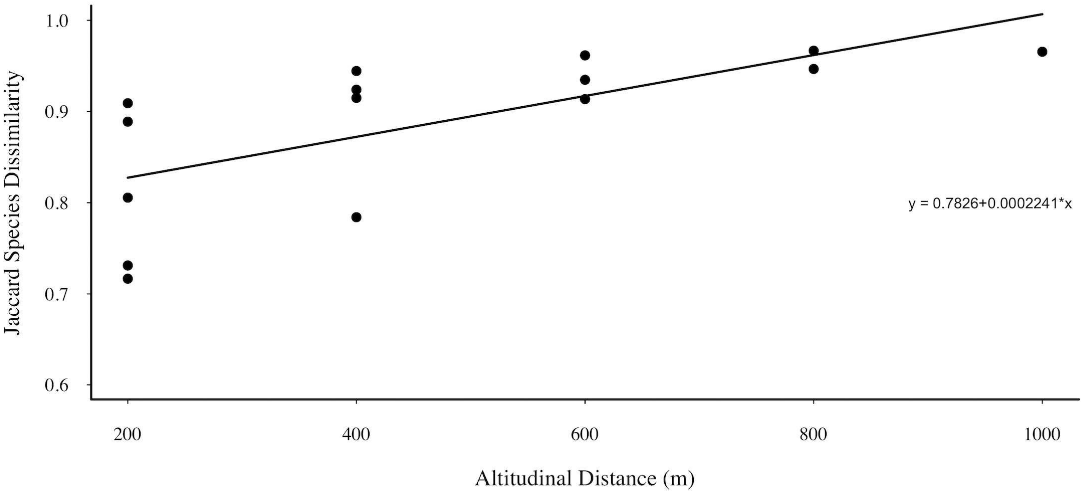

Fig 5. Relation of dissimilarity community composition with altitude. Schematic showing increasing Jaccard dissimilarity in Aculeate wasp and bee community composition with geographical altitudinal range (Mantel r = 0.85, $P < 0.01$).

Discussion

As expected, bee and wasp richness and abundance in the Caraça Mountains decreased with increasing altitude, and the causal factors behind this explanation were correlated with altitude. Further, changes in species composition (i.e., β-diversity) occurred along the altitudinal gradient and increased with altitude range. β-diversity was primarily determined by species turnover as opposed to nestedness.

Similar negative correlations between diversity and altitude were found for other insect groups (see [17]), but the possible mechanisms that produce such patterns have been less explored. Hodkinson [67] indicated that along an elevational gradient, insect species experience significant differences in environmental conditions, and interactions with other organisms may also differ. However, Hodkinson claims that the mechanisms acting on altitudinal variation in species richness are still poorly understood. Possible mechanisms promoting these patterns have been considered in studies, including lower air humidity and temperature, and higher precipitation and wind intensity with increasing altitude [23,68]. These variables are known to reduce insect flight capability and activity [24,69]. These factors are present in mountain ecosystem, and are directly correlated with altitude especially temperature that is considered the main predictor of species richness in elevational biodiversity gradients [22]. Species richness and abundance were lower at 1,000 m than at 1,200 m. This may be explained by the fact that the lower altitude plot (1,000 m) had denser vegetation with greater numbers of trees. Areas with abundant and diverse tree communities typically have higher availability of natural cavities [70,71], and this may decrease occupancy rates for trap nests [72,73]. Some studies also show that yellow Moericke traps work better in open habitats, because traps must be visible in order to capture high numbers of insects [74,75].

Few studies have evaluated the influence of altitudinal gradients on hymenopterans in Brazilian montane ecosystems (including *campos rupestres*). Our results generally agree with those of Santos and Brandão [76] in their investigation of solitary Vespidae along an altitudinal gradient at the *Parque Estadual da Serra do Mar* (São Paulo State, Brazil). Martins et al. [77] argue that some stingless bee species (Apidae) cannot persist at high altitudes, mainly due to strong winds and intense cold. Azevedo et al. [48] did a survey in Espinhaço mountain range and collected nearly 360 bee species, but emphasized the lack of information for accurate determination of their geographical distributions.

Wasp and bee communities showed significant distance decay of community similarity across the altitudinal range, with β-diversity among communities increasing with increasing distance along the altitudinal gradient. This suggests environmental filtering and dispersion limitations between low elevations and mountaintops. Geographical distance is well known to influence community dissimilarity [34,78–80], however, investigations of these effects across altitudinal distances are less common. Some examples include studies of birds [16], tropical trees [81], insect pollinators [82], and ants [83], and all of these studies showed a significant, but not always strong, relationship between species composition and altitude.

Although it was not possible to identify an altitudinal threshold that separates lowland species from those of higher elevations (as found in Silveira and Cure [46]), species composition did change with altitude. Variation in β-diversity among altitudes was primarily due to species turnover, which has also been found for other insect groups [14,15,83,84]. Our results suggest that variables which change with altitudinal gradients may serve as environmental filters [27], contributing to species turnover and thus, β-diversity [14].

We did not find any exclusive species in trap nests in higher altitudes, a result also found by Morris et al. [21] wherein numbers of insects nesting in pre-existing cavities decreased with elevation. Conversely, using Moericke traps, we found two species restricted to higher altitudes (above 1,800 m.a.s.l.): *Polybia bifasciata* Saussure, 1854 (Vespidae) and *Ceratina (Crewella)* sp.3 (Apidae). Studies indicate that the species at higher elevations typically have greater altitudinal ranges and smaller geographic distributions [42]. Moericke traps generate more reliable Aculeata species distribution data, and performed better than did trap nests. Trap nests were found to be relatively unsuitable for altitudinal surveys, mainly due to the small capture rates for Aculeata species. However, they were sufficient for production of data on species behavior and natural histories.

Species richness and abundance in colonized nests was high compared to other studies in highland regions (see [85,86]). In addition to abiotic conditions, food and nesting resource availability determines the occurrence of some species [37,87]. Soil characteristics may also be important to nesting success [38,88], because at higher altitudes, soils become more shallow [41] and compact [77], and clay and silt present become increasingly rare. These high altitude soils may hinder nest construction for Aculeata species, which utilize these types of raw material for nest construction (especially exposed nests built by wasps) [89]. Interestingly, though artificial cavities were offered in the form of trap-nests, cavity colonization was not effective. This suggests that the cavities themselves are not the only nest-limiting resource.

Environmental variables caused β-diversity to change along the mountain elevation gradient, and species turnover is influenced by high rate of singletons and doubletons. This pattern is commonly seen in tropical arthropod studies [90,91,80], even those yielding abundant specimens. Bee fauna of the *campos rupestres* in the Espinhaço Mountain Range show low abundance and high numbers of rare species [48]. This pattern has also been found in other high mountain grasslands [17]. Most surveys are carried out as part of the licensing processes for large developments, such as mining, and are thus extremely short-term. Our results highlight the need for long-term studies in order to fully assess hymenopteran diversity, specifically in mountainous areas. Our results also indicate that conservation of Aculeata diversity in tropical mountain systems such as *campos rupestres* will strongly depend on preservation of environmental heterogeneity across altitudinal strata.

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Supporting Information

S1 Table. Aculeata species occurrences and distributions along an altitudinal gradient in the Caraça Mountains, Minas Gerais, Brazil.

TÁXON	Capture method	Altitudes (m)						TOTAL
		1000	1200	1400	1600	1800	2000	
VESPOIDEA								
Vespidae								
Polistinae								
Polistes subsericeus Saussure, 1854	Moericke trap		4					4
Mischocyttarus drewseni (Saussure, 1857)	Moericke trap			1				1
Agelaia multipicta (Haliday, 1836)	Moericke trap	13	4					17
Agelaia myrmecophila (Ducke, 1905)	Moericke trap		6					6
Agelaia vicina (Saussure, 1854)	Moericke trap		23					23
Brachygastra cf. *fistulosa*	Moericke trap				1			1
Polybia bifasciata Saussure, 1854	Moericke trap					1		1
Polybia chrysothorax (Lichtenstein, 1796)	Moericke trap		1					1
Polybia dimidiata (Olivier, 1791)	Moericke trap		1					1
Polybia fastidiosuscula Saussure, 1854 Morph. *Buyssoni*	Moericke trap		4	1				5
Polybia fastidiosuscula Saussure, 1854 Morph. *fastidiosuscula*	Moericke trap			1			1	2
Polybia flavifrons Smith, 1857	Moericke trap			4		1		5
Polybia ignobilis (Haliday, 1836)	Moericke trap		1					1
Protopolybia sedula (Saussure, 1854)	Moericke trap		3					3
Eumeninae								
Ancistroceroides sp.	Trap nest			1				1
Stenodynerus sp.	Moericke trap		1					1
Monobia angulosa Saussure, 1852	Trap nest		9					9
Stenonartonia mimica (Kohl, 1907)	Trap nest	1						1
Omicron spegazzinii (Brèthes, 1905)	Moericke trap		1					1
Omicron tuberculatum (Fox, 1899)	Moericke trap		1	1				2
Scoliidae								
Scoliinae								
Campsomeris sp.1	Moericke trap		1					1
*Campsomeris*sp.2	Moericke trap			1				1

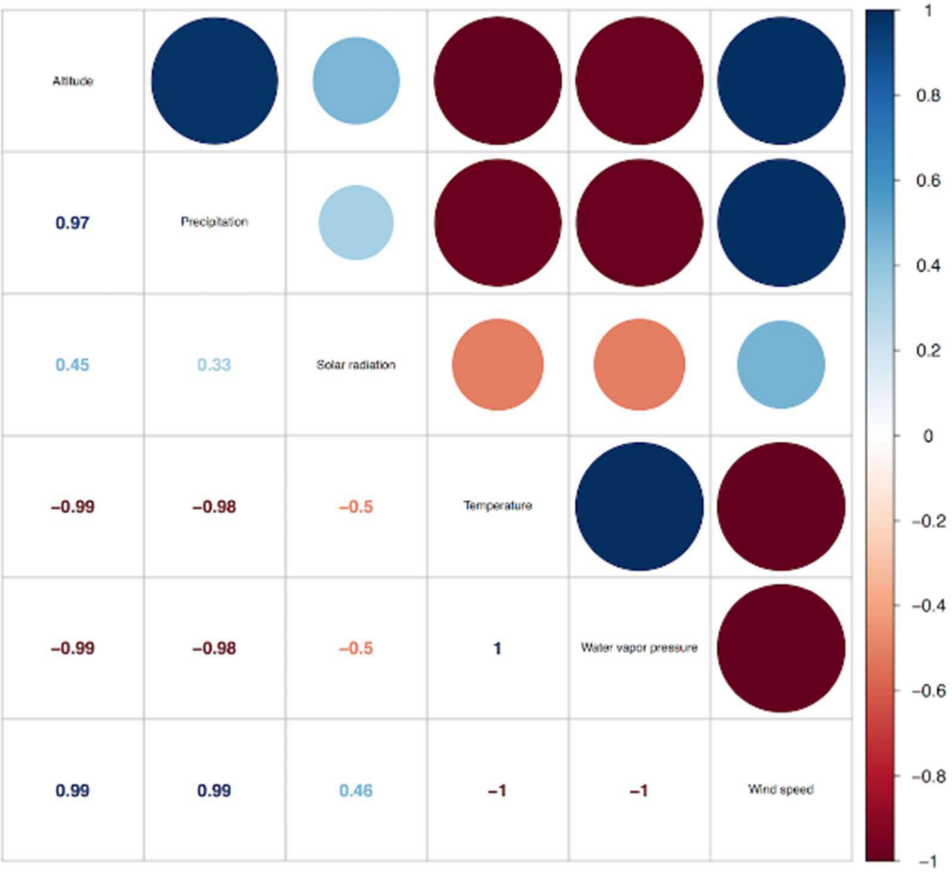
TÁXON	Capture method	Altitudes (m)						TOTAL
		1000	1200	1400	1600	1800	2000	
Pompilidae								
Pompilinae								
Agenioideus sp.	Moericke trap			1				1
*Allochares*cf. sp.	Moericke trap			1				1
Anoplius sp.1	Moericke trap	15	2					17
Anoplius sp.2	Moericke trap	1						1
Anoplius sp.3	Moericke trap		1		2			3
Aplochares sp.	Moericke trap			1				1
Aporinellus sp.	Moericke trap	3						3
Paracyphononyx sp.	Moericke trap		1					1
Poecilopompilus sp.	Moericke trap		1					1
Aporus sp.	Moericke trap				3			3
Psorthaspis sp.1	Moericke trap	4						4
Psorthaspis sp.2	Moericke trap		4	2	2			8
Ceropalinae								
Irenangelus sp.	Moericke trap	1						1
Ceropales cf. sp.	Moericke trap		1					1
Cnetocerinae								
Epipompilus cf. sp.1	Moericke trap	1	1	1				3
Epipompilus cf. sp.2	Moericke trap	2	1					3
Pepsinae								
Pepsinae sp.1	Moericke trap	1						1
Pepsinae sp.2	Moericke trap	1	1					2
Pepsinae sp.3	Moericke trap	6						6
Pepsinae sp.4	Moericke trap	3						3
Pepsinae sp.5	Moericke trap	1						1
Pepsinae sp.6	Moericke trap	1						1
Pepsinae sp.7	Moericke trap	4	1					5
Pepsinae sp.8	Moericke trap	2						2
Pepsinae sp.9	Moericke trap	1						1
Pepsinae sp.10	Moericke trap	4	1					5
Pepsinae sp.11	Moericke trap	9	3					12
Pepsinae sp.12	Moericke trap	6	6					12

TÁXON	Capture method	Altitudes (m)						TOTAL
		1000	1200	1400	1600	1800	2000	
Pepsinae sp.13	Moericke trap	1	2					3
Pepsinae sp.14	Moericke trap	1	3					4
Pepsinae sp.15	Moericke trap	4						4
Pepsinae sp.16	Moericke trap	2			3			5
Pepsinae sp.17	Moericke trap	1						1
Mutilidae								
Mutilinae								
Ephuta sp.	Moericke trap	2						2
Timulla sp.1	Moericke trap		1		1			2
Timulla sp.2	Moericke trap				1			1
Sphaerophtalminae								
Sphaeropthalmina sp.	Moericke trap	1						1
Pseudomethocina sp.1	Moericke trap	4			1			5
Pseudomethocina sp.2	Moericke trap	1						1
Xystromutilla cf. sp.	Moericke trap	1						1
Tiphiidae								
Tiphiidae sp.1	Moericke trap		1					1
Tiphiidae sp.2	Moericke trap		5		1			6
Tiphiidae sp.3	Moericke trap	5	15		2			22
Tiphiidae sp.4	Moericke trap		5	5	11			21
Tiphiidae sp.5	Moericke trap		1					1
Tiphiidae sp.6	Moericke trap	4						4
Tiphiidae sp.7	Moericke trap	1						1
APOIDEA								
Sphecidae								
Sphecinae								
Penepodium sp.	Moericke trap/Trap nest			1/2				1/2
Podium cf. sp.	Moericke trap			2				2
Ammophila sp.	Moericke trap		1					1
Ampulicidae								
Ampulicinae								
Dolichurus sp.	Moericke trap		25	15	37			77
Paradolichurus sp.	Moericke trap		2					2

TÁXON	Capture method	Altitudes (m)						TOTAL
		1000	1200	1400	1600	1800	2000	
Crabronidae								
Crabroninae								
Larra sp.1	Moericke trap		1	1				2
Larra sp.2	Moericke trap		1					1
Liris sp.1	Moericke trap	26	63	128	17			234
Liris sp.2	Moericke trap	3	25	7				35
*Tachysphex*sp.1	Moericke trap		25	17	28			70
*Tachysphex*sp.2	Moericke trap		3	3	2			8
*Tachysphex*sp.3	Moericke trap		1					1
Trypoxylon lactitarse Saussure, 1867	Trap nest		5					5
Trypoxylon sp.1	Moericke trap/Trap nest	1/0	3/2	39/0	23/3	5/2		71/7
Trypoxylon sp.2	Moericke trap	1						1
Trypoxylon sp.3	Moericke trap	9	2	5	2	1	1	20
Trypoxylon sp.4	Moericke trap		4	1	1			6
Trypoxylon sp.5	Moericke trap		1	3				4
Trypoxylon sp.6	Moericke trap	4						4
Trypoxylon sp.7	Moericke trap/Trap nest	1/6	0/1					8
Pison (pison) sp.1	Moericke trap		3	5	4			12
Pison (pison) sp.2	Moericke trap		2					2
*Nitela*sp	Moericke trap		6	1				7
Bembicinae								
Nyssonini sp.1	Moericke trap		1					1
Nyssonini sp.2	Moericke trap				1			1
Nyssonini sp.3	Moericke trap		1					1
Nyssonini sp.4	Moericke trap		2		4			6
Apidae								
Apinae								
Apis mellifera (Linnaeus, 1758)	Moericke trap		8	5	4	1		18
*Centris (Hemisiella) tarsata*Smith, 1874	Trap nest		12	2				14
Centris (Heterocentris) sp.	Trap nest	1						1
Mesocheira bicolor (Fabricius, 1804)	Trap nest		1					1
Trigona guianae Cockerell, 1910	Moericke trap	11	1					12
Trigona spinipes (Fabricius, 1793)	Moericke trap	50	180	32	4		1	267

TÁXON	Capture method	Altitudes (m)						TOTAL
		1000	1200	1400	1600	1800	2000	
Geotrigona sp.	Moericke trap		2	47	2			51
Melipona (Eomelipona) bicolor Lepeletier, 1836	Moericke trap	3	1					4
Melipona (melipona) quadrifasciata Moure 1992	Moericke trap	1						1
Paratrigona subnuda Moure, 1947	Moericke trap			1				1
Partamona ailyae Camargo, 1980	Moericke trap			1				1
Partamona cf. *combinata* Pedro & Camargo, 2003	Moericke trap	3						3
Partamona cf. *nigrilabris* Pedro & Camargo, 2003	Moericke trap	1						1
Partamona sp.	Moericke trap	1		1				2
Paratetrapedia (Xanthopedia) sp.	Moericke trap			1				1
Xylocopinae								
Tetrapedia sp	Trap nest		1					1
Ceratina (Ceratinula) sp.	Moericke trap		1				1	2
Ceratina (Crewella) sp.1	Moericke trap				1			1
Ceratina (Crewella) sp.2	Moericke trap				1			1
Ceratina (Crewella) sp.3	Moericke trap					1		1
Ceratina (Crewella) sp.4	Moericke trap				1	1		2
Andrenidae								
Panurginae								
*Anthrenoides*sp.1	Moericke trap		1	3	2			6
Anthrenoides sp.2	Moericke trap			1	1			2
Anthrenoides sp.3	Moericke trap			1	1			2
Anthrenoides sp.4	Moericke trap			1				1
Halictidae								
Halictinae								
Dialictus sp.1	Moericke trap			1	2			3
Dialictus sp.2	Moericke trap		2				3	5
Dialictus sp.3	Moericke trap				3			3
Dialictus sp.4	Moericke trap		5	1				6
Augochlora (*Augochloras.str.*) sp.1	Moericke trap		1					1
Augochloropsis sp.1	Moericke trap		1	1				2
Augochloropsis sp.2	Moericke trap			1				1
Augochloropsis sp.3	Moericke trap		1					1
Megachilidae								

TÁXON	Capture method	Altitudes (m)						TOTAL
		1000	1200	1400	1600	1800	2000	
Megachilinae								
Megachile (Austromegachile) sp.	Trap nest	4						4
Megachile (Dactylomegachile) sp.	Trap nest				1			1
Megachile (Moureapis) anthidioides Radoszkowski, 1874	Trap nest		4	1				5
Megachile (Moureapis) sp.	Trap nest	1						1
Colletidae								
Paracolletinae								
Niltonia sp.	Moericke trap	1						1
CHRYSIDOIDEA								
Chrysididae								
Chrysidinae								
Caenochrysis sp.1	Moericke trap/Trap nest	1/1	0/1					1/2
Caenochrysis sp.2	Moericke trap	2						2
Ipsiura sp.	Trap nest	1						1



S1 Fig. Pearson's correlation coefficient (*r*) between altitude and WorldClim v2 variables (1970-2000). A *r* value greater than 0.7 were the parameter to consider correlated variables. Mean values of temperature (°C), precipitation (mm), solar radiation (kJ m^{-2} day^{-1}), wind speed (m s^{-1}) and water vapor pressure (kPa).

Capítulo 2

Patterns of diversity in a metacommunity of wasps and bees of relictual mountainous forest fragments

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Patterns of diversity in a metacommunity of wasps and bees of relictual mountainous forest fragments

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ABSTRACT:

Naturally fragmented landscapes provide a very suitable opportunity to understand species dynamics under the influence of habitat fragmentation. In this context, different theoretical approaches have being used to explain patterns of species distribution and composition using landscape variables (e.g., patch size and connectivity). In this paper, we used a natural forest archipelago immersed in *campo rupestre* matrices to explore seasonal and spatial patterns of bee and wasp species (Hymenoptera: Aculeata). We evaluated the influence of environmental and landscape factors to explain richness, abundance and temporal turnover among species of wasps and bees. We found that most species are rarely sampled (singletons: 37.01%; doubletons: 13.61%) and that only three species were sampled in all forest islands. Richness and abundance of wasps and bees are higher in the summer season. We also found that there is an elevated temporal turnover among seasons (88%) with low nestedness between seasons (i.e., winter fauna is not a subset of summer species). Regarding the relationship between landscape metrics (e.g. patch size, level of isolation, distance between patches and continuous forest distance) and Aculeata diversity in natural forest fragments, only temporal turnover increases with distance from continuous forest. High species turnover can be correlated with geographic distance. Forest islands can be considered transient environments for many species. Therefore, this naturally fragmented metacommunity depends on continuous forest and its temporal dynamics is driven by the dispersion of insects among forest islands.

Key words: Spatio-temporal patterns; Nebular Forests; community structure; Landscape structure; Fragmentation; *campo rupestre*; Brazil.

RESUMO:

Os sistemas naturalmente fragmentados proporcionam uma ótima oportunidade para entender a dinâmica das espécies que são afetadas pela fragmentação do habitat. Neste contexto, diferentes abordagens teóricas têm sido utilizadas para explicar as distribuições de espécies e seus padrões de composição utilizando diferentes variáveis que caracterizam a paisagem (p. ex., tamanho do fragmento e conectividade). Neste artigo, utilizamos um arquipélago florestal natural (capões de mata) imerso em uma matriz de campo rupestre para explorar os padrões sazonais e espaciais das espécies de abelhas e vespas (Hymenoptera: Aculeata). Avaliamos a influência de fatores ambientais e de paisagem para explicar a riqueza, a abundância e a substituição de espécies ao longo do tempo (*temporal turnover*). Descobrimos que a maioria das espécies são raramente amostradas (*singletons*: 37.01 %, *doubletons*: 13.61 %). Apenas três espécies foram amostradas em todos os capões. A riqueza e abundância de vespas e abelhas foram maiores no verão. Também observamos que existe um elevado *turnover* temporal entre as estações (88%), com um baixo aninhamento entre as estações (ou seja, a fauna encontrada no inverno não é um subconjunto das espécies enconntradas no verão). Dentre as relações entre as métricas de paisagem (tais como tamanho do fragmento, nível de isolamento, distância entre os fragmentos e entre a floresta contínua) e a diversidade de Aculeata em fragmentos de florestas naturais, apenas o *turnover* temporal aumentou significativamente em relação à distância da floresta contínua. O alto *turnover* de espécies pode estar relacionado com a distância geográfica. As ilhas florestais são ambientes transitórios para muitas espécies. Portanto, essa metacomunidade naturalmente fragmentada depende da floresta continua, com sua dinâmica temporal explicada pela dispersão dos insetos entre as ilhas florestais.

Palavras-chave: padrões espaço-temporais; florestas nebulares; estrutura de comunidades; estrutura de paisagem; fragmentação; campo rupestre; Brasil.

AMONG THE SEVERAL THEORETICAL APPROACHES THAT HAVE BEEN PROPOSED TO STUDY SPATIAL EFFECTS OF HABITAT FRAGMENTATION (Harrison & Bruna 1999, Haddad *et al.* 2017), Island Biogeography Theory (MacArthur & Wilson 1967) is widely used to understand biodiversity dynamics of terrestrial fragmented habitats (Shaffer 1990, Mendenhall *et al.* 2014, Patiño *et al.* 2017). Within this scope, species-area relationship (Simberloff 1976), isolation and distance from natural remnants (Jacquemyn *et al.* 2003), proportions of different land use classes (Diaz-Forero *et al.* 2011, Saturni *et al.* 2016) and other hypotheses (Tscharntke *et al.* 2012) have drawn attention for explaining patterns of species distribution and composition in habitat archipelagos.

More recently, an additional approach to explaining diversity in fragments came from the Habitat Amount Hypothesis (Fahrig 2013), which suggests predictors that can replace the sole use of patch size and patch isolation metrics. Many studies show a positive relationship among fragmentation variables (e.g., patch size, connectivity and habitat amount) in their influence on various arthropod groups (e.g., Öckinger *et al.* 2012, Steffan-Dewenter & Tscharntke 2002, Watling & Donnelly 2006, Inclán *et al.* 2014), but there is no consensus for all invertebrate groups, such as galling insects (Julião *et al.* 2004), spiders (Nogueira & Pinto-da-Rocha 2016) and beetles (Vieira *et al.* 2008). This lack of a consistent relationship between species diversity and fragmentation variables can be attributed to the inexistence of a barrier between vegetation types or the presence of dispersal events and persistence capacity, mechanisms that could be linked to metacommunity structure (Leibold *et al.* 2004, Thompson *et al.* 2017). Metacommunity theory brought a spatial perspective to these issues (Biswas & Wagner 2012) that, coupled with the extensive literature on habitat fragmentation and processes like environmental filtering, species interactions and dispersal (Åström & Bengtsson 2011, Biswas & Wagner 2012), can be used to explain diversity patterns. Different metacommunity perspectives (patch dynamics, species-sorting, mass-effect and neutral paradigms) are useful theoretical frameworks to explain processes happening from local to regional scales (Leibold *et al.* 2004).

In this context, landscapes that are naturally fragmented are exceptionally valuable for analyzing the potential impacts of habitat fragmentation on community structure (Julião *et al.* 2004, Driscoll 2005). Although anthropically-fragmented areas are widely studied (e.g., Cook *et al.* 2002, Banks-leite *et al.* 2012, Rossetti *et al.* 2017) there have been few investigations involving natural forest fragments embedded in open matrices, particularly for certain animal groups such as arthropods (Pereira *et al.* 2017, Coelho, Neves, *et al.* 2017). Some examples with invertebrates have been performed in the Pantanal wetland system (Boff *et al.* 2013, Vieira *et al.* 2008, Corrêa *et al.* 2006, Cuissi *et al.* 2015, Julião *et al.* 2004) and in ancient forest patches in South Africa (Yekwayo *et al.* 2016a, b). Probably due to differing approaches (i.e., considering species-area, isolation or edge effect relationships in natural fragmented landscapes), no common pattern can be seen to emerge from these studies, with effects varying among the different environments, scales and taxonomic groups studied. However, environmental and habitat factors explain a relevant portion of species variation in plant patch formations in a matrix of natural grasslands (Das *et al.* 2017). Thus, there is a lack of studies on metacommunities located in naturally fragmented scenarios, especially using varied spatial structure and isolation with different taxonomic groups in tropical systems.

Seasonal variability is common in tropical forests, especially with regard to species composition (Tylianakis *et al.* 2005), which is affected by resources availability (Inclán *et al.* 2014). Furthermore, variation in plant density can be indicative of habitat complexity, and insect activity should have a positive relationship with closed habitats (Rincón *et al.* 1999, Corrêa *et al.* 2006, Oliver *et al.* 2016). Another important aspect to consider is how total diversity in a given region (i.e., γ-diversity), is partitioned between at least two components – α-diversity (i.e., number of species at the local scale) and β-diversity (i.e., differences in species composition among sites) (Whittaker 1972, Tuomisto 2010). Likewise, β-diversity can be decomposed into species replacement (turnover) and species gain/loss (nestedness) (Baselga 2010), with this distinction being particularly important for elucidating the mechanisms underlying biodiversity patterns (Baselga 2010, Solar *et al.* 2015, Perillo *et al.* 2017).

We aim to explore the spatio-temporal patterns of the wasp and bee fauna in relictual forest fragments (hereafter Atlantic Forest islands, or simply forest islands), or to be more specific, in natural forest fragments surrounded by *campo rupestre* in a mountain complex in eastern South America (Coelho *et al.* 2016). Based on several studies highlighting that environmental factors and spatial structure of the landscape (e.g., Jacquemyn *et al.* 2003, Tscharntke *et al.* 2012, Fahrig 2013), in addition to season (Tylianakis *et al.* 2005, Soares *et al.* 2013, Pereira *et al.* 2017), determine community patterns, we expect that (1) the season of the year (i.e., wasp and bee diversity will be higher in the summer) and environmental variables (such as canopy cover and understory density) positively influence species diversity, and that (2) landscape metrics (e.g., patch size, level of isolation, distance between patches and distance to continuous forest) affect species diversity with higher temporal turnover in small-sized and more isolated patches. We also aim to determine if winter fauna are subsets of summer communities.

METHODS

STUDY SITES. – We used a natural forest archipelago situated in the *Serra do Cipó* Mountains in the southern region of the Espinhaço mountain range - an important mountainous formation in Brazil with regard to biodiversity and species endemism (Giulietti *et al.* 1997, Silveira *et al.* 2016) (Table S1; Fig. S1). This mountainous range acts as a humidity barrier, dividing two Brazilian domains – *Cerrado* (Brazilian savanna) and Atlantic Forest, which together host a diverse array of threatened and endemic plant and animal species (Giulietti *et al.* 1997, Silveira *et al.* 2016). Forest island archipelagos found in the southern Espinhaço are more associated with the Atlantic Forest domain (Coelho, Carlos, *et al.* 2017), which is located nearby on the east side of the mountain range. Between these two domains biomes, predominantly associated with the Espinhaço mountaintops (beyond 900 m asl), we highlight *campo rupestre*, a grassland mosaic associated with vegetation on rocky outcrops. As Neotropical azonal vegetation complexes (Alves *et al.* 2014), *campo rupestre* form the matrix landscape and are classified as old, climate-buffered, and infertile landscapes (OCBILs) (Hopper *et al.* 2015, Silveira *et al.* 2016).

Mostly immersed in *campo rupestre* matrices, the *Capões de Mata* are natural patches of vegetation emerging on mountaintops (occurring above 1,200 m asl) with a floristic composition related to Seasonal Semideciduous Forests – a common Atlantic Forest formation in southeast Brazil (Coelho *et al.* 2016). These relictual forests have an edaphoclimatic formation, being highly dependent on climate and a specific type of soil for their development (Coelho, Neves, *et al.* 2017, Coelho, Carlos, *et al.* 2017, Coelho *et al.* 2016). Physical characteristics of the soil, such as drainage, are more relevant than their chemical characteristics, such as nutrient inputs, for the establishment and development of this plant formation. Forest islands of the Espinhaço range have a direct relationship with humidity, whereas they are located at high altitudes with significant orographic effects, producing high rates of relative humidity and nearly constant rainfall (Coelho *et al.* 2016), conditions found in other similar environments (Barbosa *et al.* 2010).

To reinforce the lack of water restriction in this environment, we verified the average temperature and humidity using a weather station installed at 1400 m asl, near our study site (Onset HOBO® U30 datalogger; Long-Term Ecological Research Program Project – *PELD Campos Rupestres da Serra do Cipó*; unpublished data). In summer (mean values of months December, January and February), the mean temperature was 19.22°C and mean humidity

88.62 percent while in winter (June, July and August mean values) the values were 14.68°C and 92.58 percent, respectively. The environment is always humid at high altitudes in the Espinhaço range due to the nebular condensation of humid air (Coelho *et al.* 2016), but temperature varies seasonally, with a mean difference of 4.54°C between summer (variance = 7.66°C) and winter (variance = 7.35°C) seasons.

SAMPLING DESIGN. – We selected 14 forest islands considering preservation status and dimensions, and excluded islands strongly impacted by fire or anthropic uses (Fig. 1; Table S1; Fig. S1). The chosen *Capões de Mata* have different dimensions (size ranged from 1.21 to 39.89 ha, with a mean area of 8.21 ha) and geometric shapes, and vary in the distances between them. In the center region of each forest patch, we established a 20 x 50 m plot. Samplings were carried out over two years with two sampling events in the summer (January-February) and two in the winter (August-September).

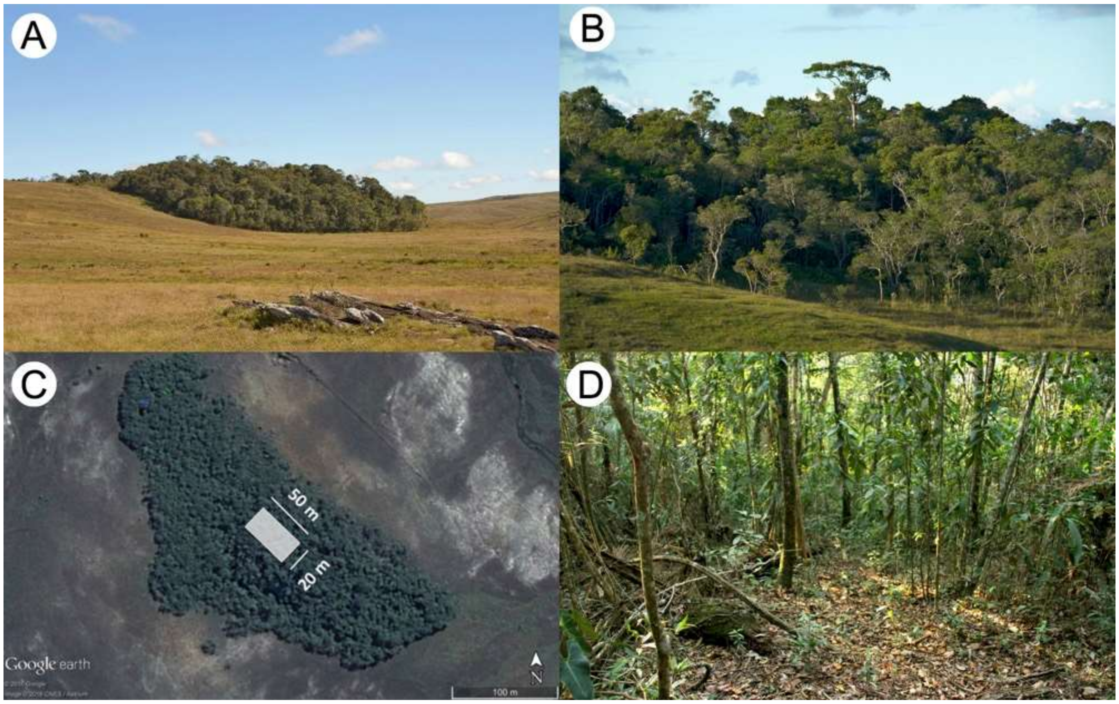

FIGURE 1. External (A-C) and internal (D) views of *Capões de Mata* in a *campo rupestre* matrix at Serra do Cipó. Minas Gerais, Brazil. (C) Schematic view of a 20 x 50 m plot

created in each Atlantic forest island.

In each sampling period we used a range of sampling methodologies in order to maximize representativeness of species diversity. In each Atlantic Forest island we installed: (1) two Malaise traps – one soil Malaise trap and one canopy Malaise Window trap; (2) ten pitfall traps (five on the ground and five attached to tree trunks); and (3) four Moericke traps (Pan traps - yellow, 25-cm diameter container filled with salty liquid). All these methodologies are used for hymenoptera surveys, such as bees and wasps (Darling & Packer 1988, Aguiar & Santos 2010). Moericke and pitfall traps remained in the field for 48 hours (Moericke: 10,752 trap-hours; Pitfall: 26,880 trap-hours), while the Malaise traps remained in the field for seven days (9,408 trap-hours each type).

All captured individuals belonging to hymenopteran families of Aculeata were considered, with the exception of Formicidae. Bees and wasps were identified to the lowest taxonomic level possible based on Fernández & Sharkey (2006) and Silveira *et al.* (2002). We were also aided by specialists in each group to confirm identifications whenever possible.

VEGETATION STRUCTURE. – As local habitat attributes, we determined the structure of vegetation in each Atlantic Forest island using digital images of the of the density shrub and herbaceous vegetation (understory) and the relative contribution of trunks and branches to canopy structure. To calculate canopy structure, we took four photos per site during each sampling using a digital camera with an 8 mm fisheye lens (see Nassar *et al.* 2008 for further details). To estimate the density of understory vegetation, we used a 100 x 100 cm white screen as a backdrop (Zehm *et al.* 2003) and took 16 photos in each site per sampling. The vegetal cover was determined from the proportion of white and black pixels in the photographs (Zehm *et al.* 2003). The canopy photos were analyzed using Gap Light Analyzer software v.2 (Frazer *et al.* 1999) and understory photos were processed using the software R package *EBImage* function (Oles *et al.* 2012, R Core Team 2017). In both cases, mean cover and density values were obtained for each sampling per forest island (for more details, see Pereira *et al.* 2017).

LANDSCAPE VARIABLES. – Individual study landscapes were defined using concentric circular sectors with a 500 m radius (78.5 ha), chosen to encompass each one of the 14 forest islands. This designated area was chosen to encompass the common foraging activities of bees, wasps and hymenopteran parasitoids species, whereas the majority of them have significant decline of species richness and abundance around 300 m distance from original location (Osborne *et al.* 1999, Zurbuchen *et al.* 2010). We also used this scale in order minimize spatial autocorrelation. Although there is high heterogeneity among *campo rupestre* herbaceous phytophysiognomies, we only classified land as "forest" and "grassland" habitats, with all landscapes partially covered by forest being classified as "forest" and all other land use classes being classified as "grasslands". The classes were mapped for each landscape using high-resolution multispectral images (RapidEye satellites, ~5 m resolution) with the package *randomForest* v4.6-12 in the software R (R Core Team 2017), which implements the ensemble learning method proposed by Breiman (2001). To construct the classification model we used all five Rapideye spectral bands plus NDVI and red edge NDVI. The landscape metrics were analyzed in the software Fragstats v4.2.1 (McGarigal *et al.* 2012), using a fixed edge depth of 20 m and no sampling strategy. The metrics were calculated for the 500-m circular sector of each forest island. We selected ten class variables (Table 1) that, in addition to other five metrics (Table 2), were used as explanatory variables. Of these five metrics, patch size, distance to continuum forest and closest forest island distance were calculated manually using Google Earth Pro tools and canopy cover and understory density were calculated as previously described. We ran correlation analyses (*psych* R package) testing all 15 explanatory variables, with those exhibiting high correlation values (Pearson correlation coefficient ≥ 0.7) being excluded sequentially (Fig. S2).

STATISTICAL ANALYSIS. – We used the software R v.3.4.0 (R Core Team 2017) to perform all statistical analyses. First, sampling efficiency was analyzed using total species accumulation curves with non-parametric estimators (Jackknife 1 and Chao). To determine the influence of season and patch variables (canopy cover and understory density) on Aculeata species richness and abundance, the identity of each forest fragment (14) was included as a random factor in a Generalized Linear Mixed Model (GLMM) to account for temporal pseudoreplication (Bolker *et al.* 2009), using Poisson error distribution. Each model (richness and abundance of Aculeata) was fitted with five fixed effect explanatory variables named season, canopy cover, understory density, season/canopy cover interaction and season/understory density interaction. We used the *lme4* package and *glmer* function. Negative binomial regression models were used and all explanatory variables were tested together. Non-significant ($P > 0.05$) variables and interactions were removed in order to simplify the model until the minimal adequate model was obtained. All models were subjected to residual analyses to check for model fit and error structure suitability (Crawley 2013).

TABLE 1. Fragstats Class Level variables considered for describing the Atlantic Forest island archipelago. Landscape classification was performed in concentric circular sectors with a 500m radius around each of the 14 forest islands. Brief description adapted from McGarigal (McGarigal 2015).

Metric Pattern Group	**Metrics**	**Acronym**	**Units**	**Brief description**
Area and Edge	Total Class Area	CA	Hectares	Measure of landscape composition; specifically, how much of the landscape is comprised of a particular patch type.
	Percentage of Landscape	PLAND	%	Quantifies the proportional abundance of each patch type in the landscape.
	Largest Patch Index	LPI	%	Quantifies the percentage of total landscape area comprised by the largest patch. As such, it is a simple measure of dominance.
	Total Edge	TE	Meters	An absolute measure of total edge length of a particular patch type.
Shape	Area-weighted mean Shape Index Distribution	SHAPE_AM	None	An adjusted measure of shape complexity based on perimeter-area ratio. We used its area-weighted mean.
Core Area	Total Core Area	TCA	Hectares	The aggregation over all patches of the corresponding patch type of the representation of the area in the patch greater than the specified depth-of-edge distance from the perimeter.
	Area-weighted mean Core Area Index	CAI_AM	%	Is a relative index that quantifies core area as a percentage of patch area (i.e., the percentage of the patch that is comprised of core area). We used its area-weighted

	Distribution			mean.
Aggregation	Number of Patches	NP	None	Works in a particular patch type as a simple measure of the extent of subdivision or fragmentation of the patch type.
	Patch Density	PD	Number per 100 hectares	Expresses number of patches on a per unit area basis, facilitating comparisons among landscapes of varying size.
	Mean Euclidean Nearest Neighbor Distance Distribution	ENN_MN	Meters	Used extensively to quantify patch isolation, is defined using simple Euclidean geometry as the shortest straight-line distance between the focal patch and its nearest neighbor of the same class.

TABLE 2. Explanatory variables considered for describing landscape and vegetation structure of each forest island.

Metric	**Acronym**	**Description**
Patch size	PSI	Size of the forest island sampled in km^2
Distance of continuum forest	DCF	Distance of each forest island from continuous to the east Atlantic Forest (km)
Closest forest island distance	CFD	Distance of each forest island from nearest forest island sampled (km)
Canopy Cover	CC_MN	Average percentage canopy cover per patch
Understory Density	UD_MN	Average percentage understory density per patch

The temporal turnover of species among seasons (sampling periods) in each forest island was calculated as the percent contribution of species turnover to total β-diversity for multiple seasons (Baselga 2010, Baselga & Leprieur 2015), using *betapart v.1.3* package. We also calculated nestedness percentage contribution between seasons in each sample year to verify if winter communities are subsets of summer fauna.

To test landscape predictors, we used generalized linear models (GLMs), considering accumulated richness, abundance and temporal turnover, using all non-correlated vegetation and landscape variables as explanatory variables (Tables 1 and 2 and Fig. S2). The best distribution errors were selected for each model (Crawley 2013) using the package *RT4Bio* and we selected Quasi-poisson errors.

RESULTS

We collected 3,402 specimens distributed among 213 morphospecies and 16 Aculeata families (Table 3; Table S2). Of these, Malaise traps collected 2,878 specimens; Moericke traps 453; Malaise/Window traps 34 specimens and Pitfall traps 33 specimens (details in

Table S2). We found a high number of rarely sampled species, with 79 singletons (37.01 percent of the total) and 29 doubletons (13.61 percent of the total). Only three morphospecies were sampled in all forest islands. According to the Jackknife 1 estimator, sampling adequacy was 71.79 percent (estimated richness: 296.70), and according to the Chao estimator it was 67.32 percent (estimated richness: 316.40) (Fig. S3). Additionally, we found 87 (41 percent) morphospecies collected exclusively in summer and 39 (18 percent) in winter. Embolemidae and Andrenidae were only collected in winter and Colletidae exclusively in summer, but they are all families of low abundance.

TABLE 3. Richness and abundance for each Aculeata (Hymenoptera) family collected in summer and winter in a Brazilian forest archipelago.

Family	**Summer**		**Winter**		**Total**	
	Richness	**Abundance**	**Richness**	**Abundance**	**Richness**	**Abundance**
CHRYSIDOIDEA						
Bethylidae	19	624	17	658	22	1282
Chrysididae	4	8	2	7	4	15
Dryinidae	8	21	5	19	9	40
Embolemidae	0	0	2	9	2	9
VESPOIDEA						
Muttilidae	12	51	7	11	16	62
Pompilidae	38	407	23	221	41	628
Scoliidae	4	26	2	19	4	45
Tiphiidae	10	319	6	94	14	413
Vespidae	11	216	9	123	14	339
APOIDEA						
Andrenidae	0	0	3	4	3	4
Apidae	20	104	11	130	22	234
Colletidae	1	2	0	0	1	2
Crabronidae	30	169	23	99	35	268
Halictidae	12	26	14	27	20	53
Sphecidae	5	7	2	1	6	8
Total	**174**	**1980**	**126**	**1422**	**213**	**3402**

Wasp and bee richness and abundance exhibited seasonal influence (summer and winter), with greater richness and abundance during summer (Fig. 2 and Fig. 3; Table 4). Despite this result, winter fauna are not a subset of summer communities, with a low contribution of nestedness between seasons (nestedness summer/winter at first sample year: 0.22 percent; nestedness summer/winter at second sample year: 0.39 percent). We observed that none of the local variables measured (understory vegetation density and canopy vegetation cover) affected species richness, but Aculeata abundance was influenced negatively by understory density in the summer (Fig. 3; Table 4).

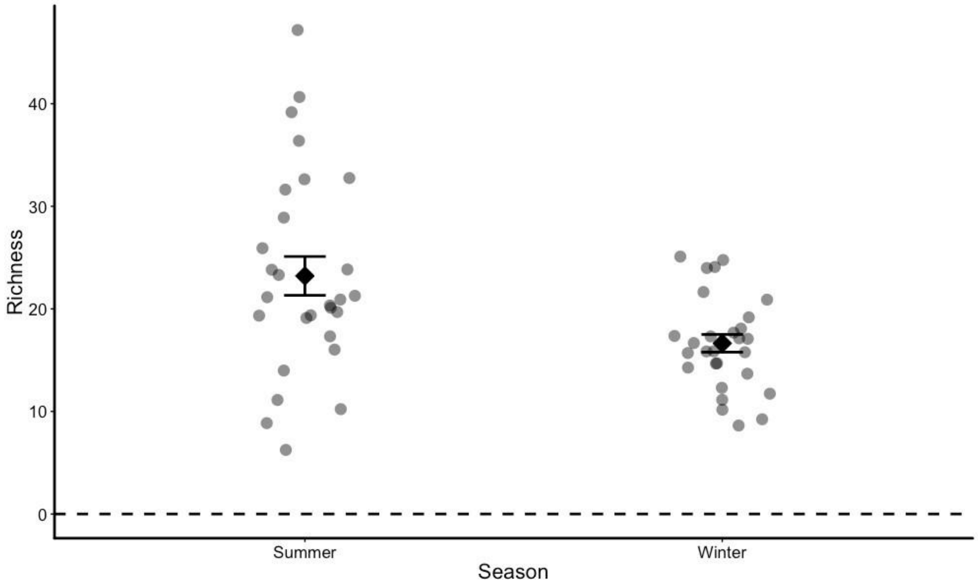

FIGURE 2. Bee and wasp species richness in summer and winter seasons in Atlantic Forest islands. Bars represent the standard deviation with the mean value (diamond).

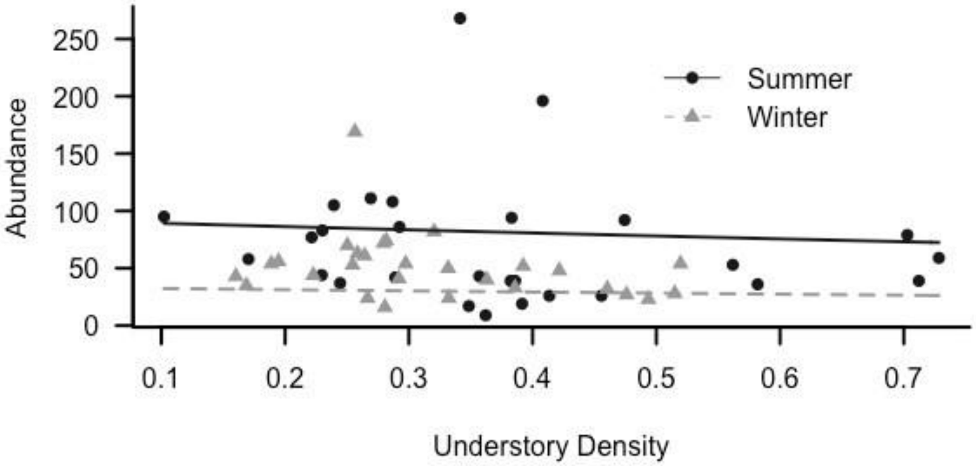

FIGURE 3. Species abundance in summer and winter seasons in Atlantic Forest islands with an understory density interaction.

TABLE 4. Results of Minimum adequate models (GLMMs), showing the effects of seasonal variables on bee and wasp species richness and abundance. Fitted to a negative binomial error distribution.

Dependent variable	**Coefficients of fixed effects**				
Richness	Parameters	Estimate	Std. Error	z-value	Pr (>|z|)
	Intercept	3.112	0.079	39.29	< 0.001
	Season	-0.322	0.076	-4.22	< 0.001
Abundance	Parameters	Estimate	Std. Error	z-value	Pr (>|z|)
	Intercept	4.5237	0.2264	19.983	< 0.001
	Season	-0.3319	0.1266	-2.621	0.009
	Understory Density	-1.0149	0.4997	-2.031	0.042

We found high temporal dissimilarity between forest islands, and species replacement (turnover) contributed relatively more to β-diversity than did nestedness for the Aculeata fauna. Between sampling periods, β-diversity represented 73 percent of total diversity, with, 88 percent of this being represented by species temporal turnover. The temporal turnover value for each forest island, used as a dependent variable, was only directly related to distance to continuous forest (Deviance = 0.15, df = 12, *P* = 0.03). Temporal turnover in forest islands increased with distance from continuous forest (DCF variable: Table 2 - Fig. 4). Besides DCF, we found no significant results (i.e., no *P*-value < 0.05) of the landscape variables (lists on Tables 1 and 2) influencing Aculeata fauna richness, abundance and temporal turnover.

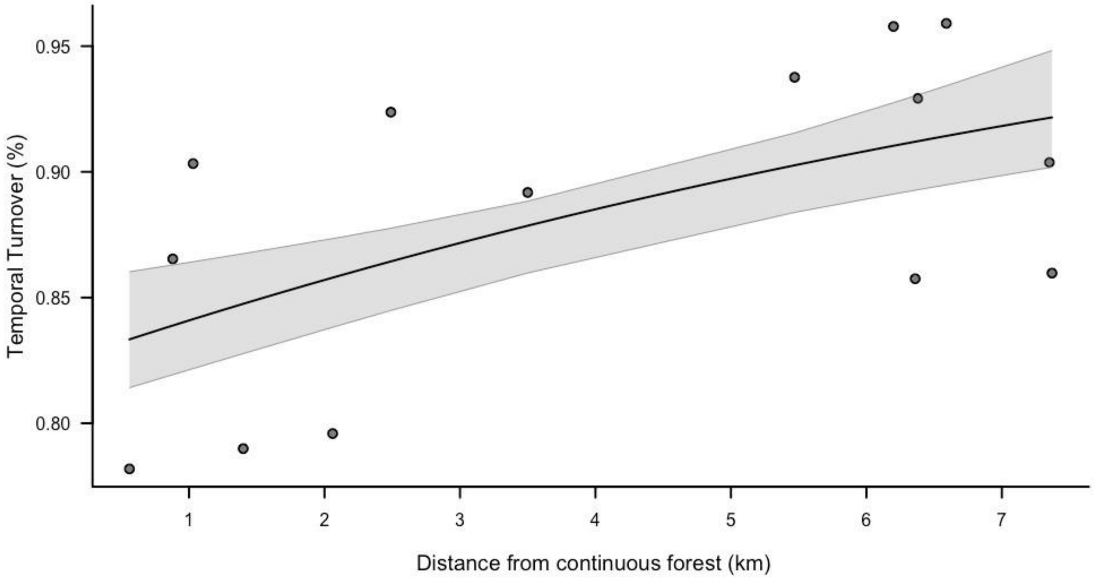

FIGURE 4. Relationship between bee and wasp species temporal turnover (%) in each Atlantic Forest island and its distance from continuous forest (km).

DISCUSSION

In general, among the environmental and landscape factors considered here, only distance to continuous forest seemed to be an important spatial factor driving species diversity of Aculeata fauna in natural forest fragments. This spatial pattern is consistent with the “patch dynamics” metacommunity paradigm (Leibold *et al.* 2004, Jamoneau *et al.* 2012), in which each patch may be occupied or unoccupied and local species diversity is limited by dispersal and species competitive ability (Leibold *et al.* 2004, Biswas & Wagner 2012). Such a pattern was observed among beetles in naturally fragmented areas, but also with species-sorting as a widely applicable metacommunity concept (Driscoll 2008). The high temporal turnover found between the studied Atlantic Forest islands has been documented in similar environments as the most important component of dissimilarity in species overtime time (Inclán *et al.* 2014, Oliver *et al.* 2016). Species turnover can also be correlated with geographic distance (Misiewicz *et al.* 2014, Perillo *et al.* 2017) and its positive relation with the distance from a continuous Atlantic Forest remnant shows its importance to species distribution dynamics, indicating a spatially explicit model (Leibold *et al.* 2004). Forest islands can be considered transient environments for many species (Vieira *et al.* 2008), where their presence can be considered a sample of the dispersers coming from the continuous forest, which can explain the existence of high rates of rare species (singletons and doubletons), despite the varied and considerable sampling effort.

Decreases in species diversity with habitat isolation and distance from forest edge are commonly related (Jacquemyn *et al.* 2003, Williams & Kremen 2007, Bailey *et al.* 2014), but not always (Lopes *et al.* 2012). The magnitude of the effects of isolation depend on resource availability (Williams & Kremen 2007), environment complexity and hostility (Tscharntke *et al.* 2002), and species dispersal or gap-crossing ability (Tischendorf & Fahrig 2000), with the amount of that habitat in the landscape also playing an important role (Fahrig 2013).

Correlations with forest proportion and landscape structure depend on which species we consider (Diaz-Forero *et al.* 2011, Banks-Leite *et al.* 2012), with each one having its own extinction threshold with a certain "loss of habitat" configuration (With & Crist 1995, Fahrig 2002). Despite of a reduced home range of most wasp and bee groups (Gathmann & Tscharntke 2002, Prezoto & Gobbi 2005), environmental factors (Osborne *et al.* 1999) and mass migrations (Vepsalainen & Savolainen 2000) can influence foraging activity in some groups. Flight distances depends on body size (Borthagaray *et al.* 2012, Carrié *et al.* 2017), with larger species foraging of greater distances (Bailey *et al.* 2014). These long foraging distances are only made by a small percentage of individuals (Zurbuchen *et al.* 2010), but still can be sufficient to guarantee low levels of genetic differentiation between distant fragments (Suni *et al.* 2014).

The high species turnover of forest islands in a wide open matrix can be associated with the presence of small habitats that contain only a proportion of the total diversity, maximizing β-diversity (Tscharntke *et al.* 2002), which allows higher regional diversity (Benedick *et al.* 2006), increasing heterogeneity and availability of resources (Cuissi *et al.* 2015) and vegetation structure (Nogueira & Pinto-da-Rocha 2016). Patch (Botzat *et al.* 2013) and matrix quality (Lion *et al.* 2016, Ås 1993) can be important, but in some cases its effects can be confounded (Haynes & Cronin 2004), showing that surrounding relationships deserve attention. The abrupt change between vegetational categories caused a near complete beetle community turnover on a very reduced scale (Spector & Ayzama 2003), but for most wasp and bee species the forest-matrix boundary is probably not an efficient barrier (Tscharntke *et al.* 2012), indicating the that matrix can also harbor an important percentage of the fauna (Cook *et al.* 2004, Driscoll 2005, Yekwayo *et al.* 2016b) and provide additional resources (Öckinger *et al.* 2012). Faria & Silveira (2011) found that the composition of the orchid bee fauna in riparian forest and *cerrado* open matrix is the same. Nevertheless, matrix core effects have multiple dimensions (see Driscoll *et al.* 2013) and more investment in insect collections in matrix grassland and continuous forest can indicate which species are specialists to a specific environment and if there exists invasions of matrix species into small habitat patches (Ås 1999, Öckinger *et al.* 2012) causing a spillover effect (González *et al.* 2016, Yekwayo *et al.* 2016b).

We found that seasonal variation in temperature could be underpinning wasp and bee activity. Likewise, there are some examples of forest islands having insect groups that respond to seasonal influence (Soares *et al.* 2013, Pereira *et al.* 2017). This pattern is explained by temporal variation in resource availability (Inclán *et al.* 2014) and changes in temperature (Oliver *et al.* 2016), and can be controlled by a competition-colonization trade-off, as indicated by the "patch dynamics" paradigm. In seasonal tropical systems, insect seasonality is determined mostly by variation in rain and humidity (Abrahamczyk *et al.* 2011, Wolda 1988), especially in dry forests (Macedo-Reis *et al.* 2016, Novais *et al.* 2016), but in some cases temperature is the main variable responsible for seasonal patterns (Silva *et al.* 2011), as verified in our study. We also found that local variables, such as canopy openness and understory density, may not have influenced species richness. Understory density was found to be negatively related to wasp and bee abundance only in summer, same as the pattern found for parasitoid hymenoptera (Dall'Oglio *et al.* 2016). Canopy variation can also negatively influence ant richness in Brazilian dry forests (Neves *et al.* 2013), but ant richness and diversity can increase in higher woody (Oliver *et al.* 2016) and herbaceous (Corrêa *et al.* 2006) plant cover. Likewise, increases in bee activity have been found in shaded microhabitats of closed forest (Rincón *et al.* 1999). This effect does not occur in winter, probably because of seasonal reduction in insect activity (Wolda 1988).

In this study, neither area, isolation, spatial connectivity nor the habitat amount hypothesis could alone explain species distribution (such as Prugh *et al.* 2008, Haddad *et al.*

2017). The species-area relationship is not a consensus, with studies recording positive (Watling & Donnelly 2006, Benedick *et al.* 2006, Öckinger *et al.* 2012, Cuissi *et al.* 2015), no (Julião *et al.* 2004, Vieira *et al.* 2008, Banks-Leite *et al.* 2012, Nogueira & Pinto-da-Rocha 2016), and even negative relationships (Lion *et al.* 2016) with species diversity indicators. Nevertheless, to better understand how these dynamics could be playing a role, we suggest that a standardized multi-taxon approach could be used to assess the species-area relationship responses of different groups (Yekwayo *et al.* 2016a). In a comparative bird density meta-analysis, patch area had a significant positive effect only with real islands, and not in habitat fragments (Brotons *et al.* 2003), showing the need of separate biogeographic theories for true islands and landscape ecosystems (Mendenhall *et al.* 2014).

Therefore, landscape variables could not explain species distribution pattern observed in the studied forest island archipelago in *campo rupestre*. Bee and wasp species distribution reflect in metacommunity processes (Leibold *et al.* 2004), and they provide a valid explanation of spatial and temporal dynamics, driven by habitat heterogeneity and environmental filters, with forest fragments connected by Aculeata dispersal among islands (Leibold *et al.* 2004, Jamoneau *et al.* 2012, Ruhí *et al.* 2017). Anthropogenic changes weaken the connectivity between patches, causing the disruption of metacommunity functioning (Jamoneau *et al.* 2012). The maintenance of forest archipelagos on a large scale, the consideration of multi-scale landscape quality (Tscharntke *et al.* 2002) and the information emerging from metacommunity dynamics (Ruhí *et al.* 2017), are the main keys to insect conservation (Samways 2007).

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DATA AVAILABILITY STATEMENT

The data used in this study are archived at the Knowledge Network for Biocomplexity (KNB) (doi:10.5063/F18G8HTR).

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SUPPLEMENTARY INFORMATION

SUPPLEMENTARY TABLES

TABLE S1. Information for the 14 Atlantic Forest island (*Capões de Mata*) chosen for the study in a *campo rupestre* matrix at *Serra do Cipó*. Minas Gerais, Brazil.

Forest island number	Patch Area (m^2)	Perimeter (m)	Distance of continuum forest (km)	Closest forest island distance (km)	Elevation (m asl)	Coordinates	
1	12,938	480	0.88	0.09	1,239	19°13'02" S	43°30'29" W
2	43,081	1,008	1.03	0.09	1,262	19°12'55" S	43°30'39" W
3	16,316	857	1.40	0.12	1,234	19°12'48" S	43°30'46" W
4	169,562	2,836	2.06	0.78	1,269	19°13'35" S	43°30'56" W
5	29,716	911	5.47	0.23	1,309	19°14'21" S	43°32'26" W
6	113,399	2,220	7.37	0.19	1,317	19°15'11" S	43°33'07" W
7	58,653	1,192	7.35	0.06	1,331	19°14'41" S	43°33'21" W
8	57,557	1,366	2.49	0.34	1,271	19°14'19" S	43°30'46" W
9	358,185	3,685	3.50	1.56	1,230	19°15'18" S	43°31'01" W
10	82,375	1,502	6.20	0.21	1,324	19°15'34" S	43°32'32" W
11	16,113	675	6.38	0.03	1,273	19°14'53" S	43°33'03" W
12	12,130	526	6.36	0.03	1,267	19°14'46" S	43°33'08" W
13	25,039	1,230	6.59	0.06	1,290	19°14'38" S	43°33'14" W
14	84,909	1,807	0.56	0.56	1,235	19°11'58" S	43°30'32" W

TABLE S2. Bee and wasp (Hymenoptera: Aculeata) morphospecies abundance, capture method and number of forest island occurrences in summer and winter seasons in Serra do Cipó. Minas Gerais, Brazil.

	Capture Method				**Summer Season**		**Winter Season**		**Total abundance**
	Malaise Window	**Malaise trap**	**Moericke trap**	**Pitfall trap**	**Islands with species occurrence**	**abundance**	**Islands with species occurrence**	**abundance**	
APOIDEA									
ANDRENIDAE									
ANDRENINAE									
Andreninae sp. 01		X			0	0	2	2	2
Andreninae sp. 02			X		0	0	1	1	1
Andreninae sp. 03			X		0	0	1	1	1
APIDAE									
APINAE									
Apinae sp. 01		X			1	1	1	1	2
Apinae sp. 02		X			1	1	0	0	1
APINI									
Apis mellifera Linnaeus, 1758	X	X	X		6	7	8	22	29
MELIPONINI									
Melipona (Melipona) quadrifasciata Lepeletier, 1836	X	X		X	5	20	13	77	97
Trigona spinipes (Fabricius, 1793)	X	X	X		7	12	3	6	18
Partamona ailyae Camargo, 1980		X			1	1	2	6	7
Trigona braueri Friese, 1900		X			3	44	2	12	56
XYLOCOPINI									
CERATININA									
Ceratina (Ceratinula) sp. 01		X			4	4	0	0	4

Ceratina (Ceratinula) sp. 02		X		1	1	1	1	2
Ceratina (Ceratinula) sp. 03		X		2	2	0	0	2
Ceratina (Ceratinula) sp. 04		X		0	0	1	1	1
Ceratina (Ceratinula) sp. 05		X		1	1	0	0	1
Ceratina (Ceratinula) sp. 06		X		1	2	0	0	2
Ceratina (Ceratinula) sp. 07		X		1	1	0	0	1
Ceratina (Ceratinula) sp. 08		X	X	1	1	1	1	2
Ceratina (Crewella) sp. 01		X		1	1	0	0	1
Ceratina (Crewella) sp. 02			X	1	1	0	0	1
EMPHORINI								
Melitoma torquata Roig-Alsina, 2009		X		1	1	0	0	1
MELIPONINI								
Scaptotrigona postica (Latreille, 1807)	X	X		0	0	2	2	2
Trigona sp. 01	X			1	1	0	0	1
Trigona sp. 02		X		1	1	1	1	2
Paratrigona lineata (Lepeletier, 1836)		X		1	1	0	0	1
COLLETIDAE								
HYLAEINAE								
Hylaeus sp.	X	X		2	2	0	0	2
HALICTIDAE								
HALICTINAE								
AUGOCHLORINI								
Neocorynura aenigma (Gribodo, 1894)		X		1	2	3	3	5
Augochloropsis sp. 01			X	0	0	1	1	1
Augochloropsis sp. 02			X	0	0	1	1	1
Augochloropsis sp. 03		X		0	0	1	1	1

Augochloropsis hebescens (Smith, 1879)	X				1	1	0	0	1
Augochlorini sp. 01		X			1	1	0	0	1
Augochlorini sp. 02		X			1	1	1	2	3
Augochlorini sp. 03		X			0	0	1	1	1
Augochlorini sp. 04		X	X		3	4	1	2	6
Augochlorini sp. 05		X			1	1	3	4	5
Augochlorini sp. 06		X			1	1	0	0	1
HALICTINI									
Dialictus sp. 01		X	X		3	3	2	6	9
Dialictus sp. 02		X			0	0	1	1	1
Dialictus sp. 03		X			1	1	0	0	1
Dialictus sp. 04		X		X	4	9	1	1	10
Dialictus sp. 05		X			0	0	1	1	1
Dialictus sp. 06		X			0	0	1	1	1
Dialictus sp. 07			X		0	0	1	1	1
Dialictus sp. 08		X			1	1	0	0	1
Halictini sp. 01		X			1	1	0	0	1
AMPULICIDAE									
AMPULICINAE									
AMPULICINI									
Ampulex sp. 01		X		X	5	5	1	1	6
Ampulex sp. 02		X			1	1	0	0	1
DOLICHURINI									
Dolichurus sp. 01		X	X		3	4	0	0	4
Dolichurus sp. 02		X			4	6	0	0	6
Dolichurus sp. 03			X		0	0	1	2	2
CRABRONIDAE									
BEMBICINAE									

ALYSSONTINI								
Didineis sp. 01		X	X	8	19	5	12	31
CRABRONINAE								
BOTHYNOSTETHINI								
Bothynostethini sp. 01		X		2	5	0	0	5
CRABRONINI								
Ectemnius sp. 01		X		2	2	3	3	5
Crabronini sp. 01		X		4	7	5	5	12
Crabronini sp. 02	X	X		4	4	7	12	16
Crabronini sp. 03	X			0	0	1	1	1
Crabronini sp. 04	X	X		1	1	2	2	3
LARRINI								
Liris sp. 01		X	X	10	34	9	20	54
Liris sp. 02			X	1	1	0	0	1
Gastroserina sp. 01			X	1	1	0	0	1
Gastroserina sp. 02		X		1	1	1	1	2
MISCOPHINI								
Miscophini sp. 01		X	X	3	6	0	0	6
Miscophini sp. 02			X	1	1	0	0	1
TRYPOXYLINI								
Trypoxylon (Trypargilum) lactitarse Saussure, 1867		X	X	1	1	1	1	2
Trypoxylini sp. 01		X	X	7	19	1	1	20
Trypoxylini sp. 02		X		4	4	1	1	5
Trypoxylini sp. 03		X		4	11	2	3	14
Trypoxylini sp. 04		X		5	6	2	2	8
Trypoxylini sp. 05		X		2	2	0	0	2
Trypoxylini sp. 06		X		2	2	1	2	4
Trypoxylini sp. 07			X	1	1	0	0	1
Trypoxylini sp. 08		X		0	0	1	1	1

Trypoxylini sp. 09	X			0	0	1	1	1
PEMPHREDONINAE								
PEMPHREDONINI								
Pemphredonini sp. 01	X	X		3	12	6	15	27
Pemphredonini sp. 02	X	X		2	2	3	3	5
Pemphredonini sp. 03	X		X	1	2	0	0	2
Pemphredonini sp. 04	X			1	1	0	0	1
SPILOMENINA								
Spilomena sp. 01	X			4	6	5	6	12
Spilomena sp. 02	X			1	3	1	1	4
Spilomena sp. 03	X			1	1	2	2	3
Spilomena sp. 04	X		X	0	0	2	3	3
PHILANTHINAE								
CERCERINI								
Eucerceris sp. 01	X			1	2	0	0	2
Eucerceris sp. 02	X			1	1	0	0	1
Eucerceris sp. 03		X		1	1	0	0	1
PHILANTHINI								
Thachypus sp. 01	X			0	0	1	1	1
SPHECIDAE								
SPHECINAE								
AMMOPHILINI								
Eremnophila sp. 01	X			1	1	0	0	1
VESPOIDEA								
MUTILLIDAE								
MUTILLINAE								
EPHUTINI								
Ephuta sp. 01	X			9	30	2	3	33
Ephuta sp. 02	X			2	7	0	0	7

Ephuta sp. 03		X			1	1	0	0	1
Ephuta sp. 04	X				0	0	1	1	1
Ephuta sp. 05		X			1	1	0	0	1
Timulla sp. 01		X			1	1	0	0	1
SPHAEROPTHALMINAE									
SPHAEROPTHALMINI									
Sphaeropthalmini sp. 01		X			1	1	0	0	1
Sphaeropthalmini sp. 02		X			2	3	1	1	4
Sphaeropthalmini sp. 03		X			0	0	1	1	1
Sphaeropthalmini sp. 04				X	1	1	0	0	1
Sphaeropthalmini sp. 05				X	1	1	0	0	1
Sphaeropthalmini sp. 06				X	0	0	1	1	1
Sphaeropthalmini sp. 07				X	1	1	0	0	1
Xystromutilla sp. 01		X			3	3	1	2	5
Xystromutilla sp. 02		X			1	1	0	0	1
Xystromutilla sp. 03		X			0	0	2	2	2
POMPILIDAE									
Pompilidae sp. 01		X			0	0	9	71	71
Pompilidae sp. 02		X	X	X	11	31	0	0	31
Pompilidae sp. 03			X		1	1	0	0	1
Pompilidae sp. 04		X	X		6	18	0	0	18
Pompilidae sp. 05			X		1	1	0	0	1
Pompilidae sp. 06		X	X		3	3	1	1	4
Pompilidae sp. 07		X	X		3	3	0	0	3
Pompilidae sp. 08		X	X		1	1	1	1	2
Pompilidae sp. 09		X	X		2	2	3	6	8
Pompilidae sp. 10		X			1	1	1	1	2
Pompilidae sp. 11		X			2	3	0	0	3
Pompilidae sp. 12		X	X		1	1	1	2	3
Pompilidae sp. 13		X	X		7	12	7	12	24

Pompilidae sp. 14		X	X		4	34	4	45	79
Pompilidae sp. 15		X			2	2	0	0	2
Pompilidae sp. 16		X	X		5	14	3	5	19
Pompilidae sp. 17			X		0	0	1	1	1
Pompilidae sp. 18		X	X	X	8	13	2	2	15
Pompilidae sp. 19		X	X		6	43	8	23	66
Pompilidae sp. 20	X	X	X		7	26	2	8	34
Pompilidae sp. 21		X			1	1	0	0	1
Pompilidae sp. 22			X		0	0	1	1	1
Pompilidae sp. 23		X	X		4	6	5	6	12
Pompilidae sp. 24		X	X		4	7	2	2	9
Pompilidae sp. 25		X	X		2	2	0	0	2
Pompilidae sp. 26		X	X		6	10	7	11	21
Pompilidae sp. 27		X			7	89	3	13	102
Pompilidae sp. 28		X	X		7	50	1	1	51
Pompilidae sp. 29		X			1	1	0	0	1
Pompilidae sp. 30		X			1	9	0	0	9
Pompilidae sp. 31		X	X		2	3	1	1	4
Pompilidae sp. 32		X	X		1	1	1	1	2
Pompilidae sp. 33		X	X		3	4	1	2	6
Pompilidae sp. 34		X	X		3	4	2	4	8
Pompilidae sp. 35		X			1	1	0	0	1
Pompilidae sp. 36		X	X		2	4	0	0	4
Pompilidae sp. 37			X		1	1	0	0	1
Pompilidae sp. 38		X			1	1	0	0	1
Pompilidae sp. 39		X			1	1	0	0	1
Pompilidae sp. 40		X	X		1	2	0	0	2
Pompilidae sp. 41		X			1	1	0	0	1
SCOLIIDAE									
SCOLIINAE									

Campsomeris sp. 01		X	X	X	6	20	5	10	30
Campsomeris sp. 02		X	X		2	4	1	9	13
Campsomeris sp. 03		X			1	1	0	0	1
Campsomeris sp. 04		X			1	1	0	0	1
TIPHIIDAE									
ANTHOBOSCINAE									
Anthoboscinae sp. 01		X			8	2	10	0	2
MYZININAE									
Pterombrus sp. 01		X			1	33	0	0	33
THYNNINAE									
ELAPHROPTERINI									
Ornepetes sp. 01	X	X			0	0	1	8	8
RHAGIGASTERINI									
Aelurus sp. 01		X	X		5	25	0	0	25
Aelurus sp. 02	X	X	X		0	12	8	0	12
Aelurus sp. 03		X			6	6	0	0	6
SCOTAENINI									
Scotaenini sp. 01	X	X	X		1	0	0	69	69
Scotaenini sp. 02		X			1	10	0	0	10
Scotaenini sp. 03		X			0	1	3	0	1
Scotaenini sp. 04		X			0	0	1	1	1
Scotaena sp. 01				X	4	0	0	1	1
TIPHIINAE									
Tiphia sp. 01	X	X	X	X	12	140	6	3	143
Tiphia sp. 02		X	X	X	5	83	0	12	95
Tiphia sp. 03		X	X		7	7	0	0	7
VESPIDAE									
EUMENINAE									
Eumeninae sp. 01	X				0	0	0	1	1
POLISTINAE									

EPIPONINI									
Agelaia multipicta (Haliday, 1836)	X	X	X		13	48	11	42	90
Agelaia myrmecophila (Ducke, 1905)		X			4	20	1	6	26
Polybia bifasciata Saussure, 1854		X			1	2	0	0	2
Polybia chrysothorax (Lichtenstein)		X			1	0	1	1	1
Polybia fastidiosuscula Saussure, 1854	X	X	X	X	2	126	1	69	195
Polybia lugubris Ducke, 1905		X			4	1	0	0	1
Polybia occidentalis (Olivier,1791)	X	X			0	5	1	1	6
Polybia sericea (Olivier, 1792)		X	X		1	6	0	0	6
Polybia sp.		X			1	1	0	0	1
MISCHOCYTTARINI									
Mischocyttarus rotundicollis (Cameron,1912)		X			2	5	0	1	6
POLISTINI									
Polistes versicolor (Olivier,1791)		X			2	1	1	0	1
Polistes lanio (Fabricius, 1775)		X		X	0	1	1	1	2
Polistes deceptor Schulz, 1905			X		0	0	1	1	1
CHRYSIDOIDEA									
BETHYLIDAE									
BETHYLINAE									
Bethylinae sp. 01		X	X		1	1	5	7	8
EPYRINAE									
Epyrinae sp. 01	X	X	X		14	92	14	99	191

Epyrinae sp. 02		X	X		9	47	4	9	56
Epyrinae sp. 03	X				0	0	1	1	1
Epyrinae sp. 04		X	X	X	3	3	2	3	6
Epyrinae sp. 05			X		0	0	1	1	1
Epyrinae sp. 06		X			1	1	0	0	1
PRISTOCERINAE									
Pristocerinae sp. 01		X			4	16	7	14	30
Pristocerinae sp. 02		X		X	4	4	3	5	9
Pristocerinae sp. 03		X			2	5	2	3	8
Pristocerinae sp. 04		X			6	6	0	0	6
Pristocerinae sp. 05	X	X	X	X	14	244	14	87	331
Pristocerinae sp. 06		X	X		13	167	14	317	484
Pristocerinae sp. 07		X			4	10	5	25	35
Pristocerinae sp. 08		X			2	2	0	0	2
Pristocerinae sp. 09		X			2	3	0	0	3
Pristocerinae sp. 10		X			2	2	0	0	2
Pristocerinae sp. 11		X			5	14	11	72	86
Pristocerinae sp. 12		X	X		3	5	5	11	16
Pristocerinae sp. 13			X		1	1	2	2	3
Pristocerinae sp. 14		X	X		1	1	1	1	2
Pristocerinae sp. 15		X			0	0	1	1	1
CHRYSIDIDAE									
AMISEGINAE									
Amisega sp. 01			X		1	1	0	0	1
CHRYSIDINAE									
Pleurochrysis sp. 01		X			1	1	3	4	5
Caenochrysis sp. 01		X	X		2	4	2	3	7
Ipsiura sp. 01		X			2	2	0	0	2
DRYINIDAE									
Dryinidae sp.		X			1	1	0	0	1

ANTEONINAE								
Deinodryinus sp. 01	X	X		0	0	2	3	3
DRYININAE								
Dryinus sp. 01	X			1	5	0	0	5
Dryinus sp. 02	X			3	3	2	2	5
Dryinus sp. 03	X	X		2	4	5	5	9
Dryinus sp. 04	X		X	3	5	0	0	5
Thaumatodryinus sp. 01	X			1	1	3	5	6
Thaumatodryinus sp. 02	X			1	1	0	0	1
GONATOPODINAE								
Neodryinus sp. 01	X	X		1	1	5	8	9
EMBOLEMIDAE								
Embolemus sp. 01	X			0	0	2	4	4
Embolemus sp. 02	X			0	0	1	1	1
TOTAL					1980		1422	3402

SUPPLEMENTARY FIGURES

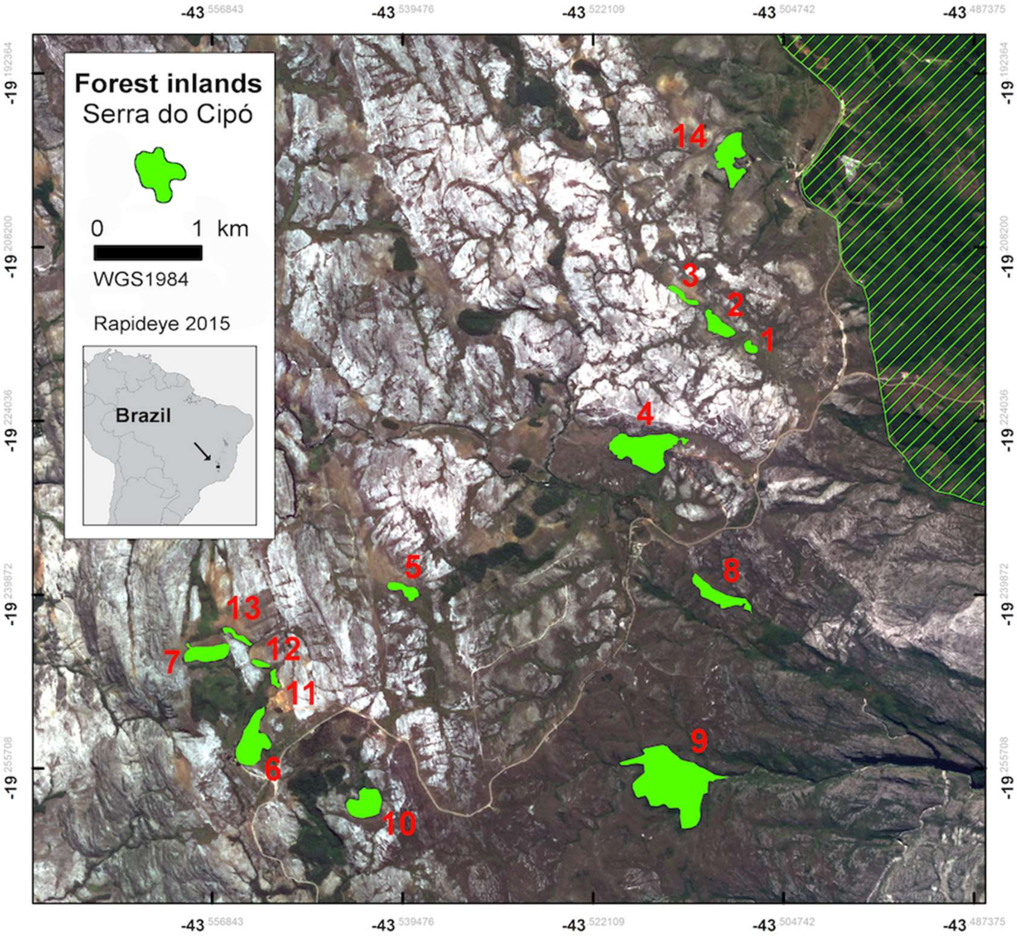


FIGURE S1. Map showing the 14 natural Atlantic Forest islands selected for sampling of Aculeata wasp and bees in a *campo rupestre* matrix at Serra do Cipó. Minas Gerais, Brazil.

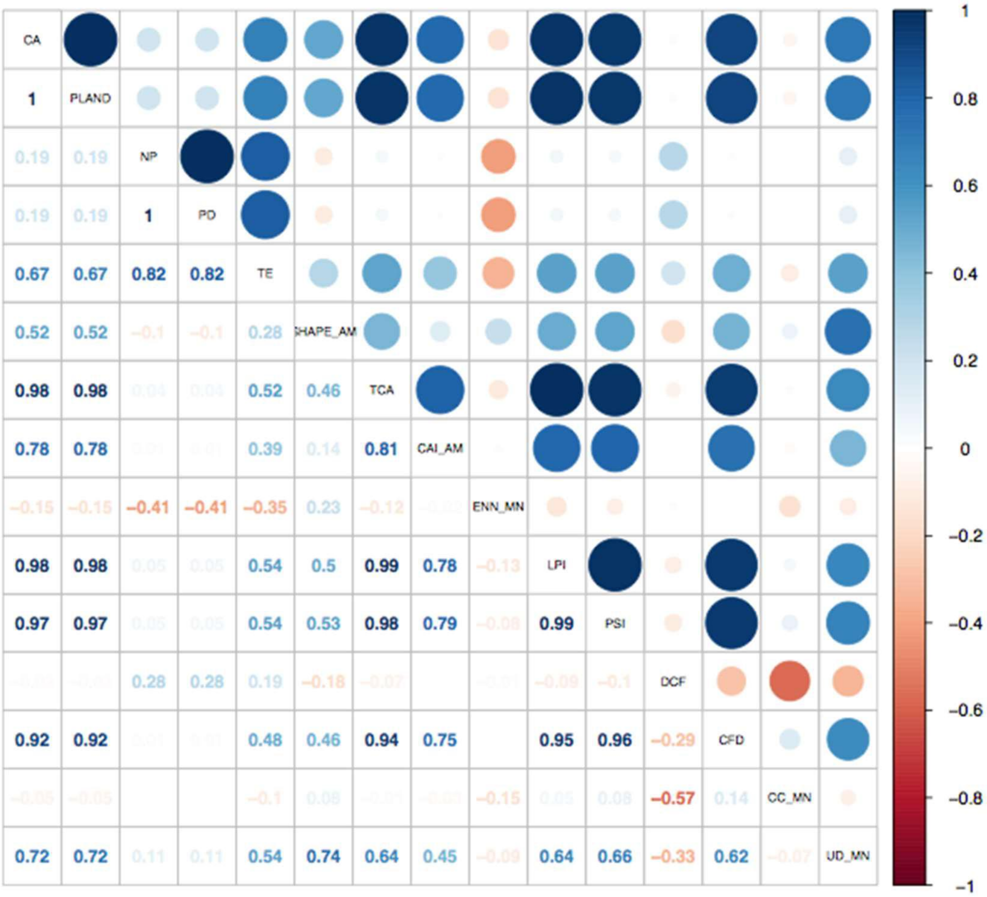


FIGURE S2. Matrix of Pearson correlations among Fragstats and other landscape and vegetation variables. Fragstats Metrics: Total Class Area (CA), Percentage of Landscape (PLAND), Largest Patch Index (LPI), Total Edge (TE), Area-weighted Mean Shape Index Distribution (SHAPE_AM), Total Core Area (TCA), Area-weighted Mean Core Area Index Distribution (CAI_AM), Number of Patches (NP), Patch Density (PD), Mean Euclidean Nearest Neighbor Distance Distribution (ENN_MN). Landscape and vegetation metrics: Patch size (PSI), Distance to Continuous Forest (DCF), Closest Forest Island Distance (CFD), Canopy Cover (CC_MN) and Understory Density (UD_MN). Red colors indicate negative correlations and blue colors indicate positive correlations while larger circles indicate higher correlation (Pearson correlation < 0.70).

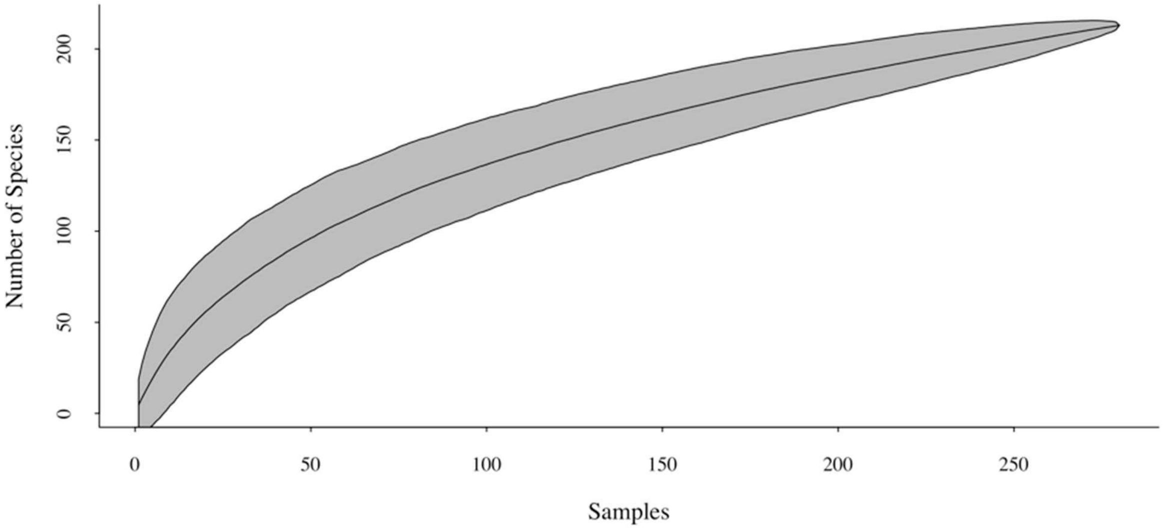
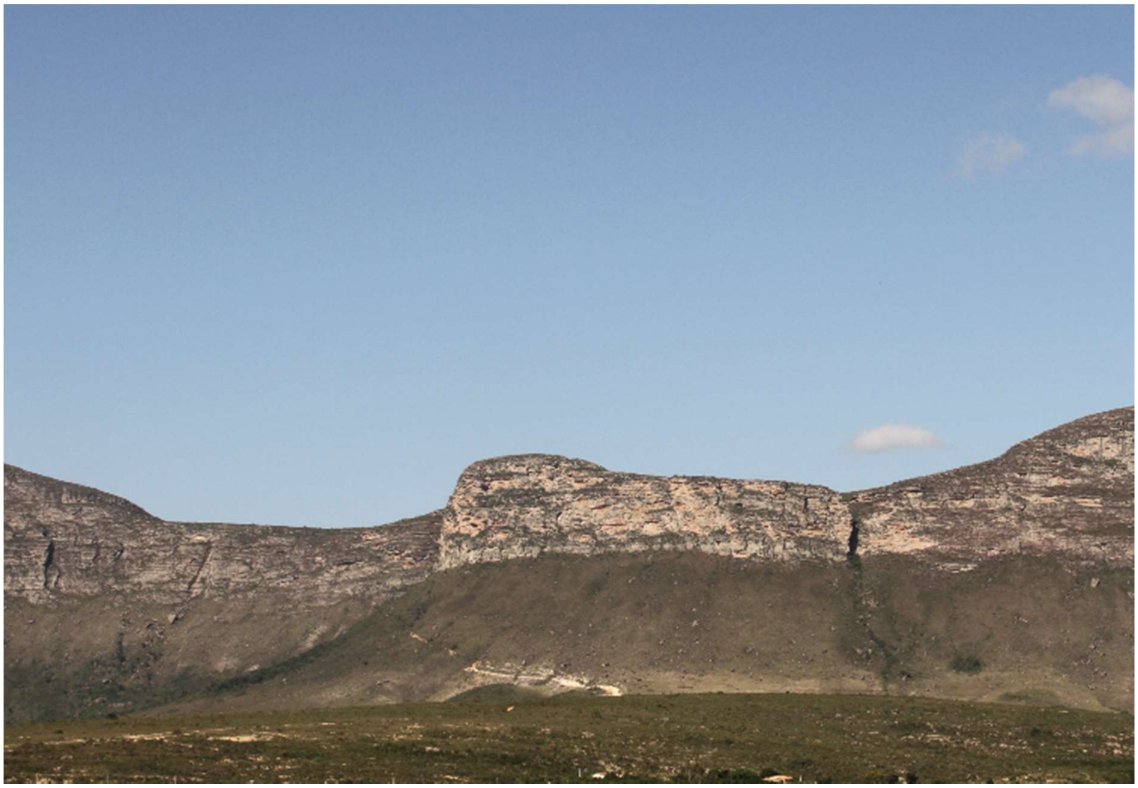


FIGURE S3. Species accumulation curve for Aculeate wasps and bees of forest islands considering all sampling methods (soil and canopy malaise, soil and arboreal pitfall, Moericke traps). Analyses using Jackknife 1 estimates.

Capítulo 3

Can we disentangle the importance of latitudinal and altitudinal gradients of variation for wasps and bees?



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Diversity and Distributions

Manuscript category: Biodiversity Research

Title:

Can we disentangle the importance of latitudinal and altitudinal gradients of variation for wasps and bees?

Running title:

Bees and wasps diversity in altitudinal and latitudinal gradients

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Abstract:

Aim: Our main objective is to disentangle effects of latitudinal and altitudinal gradients on the patterns of distribution of bees and wasps, as well as understand how climatic variables drive diversity across different spatial scales in *campo rupestre* ecosystems.

Location: Campo rupestre ecosystems in *Espinhaço* Mountain Range, southeast Brazil.

Methods: We used a standardized sampling protocol to study bees and wasps in 12 mountains, covering 1200 km from south-to-north; nine degrees of latitude and an altitudinal range from 1000 m up to 2000 m asl. We tested the relationships of bee and wasp α, γ and β-diversity with increasing latitude and elevation. To unravel possible mechanisms underpinning bees and wasps' diversity, we tested whether diversity can be explained by temperature and precipitation along the gradients.

Results: Temperature positively influenced α and γ diversities of bees and wasps and negatively influenced bees' β-diversity. The amount of species replacement was positively influenced by geographical distance.

Main conclusion: Our results provide evidence that, maintaining a single type of ecosystem (*campo rupestre*), temperature variation is the main mechanism underlying species diversity, which varies strongly associated with elevational gradient and overcomes the latitudinal gradient in tropical mountains.

Keywords: *Cadeia do Espinhaço,* Spatial patterns, α-diversity, β-diversity, γ-diversity, Latitude, Elevation, community structure, *campo rupestre*.

Introduction

Biodiversity is not evenly spatially distributed and among the recognizable patterns are the variation of species diversity with latitudinal (Pianka, 1966; Stevens, 1989; Rosenzweig, 1995) and elevational (Janzen, 1967; Lawton et al., 1987; Rahbek, 1995) gradients, which are historically described for varied systems and biological groups (Peters et al., 2016). Those spatial variations generate environmental gradients, driven by biotic and abiotic characteristics acting at both local and regional scales (Gaston, 2000). Underpinning these gradients are environmental variables - such as climate, topography and vegetation (Moura et al., 2016), as well as variations in spatial and time scales (Whittaker, 1972; Rosenzweig, 1995; Bishop et al., 2014), with rainfall and temperature emerging as the major predictors for many taxa (Sanders et al., 2007; Jaworski & Hilszczański, 2013; Andersen et al., 2015). Those two climatic variables can change communities composition through the evolutionary time (Brown, 2014) and are directly related with elevational and latitudinal conditions (McCain, 2007; Moya-Laraño, 2010).

Elevational gradients are described worldwide, with the majority of studies revealing peaks of high diversity at lower elevations (Wolda, 1987; Kraft et al., 2011; Peters et al., 2016). Changes in elevation can impose barriers to species dispersal (Qian et al., 2013; Moura et al., 2016) favoring a large number of endemic species, due to a combination of isolation effect (Körner, 2007), ecological and evolutionary processes (Rahbek, 1995; Lomolino, 2001) and allopatric speciation (Baselga et al., 2012a). An indirect effect of area can also influence the number of species (Romdal & Grytnes, 2007) through the reduction of the regional species pool (Cornell & Harrison, 2014). Latitudinal diversity gradient (LDG) also shapes the spatial distribution of biological communities (Pianka, 1966; Fine, 2015; Schemske & Mittelbach, 2017), with greater diversity associated with low latitudes (Stevens, 1989; Kraft et al., 2011; Cancello et al., 2014). Explanations range from ecological and evolutionary to geographic (Lamanna et al., 2014), involving environmental heterogeneity and stability, effective evolutionary time, temperature and productivity, interspecific interactions and abundance–adaptation hypotheses (Fine, 2015; Schluter & Pennell, 2017; Weiser et al., 2017).

Evolutionary mechanisms acting on geographic gradients can generate species richness gradients (Carnicer et al., 2012 for a detailed list). Studies performed in latitude and altitude gradients generally incorporate different ecosystems (Lamanna et al., 2014; Peters et al., 2016). Despite the large number of variables and mechanisms emanating from these gradients, the theory of ecological communities can be used to understand the processes responsible for generating and maintaining diversity in biological communities (Vellend, 2010; Graham et al., 2014). Those processes, included in selection, drift, speciation or dispersion categories, are shaped by regional and historical processes and depends on community structure and diversity of regional species pool (Karger et al., 2015; Tello et al., 2015). All species are not equal in traits (Blackburn & Gaston, 1996) or biotic interactions (Biesmeijer et al., 2005; Joern & Laws, 2013) and community structure is defined by the balance of local extinction and speciation (Schluter & Pennell, 2017) and dynamic of spatial distribution, ruled by dispersion capability (Arellano et al., 2014; Tello et al., 2015).

To understand those dynamics, a useful tool is to partition diversity across spatial scales. The relation between local (α-alpha) and regional (γ-gamma) diversities can be obtained through beta diversity (β), which indicates what makes assemblages of species more or less similar to each other at different places and times (Whittaker, 1972; Legendre et al., 2005; Baselga, 2010a; Anderson et al., 2011) and quantify the overall heterogeneity in assemblage composition among any number of sites (Tuomisto, 2010a, 2010b; Baselga, 2013). The diversity partitioning approach can provide insights to community understanding and how patterns are connected with the main processes that underlie species distribution. We used a single type of ecosystem, the endangered and megadiverse *campo rupestre*, a predominantly herbaceous-shrub ecosystem with rocky outcrops located on Brazilian mountaintops, collecting bees and wasps in different latitudes and elevations.

Invertebrates are often neglected in biodiversity conservation policies (Cardoso et al., 2011), especially in mountainous environments (Pryke & Samways, 2010). Several reasons lead to this scenario, such as the huge diversity (Basset et al., 2012), poor taxonomy (Ely et al., 2017) and large gaps in basic species surveys (Oliveira et al., 2016). We chose bees and wasps group (Hymenoptera: Aculeata) to study due to its diversification and landscape abundance (Peters et al., 2017), its importance in providing ecosystem services, such as pollination (Ollerton et al., 2011; Novais et al., 2016), sample facility and respond rapidly to environmental changes (Kremen et al., 1993).

In this paper we aimed to tackle the main effects of the latitudinal and elevational patterns acting together (i.e. lower diversity in higher elevations and higher latitudes) (Kraft et al., 2011) on bees and wasps diversity in an unique megadiverse *campo rupestre* ecosystem. We also aimed to evaluate the main climatic variables that determine diversity in different scales of diversity - α, β and γ. In addition, we want to understand whether species turnover is associated with geographic distance or environmental conditions associated with different altitudes to understand communities on those mountains.

Methods

Study sites

Our study was conducted along a latitudinal gradient ranging from 12ºS to 20ºS and elevation ranging from 700 to 2,072 m asl in a standardized sampling including only one ecosystem: *campo rupestre*. We performed a comprehensive sampling effort along the entire *Espinhaço* mountain range (Table S1; Figure 1), a mountainous formation that extends for more than 1,200 km north-south, with east-west width rarely exceeding 100 km (Schaefer et al., 2016). This mountain range is at the ecotone of three Brazilian biomes – *Cerrado* (Brazilian savanna) to the west, Atlantic rainforest to the east, and *Caatinga* (with scrubby xeromorphic vegetation, such as Dry Forests) in its northeastern. Associated with *Espinhaço* mountaintop surfaces (above 900 m asl), within all biomes represented, we highlight the *campo rupestre*, a neotropical grassland mosaic in association with azonal vegetation complexes on rocky outcrops (Fernandes, 2016; Silveira et al., 2016), formally classified as an old, climate-buffered, and infertile landscapes (OCBILs) (Hopper et al., 2015; Silveira et al., 2016). This megadiverse environment hosts a considerable number of threatened and endemic plant and animal species (Giulietti et al., 1997; Chaves et al., 2014; Silveira et al., 2016; Perillo et al., 2017).

Sampling design

Along the *Espinhaço* Mountain Range, we defined 12 sample locations. To standardize vegetation cover cross the latitudinal and altitudinal gradients, the inclusion criteria for a sampling point was always to be included in *campo rupestre* ecosystem (Table S1; Figure 1A). In each locality, to test the elevation effect, we selected two sample sites at different elevations in *campo rupestre*: one at the mountain base (Lower site: approx. at 1100 m asl) and another near the mountain summit (Upper site: ranging from approximately 1300 to 2000 m asl). We installed five set traps separated from each other by 200 m at each elevation mountain site (Figure 1B). Each set was composed by one malaise trap (field exposed for 144 hours), four pitfall traps (48 hours each) and four Moericke traps (yellow pan traps - 48 hours each), totaling 17,280 malaise trap hours, 23,040 pitfall and 23,040 Moericke trap hours divided in 120 trap sets. Those sampling methods are commonly used for Hymenoptera surveys, and were combined since each of them present different efficiencies to capture specific groups (Campbell & Hanula, 2007). Each locality was sampled once, during the rainy season (November to February). To disentangle multiscale effects on patterns of diversity across scales, we defined α-diversity as the species richness of a single trap set, γ-diversity as the total richness of each mountain elevational site (five trap sets) at a location and Whittaker's β-diversity as the heterogeneity in species composition among five trap sets in each location (Whittaker, 1972; Anderson et al., 2011) (Fig. 1B-C).

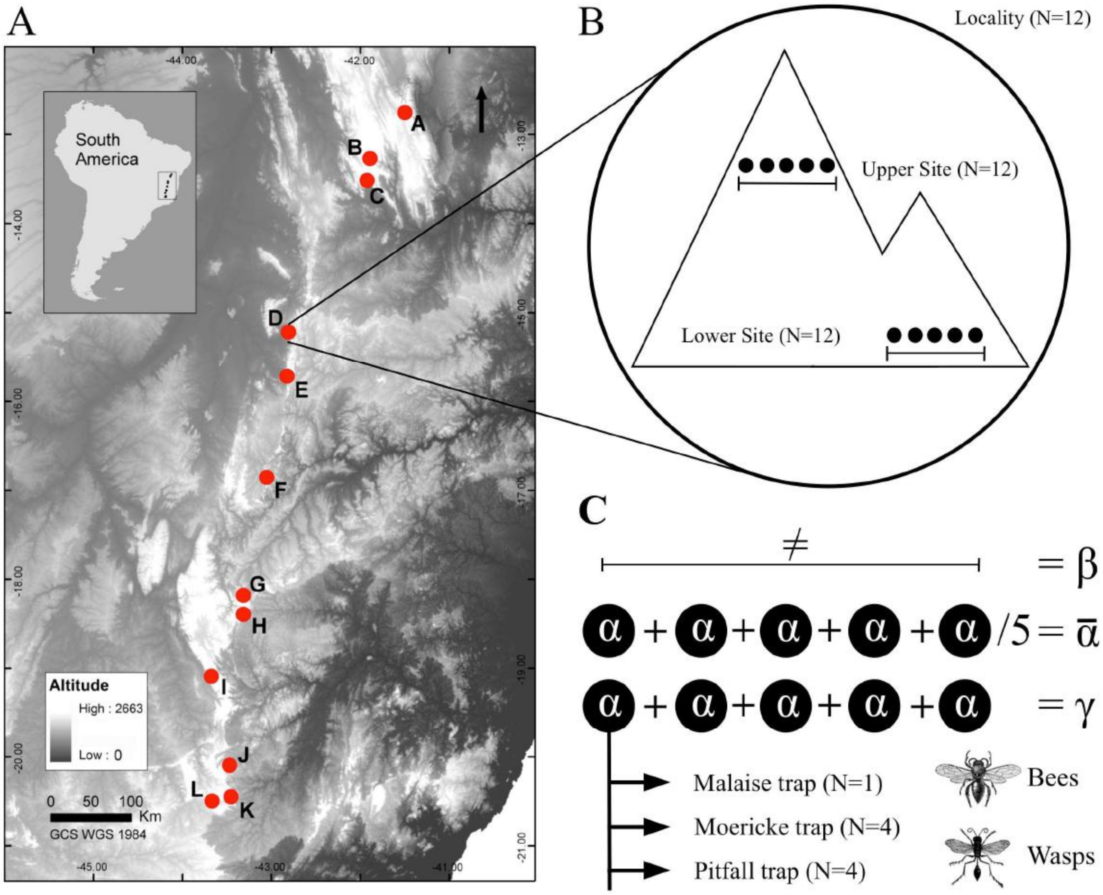

Fig. 1. (A) View of 12 sample localities thought *Espinhaço* Mountain Range. A: Parque Nacional Chapada Diamantina; B: Pico do Barbado; C: Pico das Almas; D: Pico da Formosa; E: Parque Estadual Serra Nova; F: Botumirim; G: Parque Estadual do Rio Preto; H: Parque Estadual Pico do Itambé; I: Pico do Breu; J: RPPN Santuário do Caraça. (B) Schematic sampling design with five trap sets in each elevation mountain site. Black circle correspond to a sample unit composed by 1 Malaise trap, 4 Moericke traps and 4 pitfall traps (N=120 trap sets). (C) Measurements of scales of diversity (mean alpha diversity: $\overline{\alpha}$; local gamma diversity: γ; Whittaker's beta diversity: $\beta = \gamma/\overline{\alpha}$).

All hymenopteran Aculeata families captured were considered, with exception of Formicidae and Bethylidae. To identify the specimens, taxonomic experts were consulted. When it was not possible, appropriate identification keys (Silveira et al., 2002; Fernández & Sharkey, 2006) were used to identify specimens to the lowest taxonomic level possible and deposited in the *Coleção Entomológica das Coleções Taxonômicas da Universidade Federal de Minas Gerais* (CEUFMG) in Belo Horizonte, Minas Gerais, Brazil.

Climatic variables

We used Wordclim version 2 data (1970-2000) (http:// www.worldclim.org) extracted to each collection site coordinate as explanatory variables that may rule the community patterns. Mean values of annual temperature (°C), precipitation (mm), solar radiation (kJ m^{-2} day^{-1}), wind speed (m s^{-1}) and water vapor pressure (kPa) values were submitted to correlation analyses and those that represented high correlation values (Pearson correlation coefficient ≥ 0.7) were excluded from further analysis (Fig. S1) (Zuur et al., 2010; Dormann et al., 2013). Non-correlated variables were mean temperature, precipitation and wind speed (Fig. S1) and were used as explanatory predictors to explain patterns of mean alpha ($\overline{\alpha}$), Whittaker's beta (β) and gamma (γ) diversity.

Statistical analysis

Bees and wasps data collected in different altitudes and latitudes were used to access diversity information in smaller and larger spatial scales. We calculate mean alpha diversity ($\overline{\alpha}$: mean richness between samples) and local gamma (γ: total richness of each elevational site in each locality) and also Whittaker's beta diversity ($\beta=\gamma/\overline{\alpha}$) to evaluate differences in species assemblage composition among sites (Whittaker, 1972) (Fig. 1C). Those three variables were used as response variables in further analysis. We then decomposed total β-diversity to calculate the relative contribution of species replacement (species turnover) and nestedness to total Sørensen β-diversity (Baselga, 2010b). Furthermore, to clarify the importance of the elevational range in Aculeata fauna between lower and upper elevational site in each locality, a Generalized Linear Model (GLM) was created with turnover between mountain elevational sites (N=12) as response variable and each elevational range value as explanatory variable. Total gamma was also calculated as the accumulated sample richness for each locality. All the results are arranged in Table S3 for bees and Table S4 for wasps.

To determine the influence of elevation and latitude parameters on Aculeata's diversity in smaller ($\overline{\alpha}$) and larger (γ) spatial scales and in Whittaker's β diversity, we used Generalized Linear Mixed Model (GLMM), with the identity of each location as random factor to account for the pseudoreplication due to spatial hierarchy of two altitudes in the same location. Whenever dealing with count data (i.e. α and γ diversities), we used Negative Binomial error distribution that also accounts for overdispersion (Crawley, 2013). To test for the pattern of diversity, each response variable ($\overline{\alpha}$, γ and β) was modeled with latitude and elevation (GLMM model: X ~ latitude + elevation + (1|location)). Then, to test for the possible mechanisms underpinning these patterns, we modeled each response variable against Worldclim variables (GLMM model: X ~ mean temperature + mean precipitation + mean wind speed + (1|location)). All explanatory variables were tested together in each model and non-significant variables and interactions ($p > 0.05$) were removed in order to simplify the model to obtain the minimal adequate model. For all models, we performed residual analysis to check for model adequacy and error distribution suitability (Crawley, 2013).

Finally, we used a Mantel test to analyze association patterns between distance matrices using Aculeata species β turnover (β_{sim}, pairwise between trap sets) and geographical distance matrices based on latitudinal coordinates with 10,000 permutations (Nekola & White, 1999; Castellano & Balletto, 2002). We performed all statistical analyses using R v.3.4.0 Software (R Core Team, 2017).

Results

We collected 8,906 Aculeata specimens, distributed among 674 morphospecies of 16 families, being 170 bees and 504 wasps morphospecies (Table 1; Table S2). The methods used were complementary, with Malaise trap collecting the majority of morphospecies, followed by Moericke trap and pitfall trap (see Table 1 and Fig. 2). A considerable number of rarely sampled species were found, with high capture rate of singletons, doubletons and tripletons (Table 2). Only seven morphospecies (two bees and five wasps, 1.0%) were sampled across all localities and 313 (71 bees and 242 wasps, 46.4%) were captured exclusively in a single mountain locality. Seven-dominant morphospecies were the bees *Dialictus* sp. 01 (Halictidae) and the alien and invasive species *Apis mellifera* (Apidae) and the wasps *Liris* sp. 02 and *Liris* sp. 04 (Crabronidae), *Polybia ignobilis* and *Polybia scrobalis* (Vespidae) and one unidentified Pompilidae sp. 05 (see more details in Table S2).

Table 1. Morphospecies richness and abundance collected by the different methodology types (Malaise, Moericke and Pitfall traps) distributed in each one of the 16 Aculeata families (five bees' families and 11 aculeate wasps families).

Families	**Richness**	**Abundance**	**Richness**			**Abundance**		
			Malaise	**Moericke**	**Pitfall**	**Malaise**	**Moericke**	**Pitfall**

Bees								
Andrenidae	2	53	1	2	0	3	50	0
Apidae	94	1452	85	30	4	1128	170	154
Colletidae	14	58	14	1	0	57	1	0
Halictidae	45	693	40	23	1	503	189	1
Megachilidae	15	209	15	1	0	208	1	0
Total	**170**	**2465**	**155**	**57**	**5**	**1899**	**411**	**155**
Wasps								
Chrysididae	15	78	14	6	1	46	31	1
Dryinidae	55	466	47	13	0	445	21	0
Embolemidae	3	6	3	0	0	6	0	0
Sclerogibbidae	3	109	3	0	0	109	0	0
Crabronidae	153	1906	128	70	10	1163	732	11
Sphecidae	13	78	13	4	0	72	6	0
Mutillidae	46	671	39	12	7	643	21	7
Pompilidae	126	1253	119	32	5	1083	163	7
Scoliidae	12	23	10	3	0	18	5	0
Tiphiidae	23	504	23	6	2	418	83	3
Vespidae	55	1347	53	18	1	1284	61	2
Total	**504**	**6441**	**452**	**164**	**26**	**5287**	**1123**	**31**
Grand Total	**674**	**8906**	**607**	**278**	**36**	**7186**	**1534**	**186**

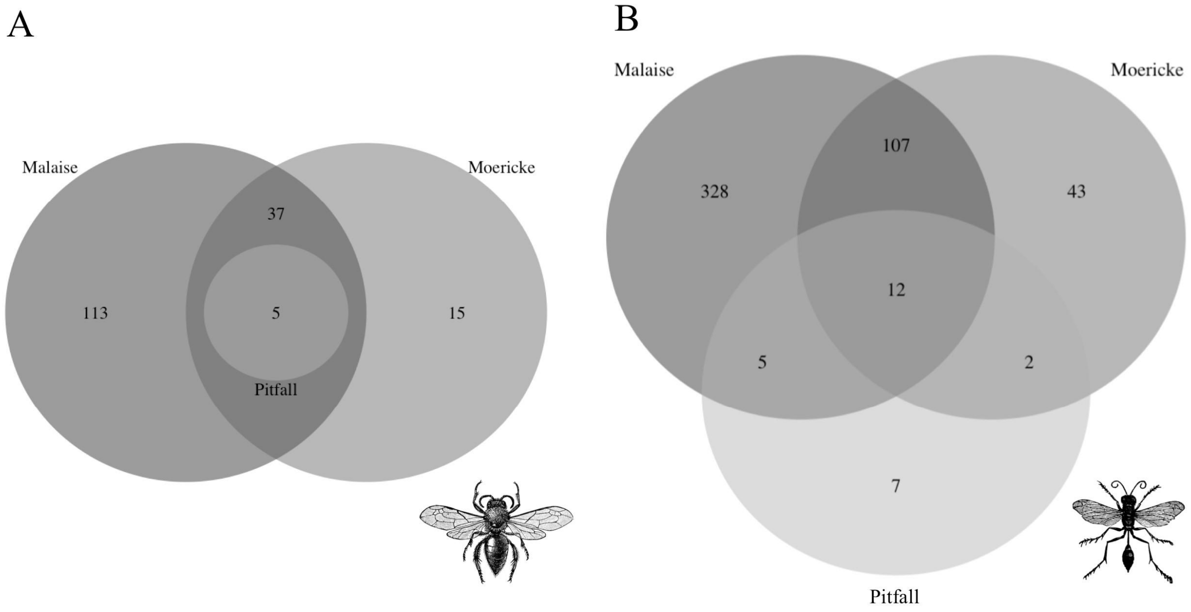

Fig. 2. Venn diagram showing bees (A) and wasps (B) morphospecies collected in Malaise, Moericke and pitfall traps.

Table 2. Number and percentages of rarely sampled bees and wasps morphospecies richness.

	Total Richness	**Singleton**		**Doubleton**		**Tripleton**	
		N	**%**	**N**	**%**	**N**	**%**
Bees	170	53	31.2	26	15.3	10	5.9
Wasps	504	174	34.5	65	12.9	50	9.9
Total	674	227	33.7	91	13.5	60	8.9

Diversity of aculeate Hymenoptera at both smaller ($\overline{\alpha}$ diversity) and larger (γ diversity) spatial scales were reduced with increasing elevation for bees (Negative Binomial - $\overline{\alpha}$: Chisq (df=1, N=12) =31.3, $p<0.001$; γ: Chisq (df=1, N=12) =29.3, $p<0.001$) (Fig. 3B) and wasps (Negative Binomial - $\overline{\alpha}$: Chisq (df=1, N=12) =48.2, $p<0.001$; γ: Chisq (df=1, N=12)

=57.3, $p<0.001$) (Fig. 3F). An inverse pattern was found for bee's β diversity (Normal: Chisq (df=1, N=12) =6.1, p=0.01) (Fig. 3D), but for wasps this relation was not significant (Normal: Chisq (df=1, N=12) =3.7, p=0.054) (Fig. 3H). We did not find relationship among latitude with bees and wasps $\overline{\alpha}$, γ or Whittaker's β diversity.

The temperature and precipitation were climatic drivers for $\overline{\alpha}$ and γ bees diversities (Negative Binomial - $\overline{\alpha}$: temperature (Chisq (df=1, N=12) =221.5, $p<0.001$) and precipitation (Chisq (df=1, N=12) =14.417, $p<0.001$); γ: temperature (Chisq (df=1, N=12) =34, $p<0.001$) and precipitation (Chisq (df=1, N=12) =8.5, $p<0.01$) (Fig. 4 A-B, D-E). Considering wasps, the same pattern occurred with temperature, but precipitation lost its importance both for $\overline{\alpha}$ and γ diversities (Fig. 4 G-H, J-K). Beta diversity was only related with temperature for bees (Chisq (df=1, N=12) =5.5, p=0.02) (Fig. 4 C, F, I, L), with decaying β values in higher temperatures (Fig. 4 C).

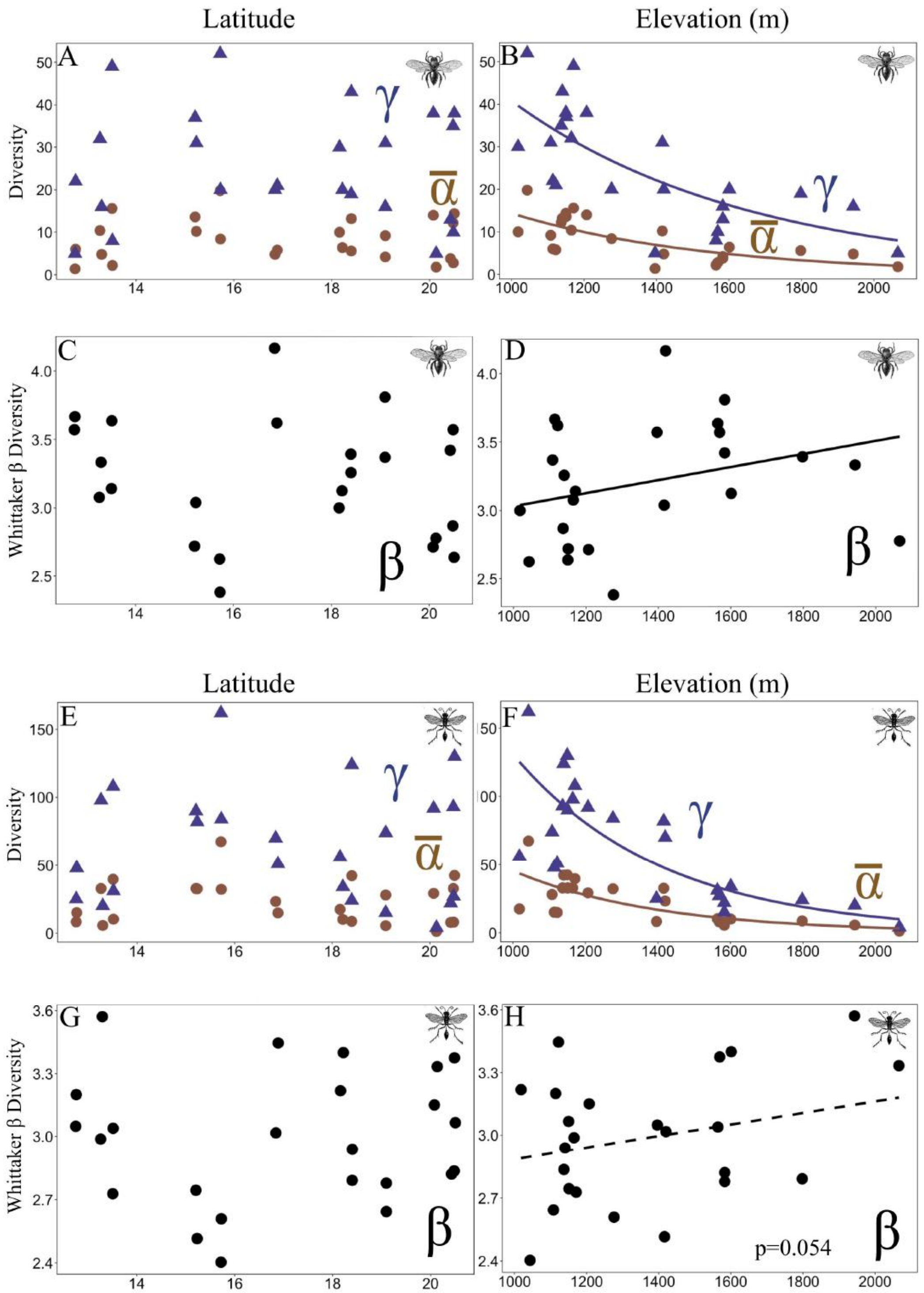

Fig. 3. Latitudinal and elevational trends in mean alpha (α), gamma (γ) and Whittaker's β diversity (β= γ/$\overline{\alpha}$) for bees (A - D) and wasps (E - H). Continuous line: $p<0.01$; Dotted line: $p<0.1$.

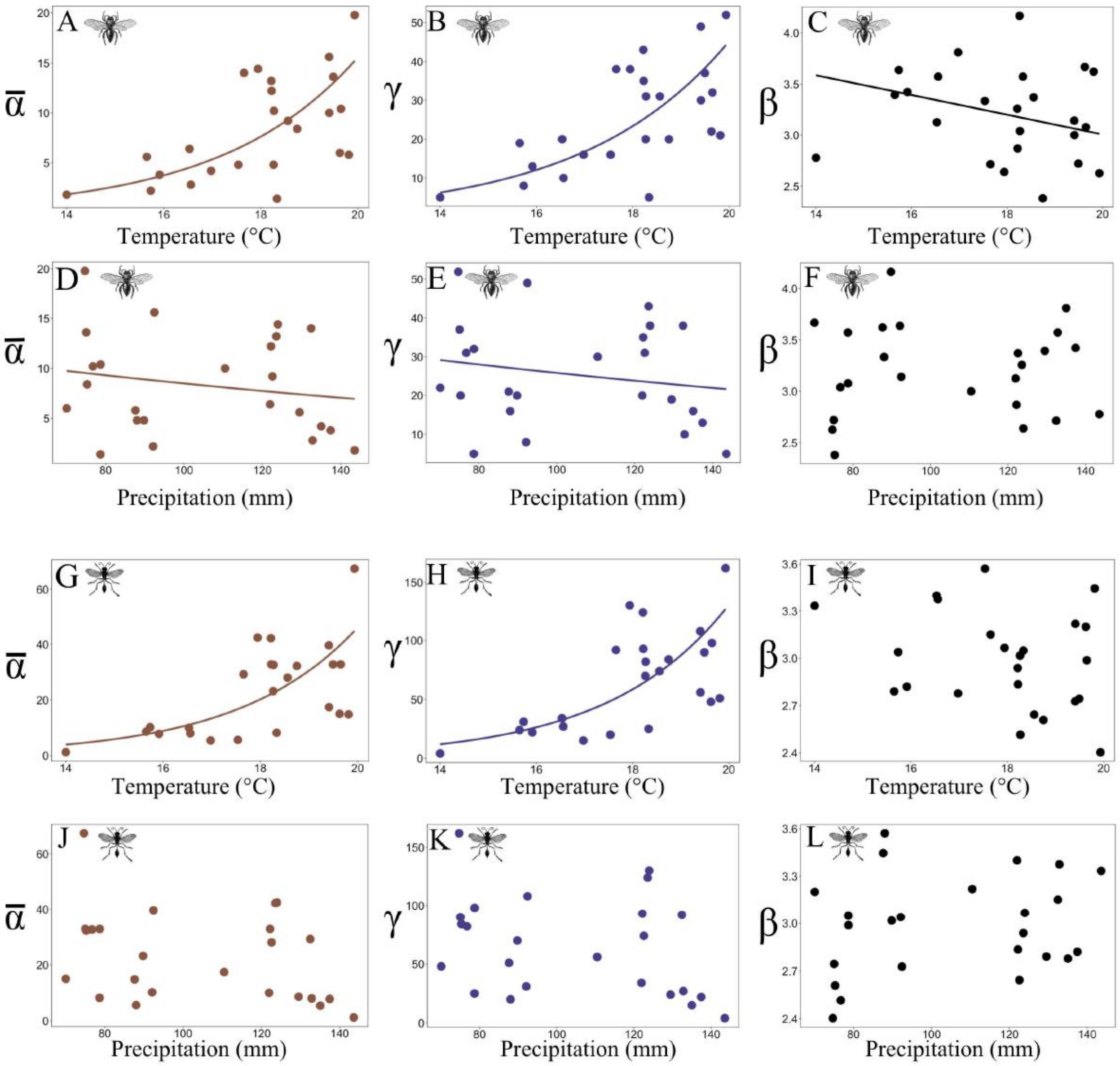

Fig. 4. Relation of Wordclim mean temperature (1970-2000) with $\overline{\alpha}$, γ and β diversity for bees (A-C) and wasps (G-I) and relation of Wordclim mean precipitation (1970-2000) with $\overline{\alpha}$, γ and β diversity for bees (D-F) and wasps (J-L).

Species turnover between mountain elevational sites had no relation with mountain elevation range (Bees: normal distribution, deviance=0.047, df=10, p=0.45) (Wasps: normal distribution, deviance=0.005, df=10, p=0.13) (Fig. 5). But species turnover between trap sets was directly related to geographic distance between sites (Bees: Mantel r=0.16, p<0.01; Wasps: Mantel r =0.28, p<0.001) (Fig. 6).

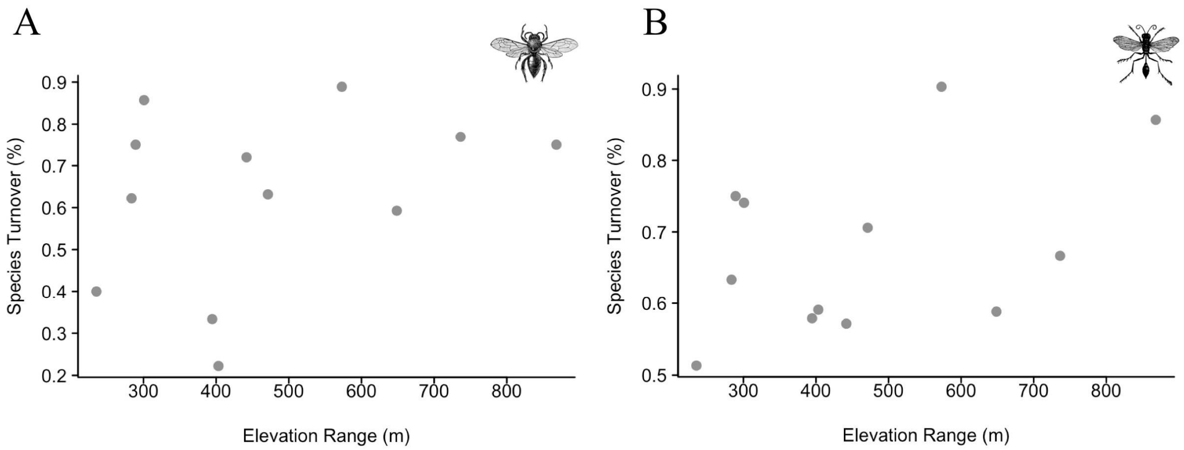

Fig. 5. Bees (A) and wasps (B) species turnover between mountain elevational sites (N=12) and elevation range (m) in *Espinhaço* mountain range localities.

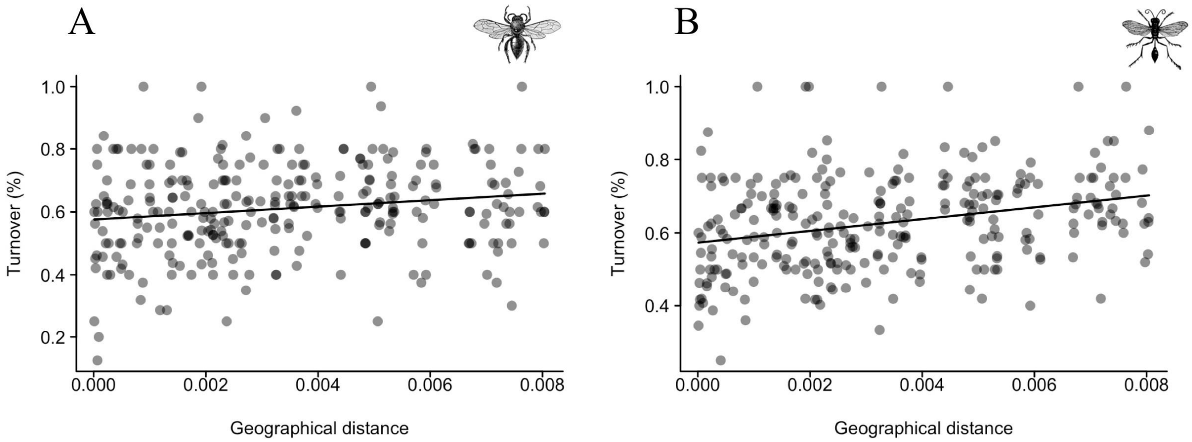

Fig 6. Relation of bee (A) and wasp (B) species turnover (pairwise β_{sim}) between trap sets with geographic distance (using geographic coordinates) (Bees: Mantel r=0.16, p<0.01; Wasps: Mantel r=0.28, p<0.001).

Discussion

Maintaining a single type of ecosystem, elevation is more important than latitude to determine distribution of diversity for wasps and bees in tropical mountains. We also found that temperature is the most important climatic variable to predict Aculeata diversity.

Despite the considerable sampling effort, we found a high number of rare sampled species (56.1% - sum of singleton, doubleton and tripletons) and a high number of species detected only in one locality (46.4%). Singletons are common on tropics (Coddington et al., 2009) and *campo rupestre* hymenopteran fauna have a high number of species with low local abundance and narrow spatial distribution documented (Azevedo et al., 2008), a common pattern found in mountain communities (McCain, 2009; Hoiss et al., 2012; Arellano et al., 2014). This high turnover also indicates high spatial genetic variation (Carnicer et al., 2012) and allopatric speciation and dispersion processes having great importance (Vellend, 2010), particularly considering that α-diversity is a small fraction of regional diversity (Jankowski et al., 2009).

The main climatic driver that underpins bees and wasps' diversity spatial scales is temperature. In *campo rupestre* system, this climatic variable is intrinsically related with elevation, contributing to the lack of latitude-diversity relationship. Unusual latitudinal diversity gradient (LDG) was also found for ants (Silva & Brandão, 2014; Andersen et al., 2015), functional traits (Lamanna et al., 2014), predation (Roslin et al., 2017) and herbivory (Moreira et al., 2015; Zhang et al., 2016). Our results are in line with several studies dealing with tropical altitudinal gradients, which also found a decrease in species richness with increasing elevation (Jankowski et al., 2009; Hoiss et al., 2012; Nunes et al., 2016; Perillo et al., 2017). The results found for both spatial scales, α and γ diversities, also agree with patterns found in studies that surveyed species diversity across spatial scales (Kraft et al., 2011; Qian et al., 2013; Peters et al., 2016). But β-diversity has a direct relation with altitude especially for bees. We highlight that despite of the limited altitudinal variation (Brazilian mountains rarely exceed 1900 m asl), we were able to find clear changes in communities along the altitudinal variations. Lower elevation quota has less severe conditions, ensuring greater concentration of species (and lower turnover), than those found on highest mountain sites. This distribution can be caused by a combination of dispersion and selection processes (Vellend, 2010). At a local scale, elevation range can cause isolation-by-adaptation with potentially high rates of *in situ* speciation (Funk et al., 2016; Schluter & Pennell, 2017), which causes spatial aggregation of taxa recently formed in more recent evolutionary events (Gastauer et al., 2015). We can also consider the indirect effect of lower available area at high elevation communities, which influence taxa that have limited dispersal potential (Romdal & Grytnes, 2007). At larger-scales, environmental filtering may not be the main driver on *campo rupestre* and dispersal limitation, caused by dispersal barriers (Baselga et al., 2012b; Gastauer et al., 2015), have a key factor on communities' differentiation (Gonçalves-Souza et al., 2015). Therefore, evolutionary processes are acting in local (such as uneven spatio-temporal mechanisms distribution) and regional scales (such as allopatric populations on great geographical distances) (Carnicer et al., 2012; Ricklefs, 2015).

Campo rupestre system is classified as an OCBIL (Silveira et al., 2016), exhibiting antiquity and climatic stability (Hopper, 2009), and some LGD theories (Pianka, 1966; Schemske & Mittelbach, 2017) cannot be applied. In *Espinhaço* mountain range, we found that temperature is not directly correlated with latitude. Rainfall also may not be a limiting factor in *campo rupestre*. Actually, there are a lot of headwaters documented for *campo rupestre* (Callisto et al., 2016) and constant fog humidity caused by the orographic effects (Coelho et al., 2016), although it is not widely available in soil (Ferrari et al., 2016). Negative correlation among precipitation and diversity was also found in *campo rupestre* dung beetle communities (Nunes et al., 2016). In fact, some bee species may prefer areas with a less seasonal precipitation regime (Nemésio & Vasconcelos, 2013). It is worth to highlight that changes in temperature (Deutsch et al., 2008) and precipitation (Zhu et al., 2014), mechanisms that are altered by climate changes, cause deleterious consequences in insects' diversity.

Despite the existence of several shared species with the Atlantic forest and the cerrado, the fauna of *campo rupestre* has its own identity and biogeographical history, favoring constant diversification of old lineages (see Silveira et al., 2016). Investments in taxonomy can help on definition of areas of endemism (Knapp, 2005) or testing other hypotheses (Chaves et al., 2014). *Campo rupestre* is a megadiverse ecosystem under threat (Fernandes et al., 2014) and due to high rates of rare species and beta diversity even small additions to protected areas could incorporate many new species (Jankowski et al., 2009). Those complex mountainous systems need urgent attention, especially in localities when human impact is higher (Nogués-Bravo et al., 2008; Pryke & Samways, 2010). These bees and wasps inventory also contribute to diminish the biodiversity knowledge shortfalls in Brazilian areas (Oliveira et al., 2016, 2017) and opens new possibilities for studies that take into account multiple mechanisms that shapes mountain communities and evidence their relationships with processes of community ecology.

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Supplementary Information

Table S1. Information of the 12 *campo rupestre* localities across *Espinhaço* Mountain Range, southeast Brazil.

Locality	**Lower Elevational Quota**			**Upper Elevational Quota**		
	Latitude	**Longitude**	**Altitude**	**Latitude**	**Longitude**	**Altitude**
P.N. Chapada Diamantina	12º 45' 48.28" S	41º 30' 40.05" W	1114	12º 45' 10.47" S	41º 30' 20.59" W	1396
Pico do Barbado	13º 15' 43.80" S	41º 52' 37.72" W	1165	13º 17' 47.70" S	41º 54' 13.08" W	1943
Pico das Almas	13º 30' 33.86" S	41º 53' 29.94" W	1171	13º 31' 01.16" S	41º 57' 29.63" W	1564
Pico da Formosa - Monte Azul	15º 12' 25.39" S	42º 48' 04.10" W	1151	15 º 13' 54.52" S	42º 48' 54.52" W	1416
P.E. Serra Nova	15º 43' 11.67" S	42º 50' 10.32" W	1043	15º 43' 33.77" S	42º 49' 42.76" W	1276
Botumirim	16º 53' 15.06" S	43º 01' 50.16" W	1122	16º 50' 27.23" S	43º 04' 15.56" W	1420
P.E. do Rio Preto	18º 09' 35.89" S	43º 19' 14.18" W	1018	18º 13' 05.21" S	43º 18' 56.35" W	1601
P.E. Pico do Itambé	18º 24' 00.45" S	43º 18' 05.42" W	1140	18º 23' 52.59" S	43º 20' 11.85" W	1798
Pico do Breu - Serra do Cipó	19º 05' 46.00" S	43º 41' 14.89" W	1108	19º 05' 44.02" S	43º 39' 56.42" W	1583
RPPN Santuário do Caraça	20º 04' 37.99" S	43º 29' 37.90" W	1207	20º 08' 07.19" S	43º 27' 08.87" W	2066
P.E. Pico do Itacolomi	20º 28' 53.04" S	43º 27' 48.14" W	1137	20º 25' 40.44' S	43º 28' 50.96" W	1583
P.E. Serra do Ouro Branco	20º 30' 20.10" S	43º 37' 23.21 " W	1150	20º 29' 12.37" S	43º 42' 43.96" W	1569

Table S2. Bees and wasps (Hymenoptera: Aculeata) morphospecies collected in *Espinhaço* mountain range, Brazil. Total abundance of each morphospecies (**A**) and the number of localities that each species was collected (**N**).

Family	**Subfamily**	**Tribe/ Subtribe**	**Morphospecies**	**A**	**N**
BEES					
ANDRENIDAE	Panurginae				
			PANURGINAE sp. 01	52	4
			PANURGINAE sp. 02	1	1
APIDAE	Apinae	Apini			
		Apina			
			Apis mellifera Linnaeus, 1758	226	12
		Meliponina			
			MELIPONINA sp. 01	3	1
		Bombini			
			Bombus Fervidobombus pauloensis Friese, 1913	11	3
			Bombus Fervidobombus morio (Swederus, 1787)	1	1
		Centridini			
			Epicharis Epicharis bicolor Smith, 1854	1	1
			Centris sp. 01	14	6
			Centris sp. 02	7	4
			Centris sp. 03	4	3
			Centris sp. 04	28	6
			Centris sp. 05	1	1
			Centris sp. 06	5	1
			Centris sp. 07	1	1
			CENTRIDINI sp. 01	1	1
		Emphorini			
			Melitoma sp. 01	1	1

Family	Subfamily	Tribe/ Subtribe	Morphospecies	A	N
			Ancyloscelis apiformis (Fabricius, 1793)	2	2
		Ericrocidini			
			Acanthopus excellens Schrottky, 1902	1	1
			Mesocheira bicolor (Fabricius, 1804)	1	1
			Mesonychium sp. 01	5	3
			Mesoplia sp. 01	1	1
			ERICROCIDINI sp. 01	1	1
		Eucerini			
			Thygater analis (Lepeletier, 1841)	1	1
			Thygater anae Urban, 1999	1	1
			Trichocerapis sp. 01	2	2
			Melissoptila sp. 01	1	1
			EUCERINI sp. 01	1	1
			EUCERINI sp. 02	2	1
			EUCERINI sp. 03	3	1
			EUCERINI sp. 04	3	2
			EUCERINI sp. 05	1	1
		Euglossini			
			Exaerete dentata (Linnaeus, 1758)	1	1
			Eufriesea nigrohirta (Friese, 1899)	2	2
			Euglossa sp. 01	2	2
			Euglossa sp. 02	1	1
		Exomalopsini			
			Exomalopsis Exomalopsis auropilosa Spinola, 1853	2	1
			Exomalopsis sp. 01	5	4
			Exomalopsis sp. 02	1	1
			Exomalopsis sp. 03	3	3
		Meliponini			
			Frieseomelitta sp. 01	1	1
			Geotrigona subterranea (Friese, 1901)	15	5
			Leurotrigona sp. 01	50	6

Family	Subfamily	Tribe/ Subtribe	Morphospecies	A	N
			Melipona Melikerria quinquefasciata Lepeletier, 1836	10	5
			Melipona (Eomelipona) bicolor Lepeletier, 1836	6	1
			Melipona (Melipona) quadrifasciata Lepeletier, 1836	6	3
			Paratrigona sp. 01	132	9
			Partamona criptica Pedro & Camargo, 2003	11	5
			Plebeia sp. 01	167	8
			Plebeia sp. 02	19	4
			Tetragonisca angustula (Latreille, 1811)	17	8
			Tetragona sp. 01	3	2
			Trigona braueri Friese, 1900	12	2
			Trigona spinipes Fabricius, 1793	198	11
			Trigonisca sp. 01	123	5
			MELIPONINI sp. 01	1	1
			MELIPONINI sp. 02	1	1
			MELIPONINI sp. 03	11	4
			MELIPONINI sp. 04	2	2
		Osirini			
			Osirinus sp. 01	1	1
			Osirinus sp. 02	1	1
			Osiris sp. 01	1	1
			Osiris sp. 02	1	1
		Tapinotaspidini			
			TAPINOTASPIDINI sp. 01	30	9
			TAPINOTASPIDINI sp. 02	4	2
			TAPINOTASPIDINI sp. 03	2	2
			TAPINOTASPIDINI sp. 04	1	1
			TAPINOTASPIDINI sp. 05	1	1
			TAPINOTASPIDINI sp. 06	14	5
		Tetrapediini			
			Tetrapedia sp. 01	17	4
			Tetrapedia sp. 02	6	3

Family	Subfamily	Tribe/ Subtribe	Morphospecies	A	N
	Xylocopinae	Ceratinini			
		Ceratinina			
			Ceratina (Ceratinula) sp. 01	52	7
			Ceratina (Ceratinula) sp. 02	13	6
			Ceratina (Ceratinula) sp. 03	2	2
			Ceratina (Ceratinula) sp. 04	2	1
			Ceratina (Ceratinula) sp. 05	12	3
			Ceratina (Ceratinula) sp. 06	9	1
			Ceratina (Ceratinula) sp. 07	17	2
			Ceratina (Ceratinula) sp. 08	1	1
			Ceratina (Crewella) sp. 01	30	9
			Ceratina (Crewella) sp. 02	45	8
			Ceratina (Crewella) sp. 03	6	4
			Ceratina (Crewella) sp. 04	12	8
			Ceratina (Crewella) sp. 05	4	4
			Ceratina (Crewella) sp. 06	7	3
			Ceratina (Crewella) sp. 07	1	1
			Ceratina (Crewella) sp. 08	1	1
			Ceratina (Crewella) sp. 09	1	1
		Xylocopini			
		Xilocopina			
			Xylocopa (Diaxylocopa) truxali Hurd & Moure, 1963	4	3
			Xylocopa (Schonnherria) anthophoroides Smith, 1874	2	2
			Xylocopa (Stenoxylocopa) sp. n1	3	3
			Xylocopa sp. 01	2	1
			Xylocopa sp. 02	1	1
			Xylocopa sp. 03	3	2
			Xylocopa sp. 04	9	3
			Xylocopa sp. 05	1	1
			Xylocopa sp. 06	1	1
COLLETIDAE	Colletinae	Colletini			

Family	Subfamily	Tribe/ Subtribe	Morphospecies	A	N
			COLLETINI sp. 01	1	1
			COLLETINI sp. 02	2	2
		Diphaglossini Caupolicanina			
			Ptiloglossa sp. 01	12	8
			Ptiloglossa sp. 02	1	1
	Paracolletinae	Paracolletini			
			Nomiocolletes sp. 01	4	2
			PARACOLLETINI sp. 01	2	1
			PARACOLLETINI sp. 02	1	1
			PARACOLLETINI sp. 03	2	2
	Xeromelissinae	Xeromelissini			
			Chilicola Oediscelis sp. 01	4	1
			Chilicola sp. 01	7	6
			Chilicola sp. 02	2	2
			Hylaeus sp. 01	17	10
			Hylaeus sp. 02	1	1
			COLLETIDAE sp. 01	2	1
HALICTIDAE	Halictinae	Augochlorini			
			Augochlora sp. 01	14	6
			Augochloropsis sp. 01	27	8
			Augochloropsis sp. 02	9	5
			Augochloropsis sp. 03	37	8
			Augochloropsis sp. 04	9	4
			Augochloropsis sp. 05	7	3
			Augochloropsis sp. 06	2	2
			Augochloropsis sp. 07	10	5
			Augochloropsis sp. 08	18	6
			Ceratalictus sp. 01	1	1

Family	Subfamily	Tribe/ Subtribe	Morphospecies	A	N
			Neocorynura aenigma (Gribodo, 1894)	13	3
			Neocorynura sp. 01	6	5
			Paroxystoglossa sp. 01	1	1
			Paroxystoglossa sp. 02	1	1
			Paroxystoglossa sp. 03	2	2
			Paroxystoglossa sp. 04	5	3
			Paroxystoglossa sp. 05	1	1
			Paroxystoglossa sp. 06	2	1
			Temnosoma sp. 01	1	1
			Thectochlora sp. 01	5	2
			AUGOCHLORINI sp. 01	6	3
			AUGOCHLORINI sp. 02	16	5
			AUGOCHLORINI sp. 03	1	1
			AUGOCHLORINI sp. 04	2	2
			AUGOCHLORINI sp. 05	9	4
			AUGOCHLORINI sp. 06	1	1
			AUGOCHLORINI sp. 07	15	5
	Halictinae	Halictini			
			Ceratalictus sp. 01	6	2
			Dialictus sp. 01	240	12
			Dialictus sp. 02	1	1
			Dialictus sp. 03	2	1
			Dialictus sp. 04	12	5
			Dialictus sp. 05	8	5
			Dialictus sp. 06	38	7
			Gnathalictus sp. 01	1	1
			Gnathalictus sp. 02	8	3
			Gnathalictus sp. 03	4	2
			Halictus sp. 01	1	1
			HALICTINI sp. 01	5	3
			HALICTINI sp. 02	14	3

Family	Subfamily	Tribe/ Subtribe	Morphospecies	A	N
			HALICTINI sp. 03	17	5
			HALICTINI sp. 04	2	1
			HALICTINI sp. 05	2	2
			HALICTINI sp. 07	110	11
			HALICTINI sp. 06	1	1
MEGACHILIDAE	Megachilinae	Anthidiini			
			ANTHIDIINI sp. 01	96	10
			ANTHIDIINI sp. 02	3	2
			ANTHIDIINI sp. 03	3	2
		Megachilini			
			Coelioxys sp. 01	14	4
			Megachile (Pseudocentron) terrestris Schrottky, 1902	27	8
			Megachile (Cressoniella) sp. 01	1	1
			Megachile Chrysosarus sp. 01	25	8
			Megachile sp. 01	3	1
			Megachile sp. 02	19	4
			Megachile sp. 03	6	5
			Megachile sp. 04	2	1
			Megachile sp. 05	2	1
			Megachile sp. 06	6	2
			Megachile sp. 07	1	1
			Megachile sp. 08	1	1
WASPS					
CHRYSIDIDAE	Cleptinae				
			Cleptidea sp. 01	6	2
	Amiseginae				
			Adelphe sp. 01	1	1
			Amisega sp. 01	21	4

Family	**Subfamily**	**Tribe/ Subtribe**	**Morphospecies**	**A**	**N**
			Amisega sp. 02	15	5
	Chrysidinae	Chrysidini			
			Caenochrysis sp. 01	9	6
			Caenochrysis sp. 02	5	3
			Caenochrysis sp. 03	4	1
			Caenochrysis sp. 04	5	4
			Caenochrysis sp. 05	1	1
			Ipsiura sp. 01	3	2
			Neochrysis sp. 01	1	1
			Neochrysis sp. 02	1	1
			Pleurochrysis sp. 01	3	2
		Elampini			
			Exallopyla sp. 01	2	1
			Holophris sp. 01	1	1
DRYINIDAE	Anteoninae				
			Anteon sp. 01	1	1
			Anteon sp. 02	1	1
			Anteon sp. 03	1	1
			Anteon sp. 04	1	1
			Anteon sp. 05	2	2
			Deinodryinus sp. 01	1	1
			Deinodryinus sp. 02	1	1
			Deinodryinus sp. 03	4	2
			Deinodryinus sp. 04	6	3
			Deinodryinus sp. 05	2	2
			Deinodryinus sp. 06	1	1
			Deinodryinus sp. 07	1	1
			Deinodryinus sp. 08	6	3
			Deinodryinus sp. 09	1	1
			Deinodryinus sp. 10	5	3
			Deinodryinus sp. 11	2	2

Family	Subfamily	Tribe/ Subtribe	Morphospecies	A	N
			Deinodryinus sp. 12	2	2
			Deinodryinus sp. 13	1	1
			Deinodryinus sp. 14	1	1
	Aphelopinae				
			Aphelopus sp. 01	5	3
			Aphelopus sp. 02	6	3
			Aphelopus sp. 03	1	1
			Aphelopus sp. 04	1	1
			Aphelopus sp. 05	1	1
			Aphelopus sp. 06	1	1
			Crovettia sp. 01	2	2
			Crovettia sp. 02	1	1
			Crovettia sp. 03	5	2
			Crovettia sp. 04	1	1
			Crovettia sp. 05	1	1
	Bocchinae				
			Bocchus sp. 1	2	2
			Bocchus sp. 2	10	5
	Dryininae				
			Dryinus piscensis (Olmi, 1984)	2	2
			Dryinus cf. *davidsoni* (Olmi, 1991)	1	1
			Dryinus forestalis (Olmi, 1984)	1	1
			Dryinus bicolor (Olmi, 1984)	1	1
			Dryinus sp. 01	1	1
			Dryinus sp. 02	1	1
			Dryinus sp. 03	42	4
			Dryinus sp. 04	20	7
			Dryinus sp. 05	4	3
			Dryinus sp. 06	2	2
			Dryinus sp. 07	5	1
	Gonatopodinae				

Family	**Subfamily**	**Tribe/ Subtribe**	**Morphospecies**	**A**	**N**
			Gonatopus sp. 01	3	2
			Gonatopus sp. 02	1	1
			Gonatopus sp. 03	1	1
			Gonatopus sp. 04	113	10
			Gonatopus sp. 05	3	1
			Gonatopus sp. 06	70	10
			Gonatopus sp. 07	66	10
			Gonatopus sp. 08	37	7
			Gonatopus sp. 09	3	2
			Gonatopus sp. 10	10	5
			Gonatopus sp. 11	1	1
			Gonatopus trichosoma Virla, Espinosa & Olmi, 2010	1	1
EMBOLEMIDAE					
			Embolemus sp. 01	4	1
			Embolemus sp. 02	1	1
			Embolemus sp. 03	1	1
SCLEROGIBBIDAE					
			Sclerogibba sp. 01	85	7
			Sclerogibba sp. 02	20	4
			Sclerogibba sp. 03	4	1
CRABRONIDAE	Bembecinae	Bembicini			
			BEMBICINI sp. 01	3	2
			BEMBICINI sp. 02	5	4
			BEMBICINI sp. 03	1	1
			BEMBICINI sp. 04	2	2
		Mellinini			
			GORYTINI sp. 01	1	1
		Mellinini			
			Mellinus sp. 01	3	2
			Mellinus sp. 02	1	1
			Mellinus sp. 03	1	1

Family	Subfamily	Tribe/ Subtribe	Morphospecies	A	N
			Mellinus sp. 04	1	1
		Nyssonini			
			NYSSONINI sp. 01	4	3
			NYSSONINI sp. 02	2	2
			NYSSONINI sp. 03	6	2
			NYSSONINI sp. 04	1	1
		Stizini			
			Bembecinus sp. 01	17	1
			Bembecinus sp. 02	1	1
			Bembecinus sp. 03	2	1
			Bembecinus sp. 04	1	1
	Crabroninae	Bothynostethini			
			Bothynostethus sp. 01	34	4
			Bothynostethus sp. 02	4	1
			Bothynostethus sp. 03	1	1
			Bothynostethus sp. 04	1	1
		Crabronini			
			CRABRONINI sp. 01	2	1
			CRABRONINI sp. 02	27	8
			CRABRONINI sp. 03	8	3
			CRABRONINI sp. 04	5	2
			CRABRONINI sp. 05	12	5
			CRABRONINI sp. 06	7	4
			CRABRONINI sp. 07	1	1
			CRABRONINI sp. 08	1	1
			CRABRONINI sp. 09	1	1
			CRABRONINI sp. 10	1	1
			CRABRONINI sp. 11	3	1
			CRABRONINI sp. 12	1	1
		Larrini			
			Liris sp. 01	63	9

Family	Subfamily	Tribe/ Subtribe	Morphospecies	A	N
			Liris sp. 02	45	12
			Liris sp. 03	26	8
			Liris sp. 04	62	12
			Liris sp. 05	4	4
			Liris sp. 06	25	6
			Liris sp. 07	3	2
			Liris sp. 08	3	1
			Liris sp. 09	6	4
			Liris sp. 10	2	2
			Liris sp. 11	2	1
			Liris sp. 12	3	3
			Liris sp. 13	2	2
			Liris sp. 14	5	3
			Liris sp. 15	1	1
			LARRINI sp. 01	72	8
			LARRINI sp. 02	78	11
			LARRINI sp. 03	14	4
			LARRINI sp. 04	1	1
			LARRINI sp. 05	26	7
			LARRINI sp. 06	12	1
			LARRINI sp. 07	2	1
			LARRINI sp. 08	10	1
			LARRINI sp. 09	40	7
			LARRINI sp. 10	92	10
			LARRINI sp. 11	6	5
			LARRINI sp. 12	2	2
			LARRINI sp. 13	2	2
			LARRINI sp. 14	1	1
			LARRINI sp. 15	2	1
			LARRINI sp. 16	1	1
			LARRINI sp. 17	32	5

Family	Subfamily	Tribe/ Subtribe	Morphospecies	A	N
			LARRINI sp. 18	3	3
			LARRINI sp. 19	18	3
			LARRINI sp. 20	16	2
			LARRINI sp. 21	1	1
			LARRINI sp. 22	22	7
			LARRINI sp. 23	8	3
			LARRINI sp. 24	1	1
			LARRINI sp. 25	5	2
			LARRINI sp. 26	5	1
			LARRINI sp. 27	19	5
			LARRINI sp. 28	4	1
		Mischopini			
			Nitela sp. 01	57	8
			Nitela sp. 02	13	5
			Nitela sp. 03	22	7
			MISCHOPINI sp. 01	31	9
			MISCHOPINI sp. 02	6	1
			MISCHOPINI sp. 03	6	4
			MISCHOPINI sp. 04	26	4
			MISCHOPINI sp. 05	3	3
			MISCHOPINI sp. 06	1	1
			MISCHOPINI sp. 07	1	1
			MISCHOPINI sp. 08	3	2
			MISCHOPINI sp. 09	20	6
		Oxybelini			
			Oxybelus sp. 01	25	7
			Oxybelus sp. 02	22	5
			Oxybelus sp. 03	5	3
			Oxybelus sp. 04	7	3
			Oxybelus sp. 05	5	3
			Oxybelus sp. 06	8	3

Family	Subfamily	Tribe/ Subtribe	Morphospecies	A	N
			Oxybelus sp. 07	9	4
		Scapheutini			
			Scapheutes sp. 01	11	1
			Scapheutes sp. 02	2	1
		Trypoxylini			
			Pisoxylon sp. 01	5	4
			Pisoxylon sp. 02	2	1
			Pisoxylon sp. 03	2	2
			Pisoxylon sp. 04	1	1
			Pisoxylon sp. 05	1	1
			Trypoxylon sp. 01	59	7
			Trypoxylon sp. 02	98	7
			Trypoxylon sp. 03	67	8
			Trypoxylon sp. 04	4	3
			Trypoxylon sp. 05	128	9
			Trypoxylon sp. 06	50	9
			Trypoxylon sp. 07	30	8
			Trypoxylon sp. 08	1	1
			Trypoxylon sp. 09	3	2
			Trypoxylon sp. 10	6	3
			Trypoxylon sp. 11	2	2
			Trypoxylon sp. 12	9	3
			Trypoxylon sp. 13	3	2
			Trypoxylon sp. 14	1	1
			Trypoxylon sp. 15	1	1
			Trypoxylon sp. 16	1	1
			Trypoxylon sp. 17	16	8
			Trypoxylon sp. 18	1	1
	Pemphredoninae	Pemphredonini			
			PEMPHREDONINI sp. 01	31	3
			PEMPHREDONINI sp. 02	4	3

Family	Subfamily	Tribe/ Subtribe	Morphospecies	A	N
			PEMPHREDONINI sp. 03	33	10
			PEMPHREDONINI sp. 04	25	8
			PEMPHREDONINI sp. 05	4	2
			PEMPHREDONINI sp. 06	9	3
		Psenini			
			PSENINI sp. 01	23	2
			PSENINI sp. 02	2	1
			PSENINI sp. 03	1	1
			PSENINI sp. 04	3	1
			PSENINI sp. 05	1	1
	Philanthinae	Aphilanthopini			
			APHILANTHOPINI sp. 01	4	3
		Cercerini			
			Cerceris sp. 01	6	2
			Cerceris sp. 02	6	2
			Cerceris sp. 03	1	1
			Cerceris sp. 04	9	3
			Cerceris sp. 05	1	1
			Cerceris sp. 06	2	2
			Cerceris sp. 07	1	1
			Cerceris sp. 08	1	1
			Cerceris sp. 09	1	1
			Cerceris sp. 10	1	1
			Cerceris sp. 11	3	2
			Cerceris sp. 12	2	1
			Cerceris sp. 13	1	1
			Cerceris sp. 14	3	3
			Cerceris sp. 15	3	2
		Philantini			
			Trachypus sp. 01	3	2
			Trachypus sp. 02	1	1

Family	Subfamily	Tribe/ Subtribe	Morphospecies	A	N
			Trachypus sp. 03	1	1
			Trachypus sp. 04	2	1
			CRABRONIDAE sp. 01	32	6
			CRABRONIDAE sp. 02	4	2
SPHECIDAE	Ammophilinae	Ammophilini			
			Ammophila sp. 01	1	1
	Sceliphrinae	Sceliphrini			
			Podium sp. 01	9	5
			Podium sp. 02	3	3
	Sphecinae	Ammophilini			
			Eremnophila sp. 01	15	7
			Eremnophila sp. 02	5	4
		Prionychini			
			Prionyx sp. 01	31	8
			Prionyx sp. 02	2	1
		Sphecini			
		Sphecina	*Isodontia* sp. 01	1	1
			Sphex sp. 01	3	2
			Sphex sp. 02	3	2
			Sphex sp. 03	2	2
			Sphex sp. 04	2	2
			Sphex sp. 05	1	1
MUTILLIDAE	Mutillinae	Ephutini			
			EPHUTINI sp. 01	59	6
			EPHUTINI sp. 02	124	10
			EPHUTINI sp. 03	24	4
			EPHUTINI sp. 04	5	1
			EPHUTINI sp. 05	14	6
			EPHUTINI sp. 06	1	1

Family	Subfamily	Tribe/ Subtribe	Morphospecies	A	N
			EPHUTINI sp. 07	1	1
		Mutillini			
			MUTILLINI sp. 01	1	1
			MUTILLINI sp. 02	1	1
			MUTILLINI sp. 03	25	8
	Sphaeropthalminae	Sphaeropthalmini			
			SPHAEROPTHALMINI sp. 01	1	1
			SPHAEROPTHALMINI sp. 02	1	1
			SPHAEROPTHALMINI sp. 03	1	1
			SPHAEROPTHALMINI sp. 04	1	1
			SPHAEROPTHALMINI sp. 05	1	1
			SPHAEROPTHALMINI sp. 06	4	1
			SPHAEROPTHALMINI sp. 07	7	3
			SPHAEROPTHALMINI sp. 08	5	3
			SPHAEROPTHALMINI sp. 09	1	1
			SPHAEROPTHALMINI sp. 10	4	2
			SPHAEROPTHALMINI sp. 11	1	1
			SPHAEROPTHALMINI sp. 12	1	1
			SPHAEROPTHALMINI sp. 13	2	1
			SPHAEROPTHALMINI sp. 14	9	5
			SPHAEROPTHALMINI sp. 15	18	5
			SPHAEROPTHALMINI sp. 16	50	5
			SPHAEROPTHALMINI sp. 17	28	6
			SPHAEROPTHALMINI sp. 18	4	1
			SPHAEROPTHALMINI sp. 19	46	5
			SPHAEROPTHALMINI sp. 20	33	4
			SPHAEROPTHALMINI sp. 21	18	2
			SPHAEROPTHALMINI sp. 22	1	1
			SPHAEROPTHALMINI sp. 23	30	3
			SPHAEROPTHALMINI sp. 24	5	4
			SPHAEROPTHALMINI sp. 25	1	1

Family	Subfamily	Tribe/ Subtribe	Morphospecies	A	N
			SPHAEROPTHALMINI sp. 26	7	4
			SPHAEROPTHALMINI sp. 27	2	2
			SPHAEROPTHALMINI sp. 28	3	1
			SPHAEROPTHALMINI sp. 29	91	10
			SPHAEROPTHALMINI sp. 30	23	5
			SPHAEROPTHALMINI sp. 31	1	1
			SPHAEROPTHALMINI sp. 32	6	4
			SPHAEROPTHALMINI sp. 33	1	1
			SPHAEROPTHALMINI sp. 34	1	1
			SPHAEROPTHALMINI sp. 35	7	3
			SPHAEROPTHALMINI sp. 36	1	1
POMPILIDAE					
			POMPILIDAE sp. 01	25	7
			POMPILIDAE sp. 02	20	5
			POMPILIDAE sp. 03	1	1
			POMPILIDAE sp. 04	215	8
			POMPILIDAE sp. 05	101	12
			POMPILIDAE sp. 06	1	1
			POMPILIDAE sp. 07	1	1
			POMPILIDAE sp. 08	1	1
			POMPILIDAE sp. 09	4	2
			POMPILIDAE sp. 10	4	3
			POMPILIDAE sp. 11	3	2
			POMPILIDAE sp. 12	9	2
			POMPILIDAE sp. 13	1	1
			POMPILIDAE sp. 14	3	2
			POMPILIDAE sp. 15	1	1
			POMPILIDAE sp. 16	1	1
			POMPILIDAE sp. 17	2	2
			POMPILIDAE sp. 18	1	1
			POMPILIDAE sp. 19	6	5

Family	Subfamily	Tribe/ Subtribe	Morphospecies	A	N
			POMPILIDAE sp. 20	1	1
			POMPILIDAE sp. 21	6	3
			POMPILIDAE sp. 22	1	1
			POMPILIDAE sp. 23	5	3
			POMPILIDAE sp. 24	6	1
			POMPILIDAE sp. 25	2	1
			POMPILIDAE sp. 26	6	5
			POMPILIDAE sp. 27	6	1
			POMPILIDAE sp. 28	2	1
			POMPILIDAE sp. 29	4	2
			POMPILIDAE sp. 30	2	1
			POMPILIDAE sp. 31	1	1
			POMPILIDAE sp. 32	1	1
			POMPILIDAE sp. 33	1	1
			POMPILIDAE sp. 34	1	1
			POMPILIDAE sp. 35	1	1
			POMPILIDAE sp. 36	1	1
			POMPILIDAE sp. 37	1	1
			POMPILIDAE sp. 38	1	1
			POMPILIDAE sp. 39	1	1
			POMPILIDAE sp. 40	1	1
			POMPILIDAE sp. 41	3	3
			POMPILIDAE sp. 42	1	1
			POMPILIDAE sp. 43	37	10
			POMPILIDAE sp. 44	1	1
			POMPILIDAE sp. 45	5	5
			POMPILIDAE sp. 46	4	3
			POMPILIDAE sp. 47	1	1
			POMPILIDAE sp. 48	1	1
			POMPILIDAE sp. 49	1	1
			POMPILIDAE sp. 50	53	8

Family	Subfamily	Tribe/ Subtribe	Morphospecies	A	N
			POMPILIDAE sp. 51	8	2
			POMPILIDAE sp. 52	1	1
			POMPILIDAE sp. 53	1	1
			POMPILIDAE sp. 54	20	6
			POMPILIDAE sp. 55	1	1
			POMPILIDAE sp. 56	6	4
			POMPILIDAE sp. 57	26	5
			POMPILIDAE sp. 58	8	5
			POMPILIDAE sp. 59	1	1
			POMPILIDAE sp. 60	3	2
			POMPILIDAE sp. 61	219	11
			POMPILIDAE sp. 62	3	3
			POMPILIDAE sp. 63	5	2
			POMPILIDAE sp. 64	18	2
			POMPILIDAE sp. 65	3	2
			POMPILIDAE sp. 66	3	1
			POMPILIDAE sp. 67	2	2
			POMPILIDAE sp. 68	4	4
			POMPILIDAE sp. 69	1	1
			POMPILIDAE sp. 70	5	3
			POMPILIDAE sp. 71	3	3
			POMPILIDAE sp. 72	3	2
			POMPILIDAE sp. 73	8	4
			POMPILIDAE sp. 74	5	2
			POMPILIDAE sp. 75	1	1
			POMPILIDAE sp. 76	2	1
			POMPILIDAE sp. 77	1	1
			POMPILIDAE sp. 78	1	1
			POMPILIDAE sp. 79	1	1
			POMPILIDAE sp. 80	2	1
			POMPILIDAE sp. 81	3	2

Family	Subfamily	Tribe/ Subtribe	Morphospecies	A	N
			POMPILIDAE sp. 82	2	2
			POMPILIDAE sp. 83	2	1
			POMPILIDAE sp. 84	3	3
			POMPILIDAE sp. 85	2	1
			POMPILIDAE sp. 86	3	2
			POMPILIDAE sp. 87	3	1
			POMPILIDAE sp. 88	1	1
			POMPILIDAE sp. 89	1	1
			POMPILIDAE sp. 90	16	4
			POMPILIDAE sp. 91	1	1
			POMPILIDAE sp. 92	1	1
			POMPILIDAE sp. 93	4	2
			POMPILIDAE sp. 94	2	1
			POMPILIDAE sp. 95	4	1
			POMPILIDAE sp. 96	1	1
			POMPILIDAE sp. 97	1	1
			POMPILIDAE sp. 98	2	1
			POMPILIDAE sp. 99	4	1
			POMPILIDAE sp. 100	1	1
			POMPILIDAE sp. 101	1	1
			POMPILIDAE sp. 102	1	1
			POMPILIDAE sp. 103	3	1
			POMPILIDAE sp. 104	9	5
			POMPILIDAE sp. 105	3	1
			POMPILIDAE sp. 106	1	1
			POMPILIDAE sp. 107	1	1
			POMPILIDAE sp. 108	18	1
			POMPILIDAE sp. 109	69	1
			POMPILIDAE sp. 110	22	1
			POMPILIDAE sp. 111	15	1
			POMPILIDAE sp. 112	84	4

Family	**Subfamily**	**Tribe/ Subtribe**	**Morphospecies**	**A**	**N**
			POMPILIDAE sp. 113	10	1
			POMPILIDAE sp. 114	4	4
			POMPILIDAE sp. 115	3	1
			POMPILIDAE sp. 116	1	1
			POMPILIDAE sp. 117	1	1
			POMPILIDAE sp. 118	16	2
			POMPILIDAE sp. 119	2	2
			POMPILIDAE sp. 120	2	1
			POMPILIDAE sp. 121	2	2
			POMPILIDAE sp. 122	1	1
			POMPILIDAE sp. 123	1	1
			POMPILIDAE sp. 124	1	1
			POMPILIDAE sp. 125	1	1
			POMPILIDAE sp. 126	1	1
SCOLIIDAE	Scoliinae	Campsomerini			
			Campsomeris Lissocampsomeris sp. 01	1	1
			Campsomeris Pygodasis sp. 01	2	2
			Campsomeris Pygodasis sp. 02	2	1
			Campsomeris Pygodasis sp. 03	1	1
			Campsomeris Pygodasis sp. 04	1	1
			Campsomeris Rhabdotomeris sp. 01	2	2
			Campsomeris Rhabdotomeris sp. 02	1	1
			Campsomeris Rhabdotomeris sp. 03	2	1
			Campsomeris Stygocampsomeris sp. 01	3	2
			Campsomeris Stygocampsomeris sp. 02	2	2
			Campsomeris Stygocampsomeris sp. 03	2	1
			Campsomeris Xanthocampsomeris sp. 01	4	3
TIPHIIDAE	Myzininae				
			Myzinum sp. 01	6	4
			Myzinum sp. 02	72	9
			Myzinum sp. 03	1	1

Family	**Subfamily**	**Tribe/ Subtribe**	**Morphospecies**	**A**	**N**
			Myzinum sp. 04	1	1
			Pterombrus sp. 01	6	2
			Pterombrus sp. 02	3	2
	Thynninae	Rhagigasterini			
			Aelurus sp. 01	6	4
			Aelurus sp. 02	13	3
			Aelurus sp. 03	1	1
		Scotaenini			
			Scotaena sp. 01	6	2
			Scotaena sp. 02	107	4
			Scotaena sp. 03	51	2
			Scotaena sp. 04	2	1
			Scotaena sp. 05	1	1
			Zeena sp. 01	49	2
			Zeena sp. 02	11	2
			SCOTAENINI sp. 01	2	2
			SCOTAENINI sp. 02	1	1
			SCOTAENINI sp. 03	2	1
			THYNNINAE sp. 01	14	4
			THYNNINAE sp. 02	12	2
	Tiphiinae				
			Tiphia sp. 01	43	5
			Megatiphia sp. 01	94	9
VESPIDAE	Eumeninae				
			Zethus sp. 01	3	3
			Zethus sp. 02	2	1
			Zethus sp. 03	1	1
			Zethus sp. 04	1	1
			Zethus sp. 05	1	1
			Zethus sp. 06	1	1
			EUMENINAE sp. 01	7	3

Family	Subfamily	Tribe/ Subtribe	Morphospecies	A	N
			EUMENINAE sp. 02	3	3
			EUMENINAE sp. 03	1	1
			EUMENINAE sp. 04	1	1
			EUMENINAE sp. 05	3	1
			EUMENINAE sp. 06	3	3
			EUMENINAE sp. 07	1	1
			EUMENINAE sp. 08	1	1
			EUMENINAE sp. 09	2	2
			EUMENINAE sp. 10	4	2
			EUMENINAE sp. 11	7	4
			EUMENINAE sp. 12	3	2
			EUMENINAE sp. 13	1	1
			EUMENINAE sp. 14	1	1
			EUMENINAE sp. 15	1	1
	Polistinae	Epiponini			
			Agelaia pallipes (Olivier, 1791)	66	9
			Agelaia sp. 01	23	6
			Agelaia sp. 02	70	3
			Agelaia sp. 03	6	4
			B*rachygastra* sp. 01	13	7
			Parachartergus sp. 01	3	2
			Polybia erythrothorax (Richards, 1978)	4	3
			Polybia ignobilis (Haliday, 1836)	115	12
			Polybia paulista von Ihering, 1896	3	2
			Polybia scrobalis Richards, 1970	371	12
			Polybia scutellaris (White, 1841)	59	6
			Polybia sericea (Olivier, 1792)	281	11
			Polybia tinctipennis Fox, 1898	4	2
			Polybia sp. 01	7	3
			Polybia sp. 02	4	3
			Polybia sp. 03	2	2

Family	**Subfamily**	**Tribe/ Subtribe**	**Morphospecies**	**A**	**N**
			Polybia sp. 04	2	1
			Polybia sp. 05	1	1
			Polybia sp. 06	1	1
			Polybia sp. 07	2	1
			Polybia sp. 08	19	6
			Polybia sp. 09	116	7
			Polybia sp. 10	1	1
			Protonectarina sylveirae (Saussure, 1854)	26	6
		Myschocyttarini			
			Myschocyttarus sp. 01	36	7
			Myschocyttarus sp. 02	1	1
			Myschocyttarus sp. 03	2	2
		Polistini			
			Polistes thoracicus Fox, 1898	1	1
			Polistes lanio (Fabricius, 1775)	16	7
			Polistes sp. 01	2	1
			Polistes sp. 02	27	9
			Polistes sp. 03	12	4
			Polistes sp. 04	1	1
			Polistes sp. 05	2	1

1910

Table S3. Bee’s diversity values of each sampled locality in mountain’s upper and lower sites. Turnover (β_{SIM}), Nestedness (β_{NES}) and overall beta diversity (β_{SOR}), measured as Sørensen multisite dissimilarity indices.

	Locality	**Site**	**Alpha (α)**	**Local Gamma (γ)**	**Beta W (β)**	**Turnover**	**Nestedness**	**Beta (β_{SOR})**	**Total (γ)**
1	P.N. Chapada Diamantina	Upper	6	22	3.67	0.60	0.25	0.85	25
		Lower	1.4	5	3.57				
2	Pico do Barbado	Upper	10.4	32	3.08	0.63	0.13	0.75	42
		Lower	4.8	16	3.33				
3	Pico das Almas	Upper	15.6	49	3.14	0.80	0.04	0.84	50
		Lower	2.2	8	3.64				
4	Pico da Formosa - Monte Azul	Upper	13.6	37	2.72	0.13	0.63	0.75	51
		Lower	10.2	31	3.04				
5	P.E. Serra Nova	Upper	19.8	52	2.63	0.45	0.05	0.50	57
		Lower	8.4	20	2.38				
6	Botumirim	Upper	5.8	21	3.62	0.25	0.33	0.58	36
		Lower	4.8	20	4.17				
7	P.E. do Rio Preto	Upper	10	30	3.00	0.75	0.01	0.76	46

		Lower	6.4	20	3.13				
8	P.E. Pico do Itambé	Upper	13.2	43	3.26	0.42	0.22	0.65	51
		Lower	5.6	19	3.39				
9	Pico do Breu - Serra do Cipó	Upper	9.2	31	3.37	0.56	0.14	0.70	40
		Lower	4.2	16	3.81				
10	RPPN Santuário do Caraça	Upper	14	38	2.71	0.60	0.31	0.91	41
		Lower	1.8	5	2.78				
11	P.E. Pico do Itacolomi	Upper	12.2	35	2.87	0.46	0.25	0.71	41
		Lower	3.8	13	3.42				
12	P. E. Serra do Ouro Branco	Upper	14.4	38	2.64	0.20	0.47	0.67	40
		Lower	2.8	10	3.57				

Table S4. Wasp's diversity values of each sampled locality in mountain's upper and lower sites. Turnover (β_{SIM}), Nestedness (β_{NES}) and overall beta diversity (β_{SOR}), measured as Sørensen multisite dissimilarity indices.

	Locality	**Sites**	**Alpha (α)**	**Local Gamma (γ)**	**Beta W (β)**	**Turnover**	**Nestedness**	**Beta (β_{SOR})**	**Total (γ)**
1	P.N. Chapada Diamantina	Upper	15	48	3.20	0.60	0.13	0.73	63
		Lower	8.2	25	3.05				
2	Pico do Barbado	Upper	32.8	98	2.99	0.50	0.33	0.83	108
		Lower	5.6	20	3.57				
3	Pico das Almas	Upper	39.6	108	2.73	0.82	0.04	0.87	121
		Lower	10.2	31	3.04				
4	Formosa - Monte Azul	Upper	32.8	90	2.74	0.42	0.32	0.74	128
		Lower	32.6	82	2.52				
5	P.E. Serra Nova	Upper	67.4	162	2.40	0.46	0.02	0.49	191
		Lower	32.2	84	2.61				
6	Botumirim	Upper	14.8	51	3.45	0.35	0.21	0.55	100
		Lower	23.2	70	3.02				
7	P.E. do Rio Preto	Upper	17.4	56	3.22	0.59	0.06	0.65	84

		Lower	10	34	3.40				
8	P.E. Pico do Itambé	Upper	42.2	124	2.94	0.42	0.39	0.81	134
		Lower	8.6	24	2.79				
9	Breu - Serra do Cipó	Upper	28	74	2.64	0.40	0.40	0.80	80
		Lower	5.4	15	2.78				
10	RPPN Caraça	Upper	29.2	92	3.15	0.75	0.23	0.98	95
		Lower	1.2	4	3.33				
11	P.E. Pico do Itacolomi	Upper	32.8	93	2.84	0.55	0.28	0.83	105
		Lower	7.8	22	2.82				
12	P. E. S. do Ouro Branco	Upper	42.4	130	3.07	0.41	0.39	0.80	141
		Lower	8	27	3.38				

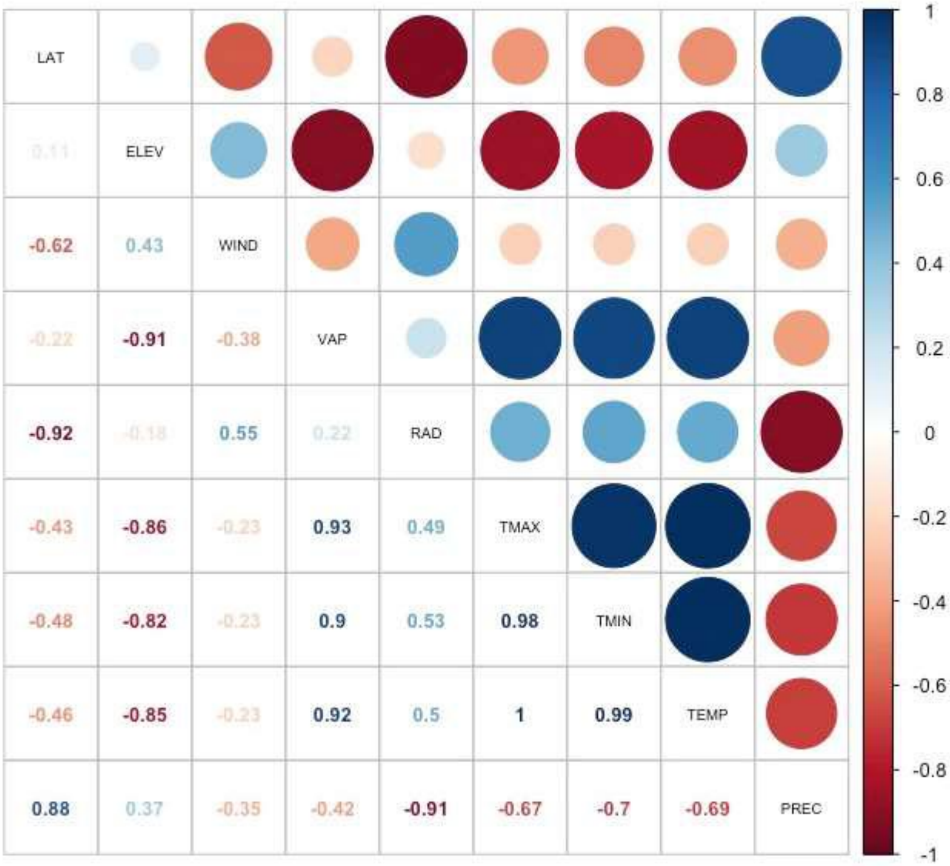

Fig. S1. Pearson's correlation coefficient (r) among latitude (LAT), elevation (m asl) (ELEV) and WorldClim v2 variables (1970-2000) for sampled coordinates. Only wind speed was not correlated with those spatial variables (latitude and elevation). Mean values of wind speed (m s^{-1}) (WIND), water vapor pressure (kPa) (VAP), solar radiation (kJ m^{-2} day^{-1}) (RAD), maximum temperature (°C) (TMAX), minimum temperature (°C) (TMIN), temperature (°C) (TEMP) and precipitation (mm) (PREC). Red colors indicate negative correlations and blue colors indicate positive correlations while larger circles indicate higher correlation. A r-value equal or greater than 0.7 were the parameter to consider correlated variables.

Considerações finais e perspectivas

Concluímos que vespas e abelhas são um bom modelo para estudos de comunidade nas montanhas brasileiras, com ressalvas para os problemas taxonômicos do grupo. Algumas importantes contribuições da tese podem ser destacadas como: (1) existe uma elevada substituição de espécies entre comunidades de diferentes faixas altitudinais; (2) uma maior distância entre fragmentos de mata e a mata contínua aumenta a substituição de espécies ao longo do tempo (turnover temporal); (3) temperatura é o principal mecanismo modelador das comunidades de vespas e abelhas nos campos rupestres; (4) variações altitudinais sobrepujam as latitudinais na determinação das comunidades de vespas e abelhas da Cadeia do Espinhaço.

Pretendemos ainda explorar a frequência das espécies comuns e raras ao longo do gradiente latitudinal e altitudinal. Importantes informações podem ser retiradas dos padrões de exclusividade em diferentes altitudes. Espécies raras nos topos de montanha podem indicar um maior risco de extinções frente ao cenário de mudanças climáticas. Os dados das espécies de formiga (Formicidae) ainda serão inseridos no Capítulo 3, abrindo a possibilidade de discussões sobre diversidade funcional devido ao fato de ser um grupo bem resolvido taxonomicamente.

É válido ressaltar a contribuição deste trabalho para reduzir a lacuna na coleta de dados de vespas e abelhas ao longo da Cadeia do Espinhaço. Ao todo, foram coletados mais de 13.000 espécimes do grupo Aculeata (sem contar as formigas). Todo o material biológico coletado está em processo de depósito na Coleção Entomológica das Coleções Taxonômicas da Universidade Federal de Minas Gerais (UFMG) e estará à disposição dos especialistas. Várias parcerias estão em andamento e até o momento temos confirmadas duas novas espécies de Dryinidae para a ciência (André Martins - UFPR). Dentre os himenópteros ainda temos prováveis espécies novas de Leucospidae, Aulacidae e Ichneumonidae (Alessandro Lima - UFMG) e Perilampidae (Chris Darling - Royal Ontario Museum). Encontramos também uma espécie nova de borboleta (Lucas Kaminski - UFRGS). Teremos outras inúmeras espécies novas para a ciência, sobretudo para grupos taxonômicos não utilizados na tese. O material coletado está sendo aproveitado em uma dissertação e duas teses em andamento.

O conhecimento das variações em diversidade e composição de espécies entre os topos e as bases das montanhas nas diferentes latitudes, somado à revisão taxonômica das espécies, pode definir parâmetros essenciais para a conservação efetiva das espécies, ecossistemas e serviços ambientais das montanhas tropicais, sugerindo áreas insubstituíveis para conservação de vespas e abelhas. Os campos rupestres merecem um constante incentivo à pesquisa.

Anexo I

Capa do artigo publicado no periódico PLOS ONE:

Perillo et al. 2017. Compositional changes in bee and wasp communities along Neotropical mountain altitudinal gradient.

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RESEARCH ARTICLE

Compositional changes in bee and wasp communities along Neotropical mountain altitudinal gradient

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Abstract

Climate conditions tend to differ along an altitudinal gradient, resulting in some species groups' patterns of lower species richness with increasing altitude. While this pattern is well understood for tropical mountains, studies investigating possible determinants of variation in beta-diversity at its different altitudes are scarce. We sampled bee and wasp communities (Hymenoptera: Aculeata) along an altitudinal gradient (1,000–2,000 m.a.s.l.) in a tropical mountainous region of Brazil. Trap nests and Moericke traps were established at six sampling points, with 200 m difference in altitude between each point. We obtained average climate data (1970–2000) from Worldclim v2 for altitudes at each sampling site. Nest traps captured 17 bee and wasp species from six families, and Moericke traps captured 124 morphospecies from 13 families. We found a negative correlation between altitude and species richness and abundance. Temperature, precipitation, water vapor pressure, and wind speed influenced species richness and abundance, and were correlated with altitude. β-diversity was primarily determined by species turnover as opposed to nestedness, and Aculeate community similarity was higher for more similar altitudinal ranges. Moericke traps seem to be more efficient for altitudinal surveys compared to nest traps. We found high occurrence of singleton and doubleton species at all altitudes, highlighting the need for long-term studies to efficiently assess hymenopteran diversity in these environments.

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Data Availability Statement: The authors confirm that all data underlying this study are fully available without restriction. Dataset are available at KNB Data Repository under the name "Lucas Perillo. 2017. Perillo 2017 Bee and Wasp RPPN Santuário do Caraça. KNB Data Repository. doi:10.5063/F1K935G9", or using the link: https://knb.ecoinformatics.org/#view/doi:10.5063/F1K935G9.

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Introduction

Beta-diversity (β) is a property of complex biological communities [1,2], and is inherently connected to large-scale measurements of species richness (i.e., gamma-diversity) through the species–area relationship found for nearly all organisms investigated thus far [3,4]. However, less attention has been paid to patterns of β-diversity [5–7], and the relative importance of environmental and geographic variables for beta diversity remains controversial. Although the importance of β-diversity to gamma-diversity has been investigated for several taxa and environments

Anexo II

Artigo publicado com participação do candidato no periódico FLORA:

Coelho et al. 2017. Forest archipelagos: A natural model of metacommunity under the threat of fire.

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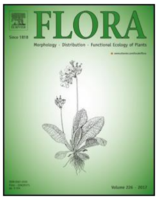

Forest archipelagos: A natural model of metacommunity under the threat of fire

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1. Introduction

One of the most important precepts of the modern conservation biology is the synergism between the efforts to protect speciose ecosystems and the ecological processes responsible for maintaining important environmental services (Kareiva and Marvier, 2012). Although the Brazilian vegetations are well studied, a unique ecosystem has received little attention by the scientific community and policy makers. Locally called *Capões de Mata* – hereafter – Atlantic forest islands, or simply forest islands – the natural islands of forests on the open grassland matrix of Espinhaço mountain range are examples of an ecosystem with relevant biodiversity associated to the protection of headwaters. The headwaters under forest islands feed important Brazilian river basins. The ecological regime – e.g. ombrophilous or semi-deciduous – dynamic of genesis and expansion, the existence of meta-community processes, and which ecoregions plays a major influence on its structure and composition – if Atlantic Rainforest or Cerrado (i.e., Brazilian savanna) – have only recently started to be deeply discussed (Coelho et al., 2016).

Despite occurring on mountaintops and in a transition zone between two phytogeographic domains, they are predominantly under influence of the Atlantic Rainforest, a biodiversity hotspot (Myers et al., 2000). The Atlantic Forest Act (Federal Law 11.428/2006) recognizes ombrophilous and semi-deciduous forests as part of the Atlantic Forest domain. However, the scale size of the thematic map which the law is mostly based on does not allow the recognition of small forest disjunctions, as the Atlantic forest islands from Espinhaço range. Although these natural islands of tropical Atlantic forest have been mostly neglected, they are part of critically endangered hotspot of biodiversity and harbor several endangered species in need of study.

The forest islands of Espinhaço Range are surrounded by a matrix dominated by the rupestrian grasslands, locally called *campo rupestre*, a fire-prone vegetation mosaic adapted to burning and largely accept as a component of cerrado savanna domain (but see Silveira et al., 2016). While fire is an important ecological force driving the evolution of the dominant grasslands and scrublands of rupestrian grasslands and its component species (Alvarado et al., 2017), it can be a significant threat to the conservation of forest islands. This discrepancy poses a dilemma to fire management policy in a mosaic of fire-sensitive and fire-tolerant vegetation.

Considering the above scenario, here we address the ecology of natural forest islands and we (i) discuss the disjunction from the Atlantic Rainforest and their conservation status; (ii) argue that fire is a major threat to forest islands conservation, proposing possible management strategies, and (iii) highlight the relevance of the islands as suppliers of ecosystem services and as an unexploited natural model for testing ecological and evolutionary hypotheses (e.g., metacommunity dynamics).

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2. Atlantic forest islands: location and landscape dynamics

The mountaintops of the Espinhaço Range are one of the few tropical areas that have remained stable during past climate changes, with emphasis on the latest considerable changes dating back to the Pleistocene period (Barbosa and Fernandes, 2016). It is likely that this ecological stability has been a driver of its high endemism (Hopper, 2009; Barbosa and Fernandes, 2016). The southern region of Espinhaço is influenced by the humid Atlantic tropical mass on its eastern face, as well as at high altitudes, leading to elevate rates of rainfall/humidity and stabilization in the form of Fronts of Stationary Nebulosity (Streher et al., 2017). The Atlantic tropical mass carries humidity from the Atlantic coast via jet streams, which fall as rain at high altitudes in the southern region of the Espinhaço Range, feeding specially the basins of the Doce river (to the east) and the São Francisco river (to the west). Thus, the Atlantic rainforest acts on the eastern face (windward), especially in the drainage zones, and maintains an influence over the higher altitudinal strata of the western face (leeward). As a result of the distinct climatic conditions, this regional landscape hosts elements of the Atlantic Forest (*sensu* Oliveira and Fontes, 2000) to the east and elements of the Cerrado to the west. Unlike the eastern face, which is mostly covered by semi-deciduous forest and, when close to the drainage and wet zones, cloud forests, the western face hosts a mosaic of vegetation' physiognomies associated with the Cerrado. The higher altitudes – mountaintops and plateaus – represent transitional zones between the two phytogeographic domains (Cerrado and Atlantic Forest) and are dominated by rupestrian grasslands (Silveira et al., 2016), gallery forests and forest islands (see Coelho et al., 2016 for a review).

The forest islands of the Espinhaço are natural islands of forest with floristic compositions very similar to the semi-deciduous forests of the Atlantic Forest domain, but with a climate system associated with cloud forests (Meguro et al., 1996; Souza, 2009; Valente, 2009; Coelho et al., 2016). These forest islands are surrounded by rupestrian grasslands (old climatically-buffered infertile landscapes - OCBIL) (Silveira et al., 2016), and established on well drained, deep and low acidic clay soil patches (Figs. 1 and 2). Therefore, the forest islands fit into environmentally suitable zones formed by quite specific soil and climate conditions (Fronts of Stationary Nebulosity), characteristics of edaphoclimatic vegetation (Rizzini, 1997). This forest ecosystem can establish in regions close to the mountains plateaus and ridges (~1200 m a.s.l.) that make up the Espinhaço Range, only under the combination of these specific environmental conditions (Coelho et al., 2016).

The landscape location and dynamics represent a rare natural opportunity to test hypotheses under relevant ecological frameworks as those related to the island biogeography and metacommunity theories (Leibold et al., 2004; Thompson, 2005). The forest archipelagos are composed by forest islands abruptly separated by a matrix of rupestrian grasslands, both comprising native ecosystems. The forest islands are of different sizes, shapes and distances to the nearest island or to the continuous forest (Fig. 2). This natural landscape feature bears similarities to other novel and fragmented ecosystems due to their high level of isolation and may bring some insights, for instance, into the effects of isolation on plant reproduction (Hagen et al., 2012). Important ecological lessons could be drawn and applied to the dominant landscape realities under conservation threat. The effects of landscape configuration on structuring communities could also be emphasized under the light of principles derived from niche theory and species-sorting models where species differ in their responses to distinct environmental conditions (Chase and Leibold, 2003). Both, dispersal processes and habitat conditions for species establishment are fundamental to understanding how communities are structured and their level of integration among islands (Jamoneau et al., 2011). Therefore, how one ecosystem gives place to the other has been recently debated in the literature, especially in the vegetations of Páramos where is clear the transition between grasslands, at the top, and forest ecosystems, at the bottom of mountains (Rehm and Feeley, 2015). The drivers behind the maintenance of these ecotones could be better understood in natural laboratories such as the forest islands.

Fig. 1. Atlantic Forest Islands from Serra do Cipó, south Espinhaço Range, Minas Gerais, Brazil. ab. Outside and inside views from typical forest islands; cd. Inside and outside views from a typical forest islands after a fire event.

3. Ecosystem dynamics and environmental services

By forming archipelagos of forest amid grassland ecosystems, the forest islands host a phylogenetically and functionally distinct flora from the surrounding matrix, increasing local and regional species diversity, and likely, serving as refuge for the local fauna (Pereira et al., 2017). Despite the existence of many animal groups endemic to the rupestrian grassland (see Fernandes, 2016), as well as those endemic to the forest islands, evidence suggest the existence of a fauna flow between the two physiognomies (Pereira et al., 2017); especially from groups responsible for ecosystem functions, such as pollinators.

Preliminary data from long-term research project (Long term ecological research from rupestrian grasslands –CRSC) points out to the existence of a dynamic of insect metacommunities among forest islands (Pereira et al., 2017). The rupestrian grassland surrounding the forest islands seem to play a key role in maintaining diversity due to its permeability and resource supply. However, we do not know yet the function of forest islands as connectors/refuges as well as the isolation level considering the complex vegetation of rupestrian grasslands mosaic, and its importance in providing resources as flowers, fruits and leaves, places to rest and nest. For-

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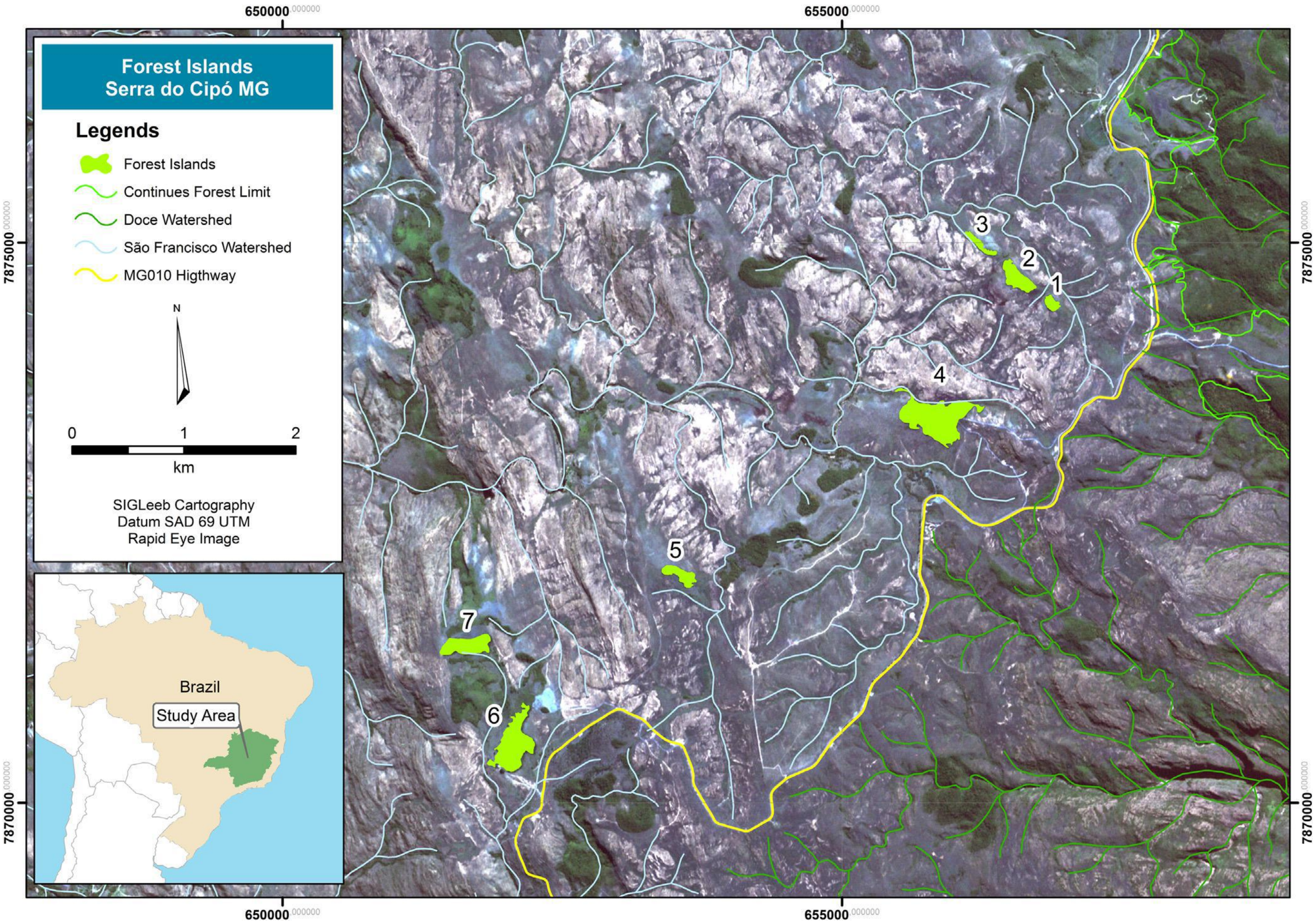

Fig. 2. Location of the seven atlantic forest islands sampled by Coelho et al. (2017) in the Serra do Cipó, south Espinhaço Range, Minas Gerais, Brazil, associated with the basins and sub-basins of the Rio São Francisco and Rio Doce rivers (source: Minas Gerais State Water Management Institute).

est islands are likely the nesting place and refuge for many animals, most of them – such as large bees and hummingbirds – are the most important long-distance pollinators of many species from the surrounded grasslands (Carstensen et al., 2014), and supporting the diversity of ecological interactions. For instance, hummingbirds pollinate up to 13% of species while large bees may account for 70% of pollination services in this ecosystem (Guerra et al., 2016) and may use the forest as shelter or nest. That proportion does not take into account the pollinators specialists of forest island species *per se*. Forest islands also host most of small mammals and several birds that also play a key role as seed dispersers (Guerra et al., 2016).

The permeability of the landscape can be altered by the plant community phenology (driven by cold winters and humid summers), as well as the action of frequent fire occurrence (Figueira et al., 2016; Alvarado et al., 2017; Streher et al., 2017). Besides their ecological importance, the forest islands establish into humid locations, with well-drained soils, associated with springs and streams (Coelho et al., 2016). The protection service of water intake environments is important, the springs responsible for feeding two of the most important Brazilian river basins, which are responsible for much of the water supply of some of the major Brazilian cities, such as Belo Horizonte (see Fig. 2, Silveira et al., 2016). Those basins are already environmentally compromised by human occupation, fishery overexploitation, exotic species introduction, constant sedimentation and damage on rivers' headwaters (see Galindo-Leal and Câmara, 2005), including one of the largest Brazilian environmental disaster, a mud tsunami caused by a mining dam rupture that invaded Rio Doce basin on 2015 (Fernandes et al., 2016). According to the Brazilian forest code (Law 12.651/2012), all springs, no matter whether perennial or seasonal, as well as mountaintops must be permanently protected. The same can be applied for gallery forests. According to the scientific definition, forest islands must be under the very restrictive terms of use as described in the Atlantic Forest Act (Federal Law N° 11.428/2006) and treated as permanent protection area by the Brazilian forest code (Federal Law N° 12.651/2012). Hence, those laws could guarantee protection of a high number of endangered species – the sampling of the forest islands already recorded 18 plant species under some threaten categories (Martinelli and Moraes, 2013). Recent findings detected important differences in species composition between gallery and the forest islands (Coelho et al., 2016), and this diversity patterns have strong implications to conservation strategies deepening on a holistic view of the landscape complexity.

4. Fire: the main threat to conservation

Fire stands out as one of the most serious threat to forest islands. Fire has been an important evolutionary factor in savannas and grasslands, as its effects exert a strong environmental filter on forest cover. Many studies have demonstrated the role of fire in re-shaping the borders of savannas as well as functional plant adaptations driving from population to ecosystems (Hoffmann et al., 2003; Veldman et al., 2015; Dantas et al., 2016).

There are three main drivers that control the boundaries between the savannas and other physiognomies (e.g. wet forests):

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climate, soil and fire. From a strictly climatic point of view, the forests that now occupy approximately 25% of the Earth's surface have the potential to expand to at least 50% area, especially covering parts of the savannas of South America and Africa (Bond et al., 2005; Veldman et al., 2015). The species comprising the forests have functional advantages over their congeneric savanna species because they have faster growth and higher productivity rates, altering the balance between the boundaries of the ecosystems (Dantas et al., 2016).

Soil may also play an important role in savanna-forest boundaries, especially under similar climate (Bond, 2010). Although some regions covered by savanna formations have a sufficient amount of nutrients for forest development in the deeper soil layers, the granulometric structure and shallow soils of rupestrian grassland are factors restricting forest expansion (Valente, 2009). The third driver is the intense and frequent occurrence of fires (Alvarado et al., 2017). Fire plays a key role in controlling forests expansion, generating environmentally suitable zones that only adapted species could occupy (Hoffmann et al., 2003; Rossatto et al., 2009). Fire is a strong environmental filter and only groups of species with specific traits are able to maintain the composition, structure and ecological dynamics of fire-prone vegetation (Veldman et al., 2015). Savanna and associated vegetation have fire resistance traits (e.g. thicker barks, sclerophylly, underground storage organs), which, in conjunction with the environmental characteristics, make savannas functionally distinct from forests (Miatto et al., 2016). In the absence of fire, fire-dependent vegetation (Bond et al., 2005; Dantas et al., 2016) suffers changes in species composition, structure and dynamics. On that new condition of fire suppression, fire-sensitive species enhance establishment over other species due to its physiological advantages (e.g. higher growth rates), changing the groups of species, canopy formation and eliminating herbaceous-shrub component (main fuel for fire occurrence and intensification) (Bond, 2008; Veldman et al., 2015).

Those particular plant communities are confined to specific soil patches that support dense and moist vegetation, composed of species more characteristic of the Atlantic Rainforest domain (Coelho et al., 2016). Tree species reaches the mountaintops, scattered through the gallery forests, stemming predominantly from the eastern face of the Espinhaço Range (Meguro et al., 1996; Souza, 2009; Valente, 2009; Coelho et al., 2016). The increase in frequency and intensity of anthropogenic fires in the last decades (Alvarado et al., 2017) have been causing a strong effect on these islands, reducing them from their borders. The forest islands have likely gradually decreased in area over dry seasons accompanied by frequent and intense fire events.

The fire burns away the array of rupestrian grassland, a vegetation high resilience to fire, with important adaptations, such as below-ground biomass storage and sclerophylly (Figueira et al., 2016; Silveira et al., 2016). The edges of the forest islands are strongly impacted because of the death of the trees, which are not fire-resistent, hence promoting a succession zone (Staver et al., 2011; Coelho et al., 2016) or even excluding the forest vegetation (Fig. 1c,d). All studies carried out on forest islands have reported on the impacts of fire (see Coelho et al., 2016 for a review). Because forest islands are high-humidity environments, with the central regions of the forest islands with large trees, fire causes greater impacts to the edges of the islands (Tabarelli et al., 2008). In a study conducted on forest islands at Rio Preto State Park (PERPreto), also located in the Espinhaço Range, Souza (2009) found significant floristic differences between the edge and the central regions of the forest islands. Tree density, stem diameter, average height of individual trees, richness and species diversity varied noticeably between the border and the central areas of the forest islands evaluated, indicating that the forest islands present a clear edge effect and fire-sensitive species (Souza 2009).

In a study of soils in a grassland-forest vegetation gradient in Serra do Cipó, Valente (2009) identified strong differences in the physical and chemical soil properties collected at different points in the forest islands. The soil conditions in the central areas were more favorable to the establishment of late successional species than in the edges (Valente, 2009).

Another likely consequence is an increase in permissiveness to biological invasion and homogenization among forest islands (Arroyo-Rodriíguez et al., 2013). Despite the inventories conducted up to date at the forest islands have no records of invasive species (Coelho et al., 2016), some pioneer species were already found, indicating the presence of disturbance (e.g., *Eremanthus erithropappus*) (Coelho et al., 2016). We suggest a stabilization of the area occupied by the forest islands in the unlikely scenario of total fire suppression, as a consequence of the strong connection on soil patches. On the other hand, the increase in fire intensity and extension could eventually lead to the extinction or drastic reduction of the forest islands, giving space to smaller islands composed predominantly by opportunistic and fast growth species. We have also observed over the last years that deep-burned edges of some forest islands/patches at Serra do Cipó have not regenerated two years after fire (Fig. 3). This instable scenario facilitates cattle access to the forests interior. Therefore, the fires regime on the Espinhaço mountaintops (see Alvarado et al., 2017), in synergy with other factors, may threaten the maintenance of the functions and ecosystem services of the forest islands, and have to be taken into account due to the contrasting roles on the rupestrian grassland matrix.

5. The need to conservation policies

Despite their relevance from an ecological and economic perspective, the forest islands of the Espinhaço Range are under increasing threat. Local landscape uses are numerous and can vary from pasture for livestock to selective logging of individual tree species for firewood (Kolbek and Alves, 2008). Because these plant formations are home to a variety of ferns and herbaceous angiosperms (orchids, bromeliads and aroids), the illegal trade of these species for use in landscaping is common (Coelho et al., 2016).

The dissemination of knowledge about the functions and services of the ecosystem performed by the forest islands associated with the Espinhaço Range is imperative. Moreover, increased monitoring by environmental agencies is a *sine qua non* condition to curb the illegal collection of species and wood for landscaping. The monitoring may also reduce fire frequency. In the face of small dimensions of the forest islands the use of unmanned aerial vehicles or drones is an alternative strategy to monitor and detect changes in the landscape over time (Fig. 3). However, when fire is inevitable, it should be managed. The implementation of firebreaks could be an alternative (Ramos-Neto and Pivello, 2000). The main disturbance responsible for a transitory increase in the biodiversity is windstorms causing mostly tree falls (Coelho et al., 2016). Fire suppression may lead to more intense and extensive fires (Alvarado et al., 2017), which imposes severe threats to forest islands. The impossibility of deploying firebreaks in all forest islands over the Espinhaço range suggests the development of strategies targeting specific islands to manage, based on their ecological dynamics, role as connectors and providers of important ecosystem services.

The forest islands must be clearly recognized as a vegetation type under the umbrella of the very restrictive terms of use provided by the Atlantic Forest Act (Federal Law N° 11.428/2006) and also treated as Permanent Protection Area (PPA) by the Brazilian forest code (Federal Law N° 12.651/2012) (Coelho et al., 2016). Thereby, even the archipelagos of natural forests lying outside protected areas would be fully protected. Brazilian society must learn about, be concerned, and draw up conservation strategies dedi-

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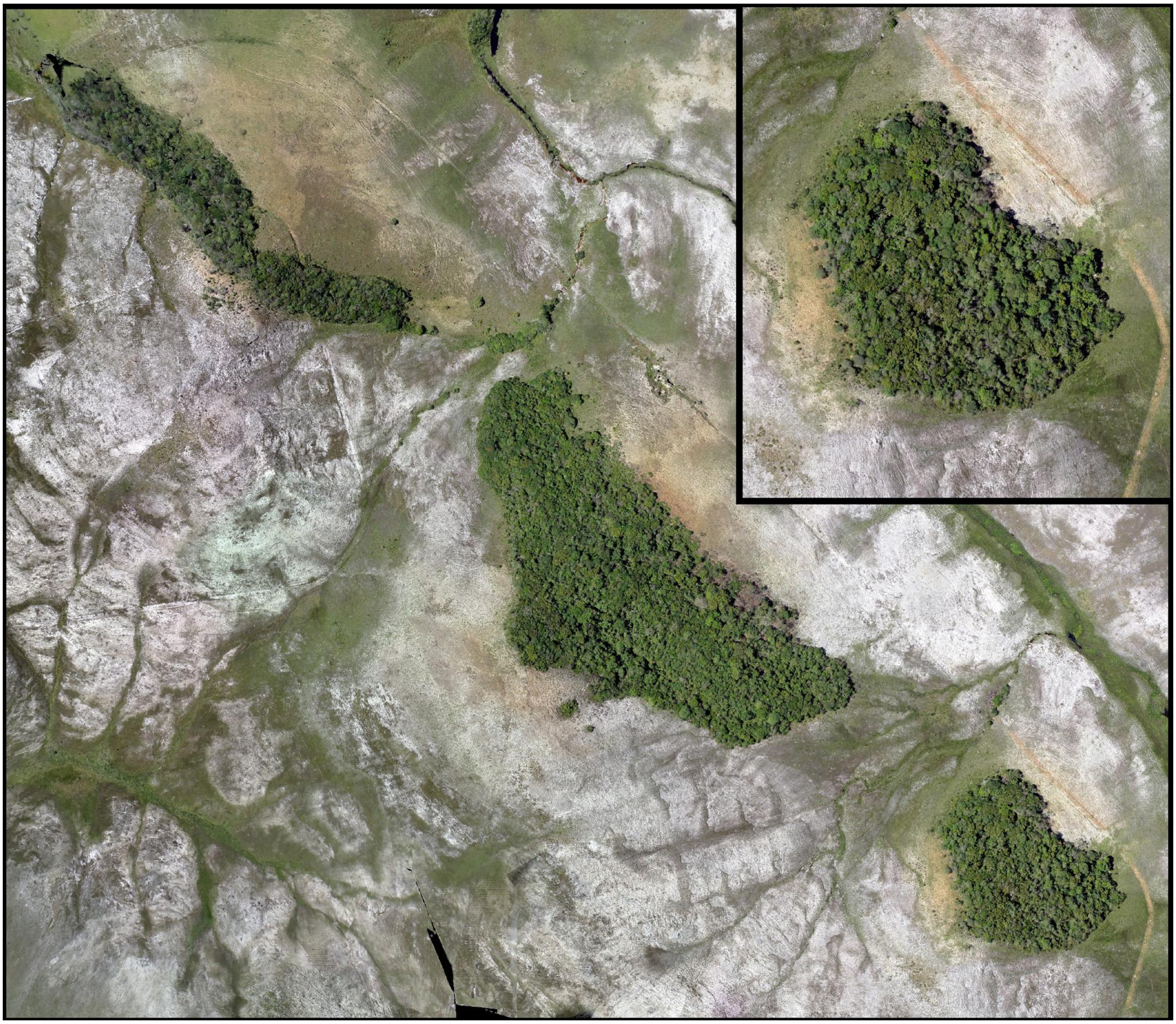

Fig. 3. Three atlantic forest islands in the Serra do Cipó, south Espinhaço Range, Minas Gerais, Brazil. The highlighted Island is impacted by fire at the edge. Image in real color acquired by unmanned aerial vehicle of fixed wing, camera Canon SX260, at a distance of 120 m from the ground, with spatial resolution of approximately 5 cm. Date: December 2016.

cated to this unique and increasingly threatened ecosystem, or they will be liable for the environmental and economic costs related to its degradation.

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Anexo III

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Capões de Mata: Arquipélagos florestais pouco conhecidos e ameaçados

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Resumo

Em regiões acima de 1.200 metros ao longo da Cadeia do Espinhaço é comum a presença de ilhas naturais de florestas associadas às nascentes de rios. O objetivo deste trabalho foi descrever as dinâmicas ecológicas das ainda pouco conhecidas e pesquisadas ilhas florestais naturais associadas à Cadeia do Espinhaço com ênfase nas principais ameaças à sua conservação e; nas perdas dos serviços ecossistêmicos associados à um possível processo de degradação. Em consequência de sua localização, Capões de Mata são influenciados pelo domínio da Mata Atlântica à leste, e pelo Cerrado à oeste. Apesar da importância para a manutenção de cabeceiras de tributários de importantes rios, a exemplo do Rio Doce e Rio das Velhas, capões de mata receberam pouca atenção de pesquisadores mesmo estando ameaçados por frequentes e intensos incêndios. Capões de Mata estão imersos em uma matriz de campos rupestres, vegetação associada ao Cerrado. Em consequência das condições climáticas, a presença do fogo é recorrente na região. O fogo tem sido um importante fator evolutivo nos ecossistemas de campos rupestres. Entretanto, a comunidade de plantas dos Capões de Mata, associada ao domínio da Mata Atlântica, não apresenta adaptações e por isso são mais suscetíveis aos impactos do fogo. As consequências são ainda mais graves quando o fogo é intensificado por causas antrópicas. O fogo pode causar colapso físico e afetar serviços ecossistêmicos, especialmente àqueles de proteção de nascentes e cabeceiras nos topos das montanhas que compõem à Cadeia do Espinhaço. Em tempo de crise hídrica, este ecossistema deve ser visto como prioritário pelas estratégias de conservação nacionais.

Palavras chave: campos rupestres, capões de mata, cerrado, fogo, mata atlântica.

Abstract

In zones above 1,200 meters along the Espinhaço Range it is common the presence of natural islands of forests associated to headwaters. The purpose of this study was to describe the ecological dynamics of the still little known and studied the natural forest islands associated to the Espinhaço Range emphasizing its main conservation threats and ecosystem services losses associated to its possible degradation process. As a consequence of its location, the islands are influenced by the Atlantic Forest to the east, and by the Cerrado to the west. Despite the importance for the maintenance of tributaries of important rivers, as the Rio Doce and Rio das Velhas, these environments have received little attention from researchers even under threat by frequent and intense fires. The islands are immersed in a matrix of rupestrian grasslands, physiognomy associated to the Cerrado. Fire is a common phenomenon as a result of the marked seasonality. Fire has played an important role in the evolution of rupestrian grasslands. However, the plant community of forest islands is associated to the Atlantic forest domain, and as it has no adaptation to deal with fire it is highly susceptible to it. The consequences are intensified when the fires have anthropogenic causes. Fire can cause physical collapse and affect ecosystem services, especially those related to headwater protection from the top mountains that make up the Espinhaço Range. In time of water crisis, this ecosystem should be seen as a priority by the national conservation strategies.

Keywords: atlantic rain forest, capões de mata, cerrado, fire, rupestrian grasslands.

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Introdução

Ilhas florestais de origem natural: padrões e processos ecológicos

Ao idealizarmos ilhas, logo construímos imagens de arquipélagos oceânicos ou estuários nos quais ecossistemas terrestres se encontram cercados por água por todos os lados. Essa visão foi muito ampliada nas últimas décadas para ecossistemas terrestres frente a uma das mais graves consequências da atual crise ambiental a qual atravessa a humanidade: a fragmentação florestal. A fragmentação florestal é o processo em que florestas contínuas são transformadas em fragmentos de menores dimensões perdendo sua conectividade, afetando a sobrevivência dos vários organismos que ali vivem (WILSON *et. al*., 2016). Um denso arcabouço teórico foi desenvolvido para detectar e entender os diversos mecanismos responsáveis pelos padrões que governam a diversidade biológica nesta nova paisagem (HILL *et al*., 2011; MAGRACH *et al*., 2014; WILSON *et al*., 2016). O Brasil, como a grande maioria dos países localizados na região tropical, testemunhou a transformação de largas extensões de alguns de seus principais domínios fitogeográficos em verdadeiros arquipélagos cercados por matrizes de cultivos agrícolas, áreas dedicadas à pecuária, estradas e empreendimentos imobiliários (TABARELLI *et al*., 2010).

Diante desta urgência, iniciativas conservacionistas, sejam públicas ou privadas, têm tentado frenar, entender, conservar e restaurar o que sobrou de algumas das suas florestas e campos mais exuberantes e ricos em biodiversidade. Entretanto, outros arquipélagos, esses naturais, continuam pouco conhecidos e apesar de também ameaçados, encontram-se negligenciados pelas políticas de conservação nacionais (COELHO, 2014).

Os capões de mata são ilhas de vegetação natural cercadas por matrizes campestres ou savânicas (MEGURO *et al*., 1996ab). Apesar de enfocarmos nesse trabalho os capões de mata localizados na Cadeia do Espinhaço, esta expressão também é aplicada às demais ilhas de florestas naturais com composição, estrutura e processos ecológicos absolutamente distintos. Estas são associadas a outros contextos biogeográficos, a exemplo dos capões de mata do Pantanal e da Mata Atlântica Ombrófila Mista da porção austral do domínio Mata Atlântica (FIG. 1 e 2).

Foto: Marcel Serra Coelho

FIGURA 1 – Arquipélago de ilhas florestais capões de mata imersos em uma matriz de campos rupestres associados à Serra do Cipó.

Fotos: Marcel Serra Coelho e Lucas Perillo

FIGURA 2 – Capões de mata associados a Serra do Cipó.
Capões de mata sem distúrbios (a, b) e com distúrbios causados pelo fogo (c, d).

A Cadeia do Espinhaço está localizada em uma zona de transição dos biomas Cerrado e Mata Atlântica, que devido ao reconhecido valor biológico e elevado nível de degradação, ganharam o título de *hotspots* em biodiversidade (MYERS, 2003). Em outras palavras, isto significa que são áreas extremamente diversas em espécies e com alto número de espécies únicas do local – endêmicas - mas que estão sob intensas pressões antrópicas. Ademais, a parte austral da Cadeia do Espinhaço, em consequência de seu valor também biológico, cênico e cultural, ganhou o título de Reserva da Biosfera (UNESCO) (FERNANDES *et al*., 2016). Os capões de mata se inserem neste cenário, embora passem quase despercebidos por cientistas e o restante da população. Estão localizados em cotas altitudinais elevadas, acima de 1.200 m, especialmente ao longo do Espinhaço meridional e sul (COELHO, 2014).

Ilhas florestais imersas em campos com diversas dimensões e formatos encontram-se espacialmente estabilizadas por alguns mecanismos, do contrário, estariam em processo de expansão ou redução de sua área (COELHO *et al*., 2016). Quando os primeiros pesquisadores se depararam com estes ecossistemas, as primeiras perguntas que surgiram foram as relacionadas ao processo de origem e estabilidade de suas dimensões espaciais. Estariam estas ilhas avançando por sobre os campos? Ou ao contrário, estariam os campos avançando por sobre as ilhas? São basicamente três os fatores que controlam de uma forma sinérgica as fronteiras entre ecossistemas florestais e campestres, muito comuns nas savanas africanas e Cerrado brasileiro (COELHO *et al*., 2016). O objetivo deste artigo é descrever os três fatores básicos que atuam na dinâmica ecológica dos capões de mata, isto é, o clima, o solo e o fogo. As descrições são baseadas, principalmente, em recentes estudos desenvolvidos na região da Cadeia do Espinhaço (COELHO, 2014; COELHO *et al*., 2016; COELHO *et al*., 2017ab, no prelo; PEREIRA *et al*., 2017, no prelo).

Clima

O clima deve prover temperatura, pluviosidade e umidade adequadas ao estabelecimento e desenvolvimento de espécies arbóreas. Não obstante a existência de microclimas gerados por características topográficas e/ou edáficas, o clima tem um carácter regional. Como tal, não atua isoladamente, mas em sinergia com fatores outros. A existência de distintas fitofisionomias hospedadas em uma região com clima semelhante é evidência deste fenômeno. A Cadeia do Espinhaço é protagonista de um interessante fenômeno orográfico com fortes consequências para o clima da região. A umidade do Oceano Atlântico trazida da costa leste por um fenômeno atmosférico, denominado massa tropical atlântica avança ao interior carreando umidade (FIG. 3) (PELOSO & SHIMABUKURU, 2010; COELHO 2014; COELHO *et al*., 2016). A umidade carreada pelos rios aéreos vai se reduzindo. Espécies da Mata Atlântica costeira mais adaptadas aos elevados índices de umidade, florestas ombrófilas, são substituídas por espécies mais adaptadas à escassez ou a disponibilidade hídrica, espécies de florestas semi-deciduais. Existem diferenças na composição da comunidade vegetal e regimes climáticos entre as matas costeiras e interioranas. As florestas costeiras são predominantemente ombrófilas enquanto as localizadas ao interior, predominantemente semi-deciduais (OLIVEIRA-FILHO *et al*., 2000).

Foto: Lucas Perillo

FIGURA 3 – Foto da massa umidade na vertente leste da Serra do Cipó.

A massa tropical atlântica alcança a vertente leste especialmente da porção meridional e sul da Cadeia do Espinhaço, dominadas por uma vegetação de Mata Atlântica e é barrada pelo relevo da vertente barlavento. Esta massa de umidade ascende em direção às cotas altitudinais mais elevadas formando a frente de nebulosidade estacionária (FIG. 4) (RIBEIRO *et al*. 2009; PELOSO & SHIMABUKURU, 2010; COELHO 2014; COELHO *et al*., 2016, 2017b, no prelo). A frente de nebulosidade estacionária tem forte influência na vertente leste, nas zonas de cumeadas, assim como nas cotas altitudinais mais elevadas da vertente oeste. Este fenômeno orográfico divide os dois domínios fitogeográficos de influência na região. A vertente leste, dominada pela

Mata Atlântica e a vertente oeste, dominada pelo Cerrado e vegetações associadas (e.g. campos rupestres, Cerrado *strictu senso*, matas secas sobre afloramentos de calcário). Os capões de mata estão imersos neste cenário (COELHO 2014; COELHO *et al*., 2016; COELHO *et al*., 2017b, no prelo).

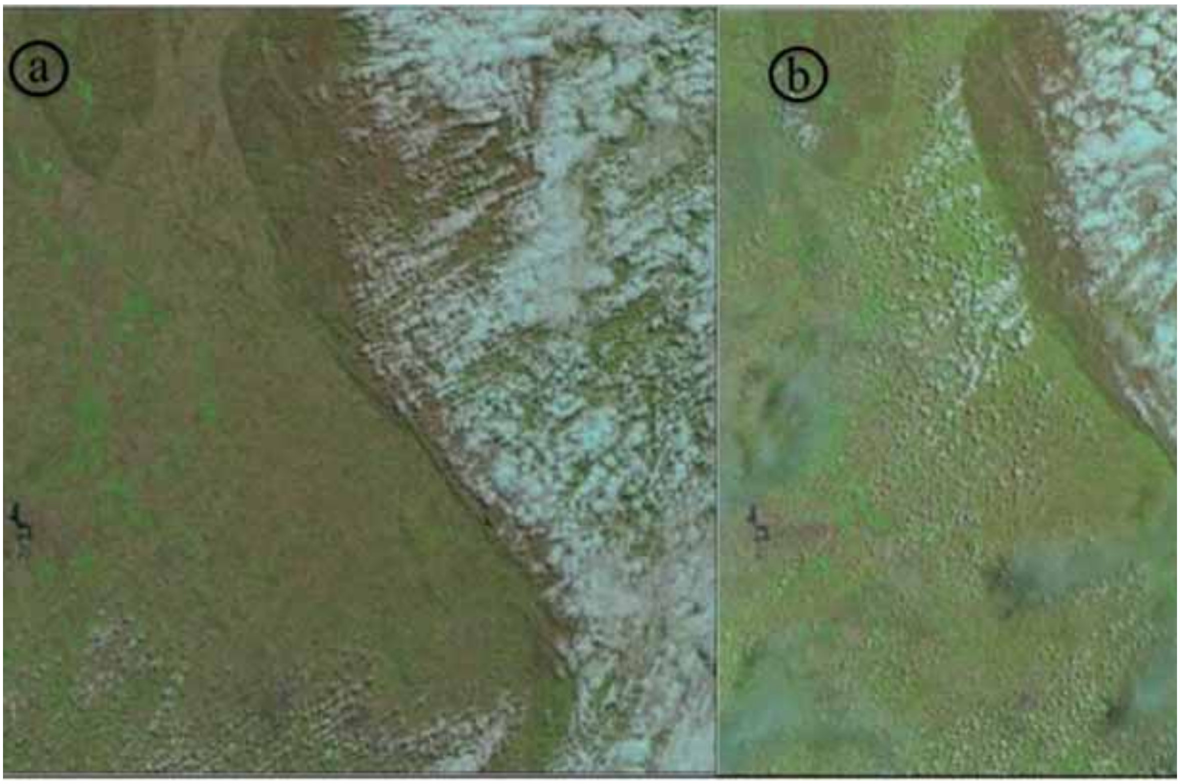

FIGURA 4 – Frente de nebulosidade estacionária sobre a Serra do Cipó. Imagens LANDSAT (Resolução = 30m).
a) Data 24/7/2013, ID – LC 82180732013205 LGN00;
b) Data 05/3/2014, ID – LC 82180732014064 LGN00.
Fonte: http;//glovis.usgs.gov

Apesar da localização e da forte influência do Cerrado e da Mata Atlântica, os capões de mata são formados predominantemente por espécies vegetais de Mata Atlântica (COELHO, 2014; COELHO *et al*., 2016; COELHO *et al*., 2017b, no prelo). Estas espécies vegetais alcançam cotas altitudinais mais elevadas dispersando-se das florestas atlânticas semi-deciduais da vertente leste até as cumeadas por meio das matas de galeria, onde encontram clima apropriado ao seu estabelecimento e desenvolvimento. A dispersão por animais (zoocoria) é a síndrome predominante (MEGURO *et al*., 1996ab; COELHO, 2014; COELHO *et al*., 2016). A abundante e constante disponibilidade hídrica advinda da frente de nebulosidade estacionária é a principal razão pela qual estas ilhas, apesar de serem alimentadas por elementos de florestas semi-deciduais, possuírem características ombrófilas, ou seja, inexistência de completa deciduidade foliar. Independente da época do ano, a frente de nebulosidade estacionária gera condições climáticas para que este tipo vegetacional se estabeleça e se mantenha (COELHO, 2014; COELHO *et al*., 2017ab, no prelo) (FIG. 4 e 5).


Foto: Marcel Serra Coelho

FIGURA 5 – Ilha florestal Capão de Mata imerso em neblina, em uma altitude de 1322m na Serra do Cipó, MG.

Solo

Além do clima, o solo exerce um importante papel para a origem dos capões de mata. Estão sempre em solos com profundidade e fertilidade adequadas ao estabelecimento e desenvolvimento de espécies de porte arbóreo (VALENTE, 2009). Características diametralmente opostas àquelas que compõem os do solo da matriz do entorno das ilhas. Campos rupestres possuem solos rasos, arenosos, ácidos, inférteis e com alta toxicidade em alumínio. Manchas de solo são as responsáveis para que as ilhas naturais de florestas estejam represadas e estabilizadas nas diversas dimensões que as encontramos (MEGURO *et al*., 1996 ab; VALENTE, 2009; COELHO, 2014; COELHO *et al*., 2016; COELHO *et al*., 2017a, no prelo). O controle é simultaneamente edáfico e climático, criando algumas zonas de adequabilidade ambiental para seu estabelecimento, sendo um processo dinâmico, que quando submetidos a mudanças do uso do solo (gado, fogo, corte) pode ter seu equilíbrio alterado. Não podendo se expandir tanto por condições de solo quanto por condições climáticas, as espécies que se estabelecem vindas da vertente leste por meio de matas de galerias formam as ilhas florestais ou capões de mata (MEGURO *et al*., 1996 ab; VALENTE, 2009; COELHO, 2014; COELHO *et al*.,2016; COELHO *et al*., 2017b, no prelo).

Alguns estudos têm demonstrado a forte adaptação às condições climáticas específicas não só de angiospermas herbáceas e monocotiledôneas epífitas (bromélias, orquídeas e filodrendos fixados em troncos de árvores) como também de vegetação arbórea (ELLER, *et al*., 2013). A absorção foliar de água pela vegetação arbórea também é um mecanismo essencial para o estabelecimento destes ecossistemas (ELLER, *et al*., 2013). A maior parte da água nestas regiões está presente sob a forma de neblina e orvalho. Assim, há evidências de que os capões de mata se assemelham às florestas nebulares onde há registros científicos de algumas espécies absorvendo significativos volumes de água pela lâmina foliar, chegando a umedecer o solo (FIG. 5), uma adaptação ambiental ainda pouco conhecida (CAMPOS, 1995; MEGURO *et al*., 1996ab; VALENTE, 2009; SOUZA, 2009; COELHO, 2014; COELHO *et al*., 2016; COELHO *et al*., 2017ab, no prelo; PEREIRA *et al*., 2017, no prelo). Assim, estando associadas às nascentes, as ilhas florestais prestam um serviço ecossistêmico muito importante de proteção de tributários que abastecem importantes bacias hidrográficas brasileiras (e.g. Rio Doce, Rio São Francisco).

Fogo

O terceiro fator de influência é o fogo de origem antrópica. O fogo é frequente e intenso em regiões de sazonalidade bem marcada, com invernos muito secos e verões úmidos. Esse é o caso de grande parte das áreas cobertas pelo Cerrado brasileiro (MISTRY, 1998). Por suas espécies armazenarem biomassa subterrânea através de órgãos especiais, assim como as que caracterizam o Cerrado típico do Brasil, as vegetações campestres também possuem conspícuas vantagens adaptativas à sobrevivência em ambientes áridos e também sujeitos à incêndios (DANTAS *et al*., 2013a,b). Muitas destas espécies podem perder a vantagem adaptativa para outras caso o fogo deixe de ocorrer. A substituição de espécies causaria então uma modificação na comunidade vegetal, descaracterizando esta fisionomia (BOND & KEELEY, 2005). São formações vegetais dependentes de fogo (DANTAS *et al*., 2013ab). Enquanto o fogo é um fenômeno previsível e necessário para manutenção de muitas formações vegetais, pode ser fator restritivo e causar distúrbios em vegetações sensíveis a ele. Estas vegetações seriam as sensíveis ao fogo (BOND & KEELEY, 2005). Portanto, muitas formações vegetais associadas ao Cerrado, especialmente em áreas transicionais (e.g. denominadas ecótonos em ecologia) podem ser fortemente alteradas pelo fogo (PIVELLO, 2011; DANTAS *et al*., 2013ab). Entre as florestas sensíveis ao fogo associadas ao Cerrado, destacamos as matas de galeria, matas secas é os capões de mata (COELHO *et al.*, 2016; COELHO et al., 2017b, no prelo).

O fogo se destaca como uma das mais graves ameaças à conservação dos capões de mata (FIG. 2). A presença do fogo em capões de mata causa a mortalidade de muitas espécies de árvores, alterando fortemente a estrutura e dinâmica sucessional. Todos os trabalhos conduzidos até o momento em capões de mata trazem relatos de distúrbios causados pelo fogo (CAMPOS, 1995;

MEGURO *et al*., 1996ab; VALENTE, 2009; SOUZA, 2009; COELHO, 2014; COELHO *et al*., 2016; COELHO et al., 2017ab, no prelo; PEREIRA et al., 2017, no prelo). Por serem ambientes de alta umidade, sendo esta mais alta nas regiões nucleares das ilhas florestais, o fogo tem seus efeitos mais intensos em suas bordas. Parâmetros como densidade, diâmetro, altura média dos indivíduos vegetais, riqueza e diversidade de espécies variam de forma conspícua entre a borda e as zonas nucleares dos capões (COELHO *et al*., 2016; COELHO *et al*., 2017b, no prelo). Estas variações evidenciam que apesar das pequenas dimensões, quando comparados às florestas contínuas, os capões de mata apresentam um claro efeito de borda (COELHO *et al*., 2016; COELHO *et al*., 2017b, no prelo). O solo também se diferencia espacialmente em suas características físico-químicas sendo suas condições em zonas nucleares mais favoráveis ao estabelecimento de espécies características de estágios tardios de sucessão (COELHO *et al*., 2016; COELHO *et al*., 2017b, no prelo). Ou seja, espécies características de florestas conservadas ou de estágio avançado de sucessão. Neste contexto, o fogo desempenha um papel importante na intensificação dos impactos associados ao efeito de borda. Uma das consequências, além das já citadas é a facilitação à invasão biológica e a regressão do desenvolvimento das ilhas florestais à estágios iniciais de sucessão. Em última análise, o aumento da frequência e intensidade do fogo podem causar o colapso deste ecossistema de ilhas naturais altimontanas, intensificado com a possibilidade de entrada de gado em seu interior (ver COELHO *et al*., 2016; COELHO *et al*., 2017b, no prelo).

Ameaças e estratégias à conservação

Fenômenos naturais como a ação do vento, muito intenso em regiões de topo de montanhas, também são responsáveis por tombamentos de árvores e aberturas de clareiras. Ademais, os capões de mata estão submetidos à intensas interferências antrópicas. O seu uso pode variar desde pastagem à supressão de árvores para aproveitamento de madeira (uso de lenha) (FIG. 6). Por hospedarem uma diversa flora de pteridófitos e angiospermas herbáceas, a coleta de espécimes para o paisagismo é comum


Foto: Lucas Perillo

FIGURA 6 – Efeito de corte seletivo de madeira em um capão de mata associado à Serra do Cipó.

frente a ainda incipiente fiscalização. Orquidaceas, Bromeliaceas e Araceas são coletadas com vistas ao comércio ilegal (COELHO 2014; COELHO *et al*., 2016 COELHO *et al*., 2017b, no prelo).

Os capões de mata, por terem dimensões reduzidas e fronteiras bem definidas, são excelentes modelos ecológicos para o teste de hipóteses ecológicas, a exemplo das dinâmicas de meta-comunidades e teorias espaciais de migrações e extinções, como àquelas descritas pela teoria da biogeografia de ilhas (COELHO, 2014; COELHO *et al*., 2016; WILSON *et al*., 2016; COELHO *et al*., 2017b, no prelo). Até hoje poucos estudos ecológicos foram realizados nestas ilhas (CAMPOS, 1995; MEGURO *et al*., 1996ab; VALENTE, 2009; SOUZA, 2009; COELHO, 2014; COELHO *et al*., 2016; COELHO *et al*., 2017ab, no prelo; PEREIRA *et al*., 2017, no prelo). Com o intuito de responder várias questões tais como diversidade de espécies relacionadas a variáveis ambientais e fluxo de indivíduos entre as manchas, foi montada uma rede de colaboração com a participação de vários laboratórios de pesquisa da UFMG. O grupo de pesquisa está investindo esforços para elucidar o que acontece dentro destes fragmentos de mata, estudando diferentes grupos taxonômicos. Resultados preliminares (herbívoros, abelhas, vespas, borboletas, formigas e besouros) apontam uma grande diversidade de insetos associados a estes capões (COELHO *et al*., 2016; COELHO *et al*., 2017b, no prelo). O início das pesquisas nestes ecossistemas representa uma nova avenida de estudos ecológicos. Além de sua importância científica, os capões de mata estão sobre nascentes de três das principais bacias hidrográficas do sudeste brasileiro: Rio Doce (a leste), Rio São Francisco e Jequitinhonha (a oeste). Prestam um serviço ambiental incalculável na proteção das nascentes destas duas bacias hidrográficas sendo ambientes estratégicos para a segurança hídrica da população brasileira (FIG. 7).

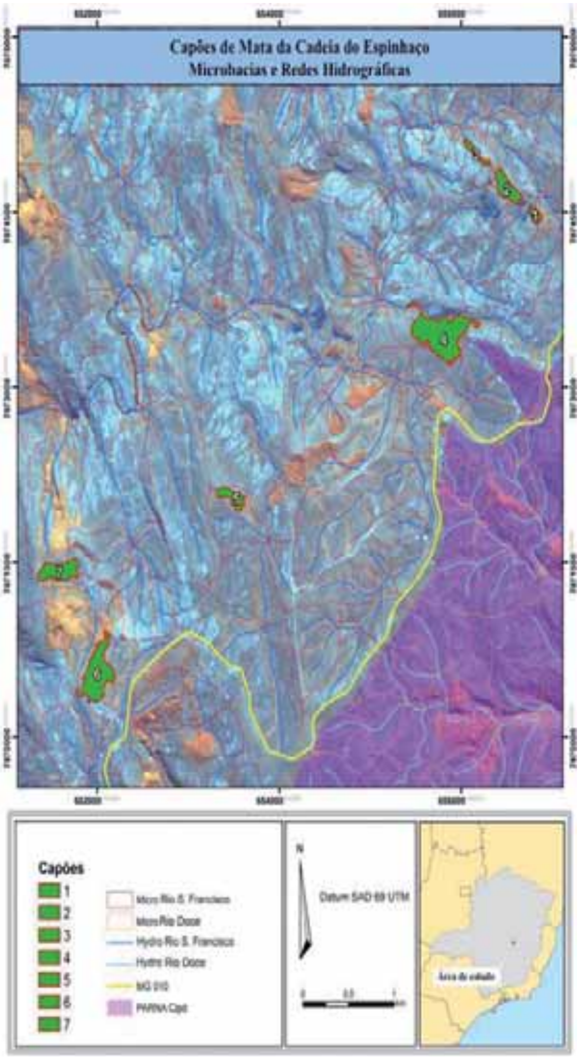

FIGURA 7 – Imagem de um arquipélago de sete Capões de Mata da Serra do Cipó, associados às bacias e microbacias do Rio São Francisco e Rio Doce.
Fonte: Imagem do satélite RapiEye cedida pelo Instituto Mineiro de Gestão das Águas – IGAM, do ano de 2010.

Considerações finais

A disseminação do conhecimento sobre as funções e serviços ecossistêmicos desempenhados pelos capões são importantes ferramentas de alerta e apontam para a sua conservação. É fundamental que saibamos onde estão localizados e qual a sua importância na paisagem com um esforço de mapeamento que pode ser realizado através de ferramentas de informação geográfica (COELHO *et al*., 2017b, no prelo). Ademais, como estão localizados em regiões extremas, podem preencher um importante papel e relevante em pesquisas envolvendo mudanças climáticas. O aumento da intensidade de fiscalização pelos órgãos competentes e planos de manejo para minimizar os impactos já existentes também são fundamentais para coibir a coleta ilegal de espécies de uso paisagístico, corte de madeira, construção de estradas mal planejadas e incêndios criminosos. Entretanto, quando o fogo é inevitável, deve ser manejado (COELHO *et al*., 2017b, no prelo). A implantação de aceiros, representa uma alternativa (RAMOS-NETO & PIVELLO, 2000). Diante do grande número de ilhas nos diversos arquipélagos de capões de mata por sobre a Cadeia do Espinhaço e da dificuldade da implantação de aceiros em todas, estratégias de escolha de ilhas específicas, baseadas em suas dinâmicas ecológicas, poderiam ser desenvolvidas (COELHO *et al*., 2017b, no prelo). A sociedade brasileira deve conhecer, preocupar-se e traçar estratégias de conservação dedicadas a este peculiar e cada vez mais ameaçado ecossistema sob pena de responder pelos custos ambientais e econômicos de sua degradação.

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