University of São Paulo
"Luiz de Queiroz" College of Agriculture
Center for Nuclear Energy in Agriculture

The effects of landscape structure and crop management on insect community
and associated ecosystem services and disservices within coffee plantation

Hugo Reis Medeiros

Thesis presented to obtain the degree of Doctor in
Science. Area: Applied Ecology

Piracicaba
2019

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versão revisada de acordo com a resolução CoPGr 6018 de 2011

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Dados Internacionais de Catalogação na Publicação
DIVISÃO DE BIBLIOTECA – DIBD/ESALQ/USP

Medeiros, Hugo Reis

The effects of landscape structure and crop management on insect community and associated ecosystem services and disservices within coffee plantations / Hugo Reis Medeiros. - - versão revisada de acordo com a resolução CoPGr 6018 de 2011. - - Piracicaba, 2019.

82 p.

Tese (Doutorado) - - USP / Escola Superior de Agricultura "Luiz de Queiroz". Centro de Energia Nuclear na Agricultura.

1. Agroecologia 2. Insetos benéficos 3. Estrutura da paisagem 4. Serviços ecossistêmicos I. Título

Dedico este trabalho à minha esposa e família, pelo amor, apoio e compreensão durante esta etapa da vida.

AGRADECIMENTOS

Primeiramente, agradeço minha esposa Mariana, por estar ao meu lado nessa fase da vida e me dar forças principalmente nos momentos difíceis. Muito obrigado pelo amor, carinho, confiança, parceria e compreensão!

Aos meus pais, Sonia e José Inácio, e irmão Lucas pelo incentivo, apoio irrestrito e amor incondicional.

Aos meus orientadores Prof. Ciro Righi e Prof. Milton C. Ribeiro pela oportunidade, confiança e motivação. Muito obrigado pelo grande aprendizado, além da parceria e amizade ao longo desses anos.

Aos parceiros Carlinhos, Felipe Martello, Juliana Silveira, Calebe e Rafael (Urucum) do Departamento de Ecologia da UNESP-RC. Muito obrigado pela parceria, amizade, trabalho duro e aprendizado durante esses anos.

Ao parceiro Dr. Yuri Grandinete responsável pela identificação das vespas e aos parceiros Prof. Eduardo Almeida e Prof. Ximo Mengual responsáveis pela identificação de abelhas e sirfídeos, respectivamente.

Aos parceiros canadenses Profa. Karen Harper, Prof. Peter Tyedmers, Prof. Chris Cutler e Dr. Paul Manning. Muito obrigado pela oportunidade e aprendizado, sobretudo Profa. Karen, responsável por viabilizar meu intercâmbio no Canadá.

Aos Professores Wesley A. C. Godoy, Carlos A. Vettorazzi, Hilton Thadeu Z. Couto, Danilo Boscolo. Muito obrigado pelo acolhimento e conversas durante o desenvolvimento deste trabalho.

Ao CNPQ e ao Governo Canadense pelas bolsas de estudos. À Fundação Rufford e FAPESP pelo apoio financeiro fundamental para a realização dos trabalhos de campo e de laboratório.

Agradeço imensamente à Universidade de São Paulo e ao Programa de Pós-Graduação em Ecologia Aplicada (Interunidades). Aos coordenadores, docentes, alunos e à secretária do PPGI-EA, Mara Casarin, pelo suporte e acolhimento. Obrigado!

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RESUMO

Os efeitos da estrutura da paisagem e do manejo agrícola sobre a comunidade de insetos e seus serviços e desserviços em plantações de café

A fragmentação e perda de habitats são consideradas as maiores ameaças à biodiversidade em escala global. A principal força condutora desses processos é a intensificação da agricultura, que se baseia no uso excessivo de pesticidas e expansão das monoculturas, resultando na simplificação da paisagem e na perda de espécies e de serviços ecossistêmicos associados a eles. Apesar da reconhecida importância, pouco se sabe sobre como a intensificação da agricultura afeta a ocorrência de diferentes grupos funcionais de insetos em múltiplas escalas espaciais na região Neotropical. Nesse contexto, o objetivo deste estudo foi analisar como a estrutura da paisagem e fatores locais (ex. microclima, pesticidas) afetam a comunidade de insetos e a provisão de serviços e desserviços na matrix agrícola. Para tanto, vespas (inimigos naturais), abelhas e sirfídeos (polinizadores) foram coletados em 16 plantações de café e em 16 fragmentos florestais adjacentes, situados em diferentes contextos de paisagem na região Sudeste do Brasil. Além disso, a abundância do inseto praga *Leucoptera coffeella* e sua taxa de mortalidade relacionada à predação (controle biológico) foram estimadas no interior dos cafezais. A estrutura da paisagem foi representada pelas métricas: porcentagem de cobertura florestal, diversidade da paisagem e densidade de bordas. Elas foram calculadas em quatro escalas espaciais: 250, 500, 750 e 1000 metros, no entorno das interfaces café-floresta. Dentre os resultados, destacamos que ao longo de 13 meses foram coletadas 13658 vespas - distribuídas em 86 espécies e 26 gêneros; 8393 abelhas - distribuídas em 116 espécies 73 gêneros; e 4984 sirfídeos - compreendendo 63 espécies e 20 gêneros. A abundância da praga e o controle biológico variaram de 5.3 a 32.5 % e de 12.7 a 72.8 %, respectivamente. A abundância de *L. coffeella* apresentou correlação negativa com o aumento de cobertura florestal e diminuição da temperatura. A riqueza de espécies e abundância de vespas e a riqueza de espécies de abelhas aumentaram com o incremento da cobertura florestal. A diversidade beta de vespas e abelhas apresentaram altos valores do componente “nested” entre pares de interfaces localizadas em paisagens com alta e baixa cobertura florestal, indicando a perda de espécies em paisagens simplificadas dominadas por monoculturas. Esses resultados foram encontrados em todas as escalas espaciais, entre 250 e 1000 metros, sugerindo que a conservação e restauração florestal podem melhorar o balanço entre a produção agrícola e a conservação da biodiversidade e que devem ser implantadas em escala de paisagem. O aumento de cobertura florestal em paisagens estruturalmente simplificadas pode aumentar a disponibilidade de recursos resultando no aumento de diversidade de espécies e da provisão de serviços ecossistêmicos como a polinização e o controle biológico de pragas.

Palavras-chave: Diversidade de insetos; Estratégias agroecológicas; Estrutura da paisagem; Serviços ecossistêmicos

ABSTRACT

The effects of landscape structure and crop management on insect community and associated ecosystem services and disservices within coffee plantations

Habitat loss and fragmentation are considered the major threat to biodiversity at global scale. The main driving force behind this process is agricultural intensification that is based on pesticide overuse and expansion of monocultures resulting in landscape simplification as well as loss of species and associated ecosystem services. Despite recognized importance, little is known about how agricultural intensification affects the occurrence of different insect functional groups at multiple spatial scales in the Neotropical region. The aim of this study is investigate how landscape structure and local factors (e.g. microclimate and pesticides) affect insect community and the provision of ecosystem services and disservices in crop matrix. For this, wasps (natural enemies), bees and flower flies (pollinators) were collected in 16 coffee plantations and in 16 forest fragments located in different landscape contexts in southeast Brazil. Moreover, the abundance of the coffee leaf miner *Leucoptera coffeella* (pest) and mortality rates related to predation (biological control) were estimated within coffee plantations. Landscape structure was represented by the following metrics: percentage of forest cover, landscape diversity and edge. These metrics were calculated at four spatial scales 250, 500, 750 and 1000 meters in the surroundings of coffee-forest interfaces. Over 13 months, we collected 13,658 wasps distributed in 86 species and 26 genres; 8,393 bees belonging to 116 species and 73 genres; and 4,984 flower flies within 63 species and 20 genres. Pest abundance and biological control varied from 5.3 to 32.5 % and from 12.7 to 72.8 %, respectively. Pest abundance was negatively correlated with the increment of forest cover and decreasing temperature. Species richness and abundance of wasps and bee species richness increased with increasing forest cover. The beta diversity of wasps and bees presented high values of nested component between pairs of interfaces located in landscapes with high and low forest cover indicating species loss in structurally simple landscapes dominated by monocultures. These results were found at all spatial scales from 250 to 1000 meters suggesting that forest conservation and restoration can enhance the balance between crop production and biodiversity conservation, and that it should be promoted at landscape scale. Increasing forest cover in crop dominated landscapes can result in higher availability of resources resulting in the high species diversity and provision of associated ecosystem services such as pollination and pest biological control.

Keywords: Agroecological strategies; Insect diversity; Landscape structure; Ecosystem services

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INTRODUÇÃO GERAL

A fragmentação e perda de habitat são consideradas as maiores ameaças à biodiversidade em escala global (TILMAN et al., 1994, FAHRIG, 2003). A principal força condutora desse processo é a intensificação da agricultura, que afeta a biodiversidade e seus serviços ecossistêmicos em múltiplas escalas espaciais (LOSEY; VAUGHAN, 2006; GARDINER et al. 2009; CHASE; BENGTSSON, 2010).

Em escala local, as mudanças ambientais decorrentes do manejo agrícola, tais como a colheita e aplicação de fertilizantes e pesticidas, afetam negativamente a biodiversidade (ROSCHEWITZ et al., 2005; BIANCHI et al. 2006; MEEHAN et al., 2011). O uso de pesticidas aumenta as taxas de mortalidade e os efeitos subletais em insetos não alvo como, por exemplo, os agentes de controle biológico (GEIGER et al., 2010; STAPEL et al., 2000). Em escala de paisagem, a intensificação da agricultura promove a expansão das monoculturas, resultando na simplificação da paisagem e na fragmentação dos ecossistemas naturais, reduzindo-os a fragmentos pequenos e isolados (MENALLED et al., 1999; ROSCHEWITZ et al., 2005; FLOHRE et al., 2011).

A intensificação da agricultura implica na substituição de comunidades com alta diversidade de espécies por um pequeno número de plantas cultivadas e animais domesticados (RAMANKUTTY; FOLEY, 1998; ALTIERI, 1999). De fato, entre os anos de 1990 e 2010, na América Latina, 88 milhões de hectares de floresta foram convertidos em pastagens, monoculturas e áreas urbanas (FAO, 2010). As previsões mais otimistas preveem que os parques e as demais categorias de unidades de conservação protegerão apenas 10% da cobertura original dos ecossistemas tropicais (GRADWOHL; GREENBERG, 1991).

Diante desse cenário, as monoculturas são os elementos dominantes na paisagem e, embora os diferentes cultivos sejam percebidos distintamente pelas espécies (HONĚK, 1982; DUELLI et al., 1999), todas as plantações são habitats efêmeros submetidos a frequentes e intensos distúrbios decorrentes da ação antrópica (ALTIERI, 1999; LANDIS; MARINO, 1999). Consequentemente, grande parte da biodiversidade em paisagens agrícolas depende da existência de remanescentes de ecossistemas naturais, que são fontes de recursos e habitats relativamente estáveis e permanentes (ALTIERI, 1999; LANDIS et al., 2000; KLEIJN et al., 2001). Portanto, remanescentes de ecossistemas naturais em paisagens agrícolas exercem um papel fundamental na conservação da biodiversidade e na manutenção dos serviços ecossistêmicos em múltiplas escalas espaço-temporais.

OBJETIVO GERAL

A presente tese de doutorado tem como objetivo investigar os efeitos da composição e configuração da paisagem e do ambiente local (ex. manejo agrícola e microclima local) afetam a ocorrência de insetos pragas, a diversidade de insetos benéficos e seus serviços ecossistêmicos. Para tanto, populações de *Leucoptera coffeella*, a comunidade de insetos benéficos (abelhas, vespas e sirfídeos), e o serviço de controle biológico foram monitorados em interfaces café-floresta localizadas em diferentes contextos de paisagem e intensidade de manejo.

REVISÃO DE LITERATURA

Com base na problemática apresentada, a breve revisão a seguir discorrerá sobre os padrões e os processos da biodiversidade em paisagens agrícolas, com ênfase na importância dos ecossistemas naturais e da estrutura da paisagem para a conservação de grupos funcionais de artrópodes e a manutenção de seus serviços ecossistêmicos. Além disso, será realizada uma descrição sobre o sistema utilizado como modelo de estudo que consiste em plantações de café, o inseto praga *Leucoptera coffeella* e os insetos benéficos associados representados pelas vespas (inimigos naturais) e abelhas e sirfídeos (polinizadores).

Serviços ecossistêmicos na agricultura

Os serviços ecossistêmicos são resultantes de processos químicos, físicos, geológicos e biológicos dos quais os humanos dependem, tais como a polinização, a ciclagem de nutrientes, os recursos genéticos, o controle biológico de pragas, a regulação climática e a conservação do solo e da água (HAYCOCK et al., 1993; USDA, 2000; KEARNS et al., 1998; ALTIERI, 1999; DAILY, 1999; LOREAU et al., 2002; KREMEN, 2005; LOSEY; VAUGHAN, 2006). De acordo com Millennium Ecosystem Assessment (2005), os serviços ecossistêmicos podem ser classificados em quatro categorias: serviços de suporte (ciclagem de nutrientes, polinização, formação de solo), regulação (regulação climática, controle de pragas e doenças), provisão (água potável, combustíveis, fibras) e cultural (valores estéticos, espirituais, recreacionais). Os serviços ecossistêmicos têm sido degradados e utilizados de forma insustentável pelo homem, por meio do processo de fragmentação e perda de habitat (simplificação da paisagem), uso indiscriminado de agrotóxicos, exploração predatória dos recursos naturais e da biodiversidade (MEA, 2005). Mudanças ambientais ocasionadas por ações antrópicas também podem resultar no aumento de desserviços, como a intensificação de processos erosivos e de danos causados por pragas agrícolas, extinção de espécies e de serviços associados como polinização e controle biológico, lixiviação de nutrientes, contaminação de águas superficiais e subterrâneas (MEA, 2005; ZHANG et al., 2007).

Dentre os serviços ecossistêmicos relevantes para a agricultura podemos destacar os serviços de polinização e controle biológico fornecidos por insetos benéficos que são de extrema importância para o aumento na produção de alimentos. Insetos benéficos e seus serviços de polinização, decomposição e controle biológico de pragas foram valorados em aproximadamente US\$ 71.3 bilhões anualmente apenas nos Estados Unidos (LOSEY; VAUGHAN, 2006) - valores corrigidos com base no ano de 2018. Aproximadamente 30% da produção global de alimentos depende da polinização mediada por animais (KLEIN et al., 2007) contribuindo com US\$235–577 bilhões para a produção agrícola em escala global (POTTS et al., 2016). De maneira similar, o serviço de controle biológico de pragas foi valorado em US\$619/ha em escala global (CONSTANZA et al., 1997). Apesar da reconhecida importância, os serviços de polinização e controle de pragas são particularmente ameaçados pela fragmentação e perda de habitat, uma vez que essas espécies dependem da presença dos ecossistemas naturais para persistirem em paisagens agrícolas submetidas a constantes mudanças ambientais (ALTIERI, 1999; LANDIS et al., 2000; BIANCHI et al., 2006). Dessa forma, o próximo tópico discorrerá sobre a importância dos habitats naturais e da estrutura da paisagem sobre a biodiversidade e seus serviços ecossistêmicos.

A função dos ecossistemas naturais para a biodiversidade e os serviços ecossistêmicos em paisagens agrícolas

Os ecossistemas naturais atuam como fontes de populações que recolonizam regularmente os agroecossistemas (LANDIS et al., 2000; BIANCHI et al., 2006; LARRIVÉE et al., 2008). Isto é particularmente verdade para espécies de artrópodes benéficos, como os inimigos naturais de pragas agrícolas e polinizadores que são capazes de forragear na matriz agrícola (KLEIN et al., 2002; KRUESS, 2003; SCHMIDT; TSCHARNTKE, 2005b). Por exemplo, no Brasil Demite e Feres (2005) verificaram que a árvoreta apoiante nativa *Celtis iguanea*, comum nas bordas dos fragmentos de Mata Atlântica, possui interação com ácaros predadores. Fadini et al. (2001) constataram aumento na diversidade e na abundância de inimigos naturais em vinhedos com terraços vegetados. Thomson e Hoffmann (2010) detectaram elevadas taxas de predação nas proximidades de fragmentos florestais.

Nesse contexto, os remanescentes de ecossistemas naturais existentes em paisagens agrícolas fornecem segurança espaço-temporal para a biodiversidade, resultando na provisão regular de seus serviços ecossistêmicos nos agroecossistemas adjacentes. A vegetação associada aos ecossistemas naturais abriga presas e hospedeiros alternativos para insetos predadores e parasitoides (ALTIERI, 1999; CRONIN; REEVE, 2005; BIANCHI et al., 2006). Sobre isso, Landis e Menalled (1998) reportaram que mais de 60% dos hospedeiros alternativos de parasitoides generalistas foram encontrados nos ecossistemas naturais adjacentes às plantações. Além disso, esses ambientes atuam como fontes estáveis de pólen e néctar (TYLIANAKIS et al., 2004; HAENKE et al., 2009; SCHEID et al., 2011) e fornecem um microclima mais ameno quando comparado às monoculturas (FORMAN; BAUDRY, 1984). O consumo desses recursos tem sido associado ao aumento na fecundidade (CHAPMAN, 1998), longevidade (BERNDT; WRATTEN, 2005) e maturação dos ovos (HASLETT, 1989; HICKMAN et al., 1995) em espécies de inimigos naturais. As condições microclimáticas mais amenas são relevantes para espécies intolerantes, como parasitoides que apresentam baixa expectativa de vida em altas temperaturas (HAILEMICHAEL; SMITH, 1994).

Além disso, os ecossistemas naturais fornecem micro habitats específicos para nidificação e oviposição de importantes grupos funcionais, como abelhas, vespas e sirfídeos (SOMMAGGIO, 1999; SPEIGHT, 2006; HOLZSCHUH et al., 2009; SOBEK et al., 2009). Estudos mostram que insetos benéficos forrageiam na matriz agrícola, mas dependem da presença de remanescentes de floresta para encontrar múltiplos recursos e locais seguros para nidificação, incluindo vespas predadoras (EDWARDS, 1980; MATSURA; YAMANE, 1984; SOUZA et al., 2010, 2014, 2015) e abelhas (LAGERLOF et al. 1992; CHACOFF; AIZEN, 2006). Até mesmo as espécies associadas à matriz agrícola utilizam os ecossistemas naturais como refúgio em períodos de distúrbios, como a colheita e a aplicação de pesticidas (RAND et al., 2006, RAND; TSCHARNTKE, 2007). Sendo assim, entende-se que os remanescentes naturais são fundamentais para a manutenção da biodiversidade e de seus serviços ecossistêmicos em paisagens agrícolas.

Em contraste, os ecossistemas naturais podem falhar na promoção da biodiversidade de seus serviços ecossistêmicos. Tcharntke et al. (2016) propuseram cinco hipóteses sobre quando e porque os habitats naturais podem falhar na manutenção e promoção de inimigos naturais e a provisão do serviço de controle biológico de pragas agrícolas:

1 - Quando as populações de praga não possuem comunidade efetiva de inimigos naturais na região. Nesse caso, as populações da praga podem não ser controladas por inimigos naturais e sim por outros fatores, como a disponibilidade de plantas hospedeiras, manejo agrícola ou mesmo predação intra-guilda. Por exemplo, os insetos-praga *Diabrotica virgifera* e *D. barberi* são regulados pela área cultivada de milho independentemente do tamanho das

populações de inimigos naturais (O'ROURKE et al., 2011). A mariposa do repolho (inseto praga) apresentou correlação positiva com a quantidade de habitats naturais devido ao aumento da predação intra-guilde ocasionada por pássaros, liberando, assim, a mariposa do repolho do controle biológico realizado por insetos predadores, como as vespas (MARTIN et al., 2013).

2 - Quando os habitats naturais fornecem mais pragas que inimigos naturais. Ecossistemas naturais podem abrigar alta densidade de inimigos naturais com baixa capacidade de dispersão, enquanto que insetos praga migram dos ecossistemas naturais em direção à matriz agrícola (BLITZER et al., 2012). Tscharnkte et al. (2008) observaram que aves insetívoras (inimigos naturais) em florestas tropicais não forrageiam em áreas abertas, como as plantações e pastagens.

3 - Quando a matriz agrícola fornece mais recursos para os inimigos naturais que os ecossistemas naturais. Em alguns casos os habitats naturais possuem baixa produtividade e suportam populações pequenas de inimigos naturais quando comparado à matriz agrícola. Costamagna et al. (2015) verificaram que os inimigos naturais se correlacionaram positivamente com a matriz agrícola e negativamente com os habitats naturais na região semiárida da Austrália. Esses resultados podem ser associados ao fato de que a matriz é irrigada enquanto que os habitats naturais são submetidos a longos períodos de estiagem, tornando-os improdutivos e inóspitos.

4 - Quando a proximidade e a quantidade de ecossistemas naturais são incapazes de fornecer populações de inimigos naturais necessárias para o controle biológico efetivo. O aumento de eficiência do controle biológico ocorre quando a quantidade e a conectividade entre os habitats naturais são suficientes para diminuir a distância entre habitats naturais e matriz agrícola. Em plantações de frutas na África, Henri et al. (2015) observaram um declínio nas populações de inimigos naturais e do controle biológico devido o aumento na distância das plantações em relação aos habitats naturais. Esse declínio foi mais acentuado entre as espécies de inimigos naturais especialistas que possuem capacidade de dispersão limitada e que são menos eficientes na colonização de plantações isoladas.

5 - Quando as práticas agrícolas contrabalanceiam o estabelecimento de inimigos naturais e o serviço de controle biológico fornecidos pelos ecossistemas naturais. Pesticidas de amplo espectro, aragem dos solos, variedades de alta suscetibilidade e a baixa diversificação das lavouras afetam negativamente os inimigos naturais, resultando em alta mortalidade de inimigos naturais e, consequentemente, liberando as pragas do controle via *top-down*. Diversos estudos verificaram a elevada diversidade de inimigos naturais e altas taxas de controle biológico em plantações orgânicas quando comparada com plantações convencionais submetidas a um manejo agrícola intensivo (LETOURNEAU; BOTHWELL, 2008).

Tscharnkte et al. (2005) destacam que o entendimento dos efeitos positivos e negativos da intensificação da agricultura e dos habitats naturais sobre a biodiversidade e seus serviços ecossistêmicos necessita de uma perspectiva de paisagem, uma vez que as espécies e suas interações tróficas respondem à quantidade de habitats naturais e dos outros elementos da estrutura da paisagem em múltiplas escalas espaciais. Portanto, a composição de espécies e a manutenção dos serviços ecossistêmicos são reguladas pela distribuição espacial dos habitats agrícolas e naturais em escala local e principalmente de paisagem.

Efeitos da estrutura da paisagem sobre a biodiversidade e serviços ecossistêmicos

As espécies variam em suas habilidades de dispersão e respondem ao arranjo espacial dos habitats em escala local e de paisagem (TSCHARNTKE et al., 2005a, 2012). As variações ambientais locais são provavelmente de maior importância para os organismos com baixa capacidade de dispersão (BIANCHI et al., 2006) e, por outro lado,

a ocorrência de organismos mais vágéis é primariamente determinada pela composição e configuração espacial dos habitats em escala de paisagem (BENGTSSON, 2010; FARHING, 2011). Espécies com ampla capacidade de dispersão, como as abelhas e sirfídeos, respondem à composição da paisagem na escala de quilômetros (STEFFAN-DEWENTER et al., 2002; BOSCOLO et al., 2017; MEDEIROS et al. 2018), enquanto que vespas predadoras respondem em uma escala de até 300 metros (SANTOS et al., 2000; CRUZ et al., 2006; RIBEIRO-FILHO et al., 2008). Nesse contexto, paisagens estruturalmente complexas suportam uma maior diversidade de espécies quando comparadas àquelas simplificadas e dominadas por monoculturas (BENGTSSON et al., 2003; TSCHARNTKE et al., 2007). Paisagens complexas apresentam amplas interfaces entre as plantações e os ecossistemas naturais, o que fornece maior oportunidade para a migração de ambos os organismos com alta e baixa capacidade de dispersão (CRONIN; REEVE, 2005; TSCHARNTKE et al., 2007, 2012). Paisagens complexas fornecem recursos de forma contínua no espaço e no tempo, o que resulta na resiliência e estabilidade de processos ecológicos em ambientes periodicamente perturbados ou em constante mudança (YACHI; LOREAU, 1999). Em contrapartida, em paisagens simplificadas apenas os organismos com alta habilidade de dispersão são capazes de acessar os recursos existentes nos poucos, pequenos e isolados ecossistemas naturais (TSCHARNTKE et al., 2005a; RAND; TSCHARNTKE, 2007) resultando na perda de espécies e de seus serviços. Portanto, a simplificação da estrutura da paisagem por meio da destruição e a fragmentação de habitats naturais, alteram a estrutura das comunidades de modo a selecionar e eliminar grupos funcionais (SWIFT; HANNON, 2010). Assim, enquanto espécies raras, especialistas ou endêmicas tendem a se tornar extintas após a ocorrência de tais distúrbios ambientais, espécies generalistas, com grande capacidade de adaptação e dispersão, tendem a se tornar dominantes (TSCHARNTKE et al., 2012). As consequências negativas da simplificação da estrutura da paisagem sobre a biodiversidade resultam na perda de espécies e de serviços ecossistêmicos associados como o controle biológico e polinização (TSCHARNTKE et al., 2005a). Saturni et al. (2016) verificaram que o aumento na cobertura florestal em escala de paisagem afetou positivamente a riqueza, abundância e diversidade de abelhas em cafezais, resultando em um aumento de 28% na formação dos frutos. Hipólito et al. (2018) verificaram que plantações de café localizadas próximas a habitats naturais e sob baixa intensidade de manejo apresentaram grande potencial para conciliar produção e conservação da biodiversidade. O efeito combinado dos habitats naturais e da baixa intensidade de manejo beneficiou os polinizadores que, por sua vez, foram responsáveis por um aumento de 30% na produtividade (HIPÓLITO et al. 2018). De forma similar, Bianchi et al. (2005) verificaram que plantações situadas em paisagens complexas apresentaram maiores taxas de predação de pragas quando comparadas àquelas situadas em paisagens simplificadas.

A estrutura da paisagem também pode determinar o sucesso de iniciativas voltadas para a conservação da biodiversidade e otimização de serviços ecossistêmicos, como a polinização e o controle biológico de pragas. Estudos indicam que tais iniciativas são mais efetivas em paisagens de complexidade estrutural intermediária quando comparada a paisagens estruturalmente complexas ou a paisagens simplificadas dominadas por monoculturas (TSCHARNTKE et al., 2012). Nesse sentido, medidas como o plantio de cordões vegetados e a adoção de agricultura orgânica, por exemplo, são mais efetivas em paisagens de estrutura intermediária (BATÁRY et al., 2010). Paisagens de complexidade intermediária apresentam um pool de espécies reduzido, mas que são capazes de se recuperar com um aumento na conectividade entre habitats agrícolas e não agrícolas e com o incremento na disponibilidade de recursos (TSCHARNTKE et al., 2012). Por outro lado, os efeitos dessas medidas conservacionistas não são visíveis em paisagem complexas onde diversidade e a densidade de espécies são altas em toda a área. Em paisagens simplificadas, os efeitos também não são visíveis, devido ao pool regional de espécies muito reduzido, incapaz de responder a esses estímulos (GEIGER et al. 2010; TSCHARNTKE et al. 2005a).

A estrutura da paisagem também modera a dissimilaridade entre as comunidades locais, superando os efeitos negativos da fragmentação e do manejo agrícola em escala local (TSCHARNTKE et al., 2012). A perda de habitat e a fragmentação *per se* são consideradas as principais forças condutoras da redução de biodiversidade (COLLINGE, 2009), entretanto o conceito de fragmentação tem sido amplamente criticado, devido à sua ambiguidade (FAHRIG, 2003). Os efeitos da fragmentação (alteração do arranjo espacial dos habitats remanescentes existentes na paisagem) sobre a perda de biodiversidade vêm sendo superestimado, resultando na subestimativa da diversidade beta como condutora da biodiversidade na escala de paisagem e de região (TSCHARNTKE et al., 2012). De fato, os mecanismos condutores dos padrões de biodiversidade em paisagens fragmentadas não incluem apenas os efeitos separados da perda de habitat e da fragmentação *per se*, mas também a interação desses fatores com a heterogeneidade espacial da paisagem anterior e posterior à modificação resultante da ação antrópica, assim como a extensão da paisagem. O aumento da heterogeneidade espacial da paisagem resulta em maior dissimilaridade na composição de espécies entre os habitats remanescentes que são separados por distâncias maiores, uma vez que habitats próximos apresentam maior similaridade nas condições ambientais quando comparados aos habitats distantes (FORTIN; DALE, 2005). Portanto, quando a área de habitat é distribuída na paisagem via fragmentação (vários pequenos fragmentos), e não concentrada em um grande e único remanescente de habitat, a diversidade beta aumenta - apesar da diminuição das populações locais (TSCHARNTKE et al., 2012). Por exemplo, Tschamntke et al. (2002) mostraram que 10 hectares de área protegida distribuídas em 29 pequenos fragmentos suportaram maior número de espécies, incluindo espécies raras e especialistas, que a mesma área distribuída em dois fragmentos grandes. Ademais, os efeitos da fragmentação são amenizados quando a matriz agrícola não é totalmente hostil e contém importantes recursos complementares, o que nos mostra a limitação dos efeitos da fragmentação *per se* e da aplicabilidade das teorias de metapopulação e da biogeografia de ilhas.

As mudanças espaciais e temporais na composição da paisagem podem causar concentração e diluição temporária das populações, sobretudo em paisagens agrícolas (HOLT; HOCHBERG, 2001). A alta disponibilidade de recursos por curtos períodos na matriz agrícola pode resultar na concentração das populações nas plantações via o processo de *bottom-up* (HOLT, 2008). Essa dinâmica de diluição e concentração pode ter consequências funcionais, principalmente em paisagens simplificadas que suportam populações reduzidas. Nesse sentido, Holzschuh et al. (2011) verificaram que as florações em massa em plantações de canola ocasionaram a concentração das populações de polinizadores na matriz, resultando em efeitos negativos para a polinização de plantas ameaçadas de extinção dos habitats naturais adjacentes. Espécies especialistas (ex. parasitoides) e de altos níveis tróficos (predadores no topo da cadeia alimentar) parecem ser mais afetadas pela dinâmica de concentração e diluição resultantes de distúrbios e mudanças ambientais e ecológicas quando comparadas às espécies que ocupam a base da cadeia alimentar (ex. insetos praga) (TSCHARNTKE et al., 2005a).

A simplificação da estrutura da paisagem resultante da destruição e fragmentação dos habitats naturais não afeta igualmente todas as espécies. Os efeitos dependem de características das espécies e da dinâmica espaço-temporal das paisagens (SWIFT; HANNON, 2010). Nesse sentido, a estrutura da paisagem seleciona grupos funcionais regulando as interações interespecíficas, assim como os processos evolucionários e ecológicos, e as dinâmicas de dispersão e colonização que estruturam as comunidades (URBAN et al., 2008). A evolução adaptativa e genética em decorrência de mudanças ambientais em paisagens agrícolas está ligada à seleção de espécies por meio de filtros ambientais, resultando no aumento da colonização e extinção de diferentes grupos funcionais. A persistência das espécies em paisagens antropizadas requer que as espécies sejam capazes de usar uma ampla gama de recursos e de forragear em diferentes habitats (RAND; TSCHARNTKE, 2007). Por exemplo, espécies de aves adaptadas às

mudanças ambientais em paisagens agrícolas são capazes de utilizar uma ampla gama de recursos e habitats em comparação às espécies existentes em paisagens florestais (TSCHARNTKE et al., 2008). Espécies com alta capacidade de dispersão em paisagens naturais e espécies no topo da cadeia alimentar especializadas em recursos e habitats específicos tendem a ser mais suscetíveis às mudanças ambientais existentes em paisagens agrícolas (FAHRIG, 2007). Além disso, a estrutura da paisagem pode selecionar grupos funcionais inteiros (PETCHEY; GASTON, 2006). Tscharnkte et al. (2008) verificaram que a diversidade de aves insetívoras, insetos predadores e de abelhas declina com a simplificação da paisagem resultante da intensificação da agricultura.

A estrutura da paisagem pode otimizar a diversidade funcional e a provisão de serviços ecossistêmicos sem contemplar a proteção de espécies raras e ameaçadas. Nesse sentido, o mosaico de habitats agrícolas e não agrícola existente na paisagem pode maximizar a provisão dos serviços ecossistêmicos, como a polinização (KLEIN et al., 2007), controle biológico de pragas (MEEHAN et al., 2011) e serviços ecossistêmicos culturais oriundos da beleza estética da paisagem (TSCHARNTKE et al., 2012). Paisagens complexas com alta diversidade de habitats agrícolas e não agrícolas são ambientalmente mais favoráveis para a biodiversidade e aumentam a dispersão e sobrevivência das populações (PERFECTO et al., 2009). Essas paisagens multifuncionais beneficiam espécies bem adaptadas às mudanças ambientais decorrentes da ação antrópica, entretanto, espécies raras, endêmicas, ameaçadas e especialistas continuam em risco. Por exemplo, a diversidade de aves nos trópicos pode ser alta em paisagens agrícolas, mas espécies especializadas em habitats florestais são raras nessas paisagens fragmentadas (MAAS et al., 2009). De maneira similar, a redução no sombreamento de 80% para 40% no interior de sistemas agroflorestais resultou no aumento de produtividade e de biodiversidade, mas a maioria das espécies florestais foi perdida (STEFFAN-DEWENTER et al., 2007; TSCHARNTKE et al., 2011).

A presente revisão destacou que a estrutura da paisagem pode afetar positiva e negativamente a biodiversidade e seus serviços ecossistêmicos por meio de múltiplos processos. Dessa forma, a definição de estratégias prioritárias que conciliem a conservação da biodiversidade com a produção de alimentos depende do entendimento de como as espécies percebem as mudanças ambientais em escala local e de paisagem. Nesse contexto, pesquisadores e conservacionistas propuseram a estratégia de “*land sparing and land sharing*” como meio para a conservação da biodiversidade em paisagens agrícolas (HERZOG; SCHÜEPP, 2013). A estratégia de *land sparing* consiste na maximização da agricultura com o objetivo de elevar a produtividade sem aumentar a área cultivada, resultando em maior número de áreas que podem ser destinadas para a conservação da biodiversidade, enquanto que a estratégia de *land sharing* concilia a produção agrícola e a conservação da biodiversidade por meio da adoção de práticas de manejo mais sustentáveis (BALMFORD et al. 2012). Phalan et al. (2011) concluíram que a conservação de espécies arbóreas e de aves em Gana e na Índia é mais efetiva utilizando a estratégia de *land sparing* para minimizar os impactos negativos do manejo agrícola intensivo nas plantações. Em contraste, estudos mostram que a estratégia de *land sharing* por meio da implantação sinérgica de práticas de manejo mais sustentáveis com a adoção de sistemas orgânicos e de restauração de habitats naturais em áreas de baixa aptidão agrícola resultou no aumento de biodiversidade e de serviços ecossistêmicos (BENGTTSSON et al., 2005; FISCHER et al. 2011; HAYASHI, 2011; GABRIEL et al., 2013). Os resultados contrastantes entre *land sparing* e *land sharing* encontrados em regiões tropicais e temperadas dificultam a inferência de generalizações sobre a efetividade dessas estratégias. Entretanto, essa discussão traz à tona a necessidade de se adotar práticas de manejo mais sustentáveis, que permitam conciliar a produção agrícola com conservação da biodiversidade, resultando na persistência em longo prazo de diferentes grupos funcionais e de seus serviços ecossistêmicos.

Descrição do sistema de estudo: a cultura do café, a comunidade de insetos e suas interações tróficas.

O café é a segunda bebida mais consumida no mundo, ficando atrás apenas da água (TNS-Interscience, 2008) e o Brasil é o maior produtor mundial de café produzindo aproximadamente 49 milhões de sacas (COCAPEC, 2017). Existem mais de 100 espécies no gênero *Coffea* (Rubiaceae), entretanto apenas as espécies *C. arabica* e a *C. canéfora* são de interesse econômico. A espécie *C. arabica* é unicaule, autógama com taxa de fecundação superior a 90% (REDDY et al., 1988) e se desenvolve bem em temperaturas entre 18°C e 22°C, balanço hídrico superior a 120 mm e altitude acima de 800 metros (WALLER et al., 2007). A espécie *C. canephora* é multicaule, alógama com 100% de polinização cruzada (WILLMER AND STONE, 1989) e apresenta maior produtividade em temperaturas entre 22°C a 26°C, balanço hídrico inferior 150 mm e altitudes abaixo de 700 metros (WALLER et al., 2007). O fruto maduro de ambas as espécies apresenta coloração vermelha e é constituído de uma polpa carnosa (mucilagem) que envolve a semente de formato elíptico alongado de 15 a 18 mm de comprimento (SOCIETY OF MEDICINAL PLANT, 2004). Segundo Waller et al., (2007), ambas as espécies são originárias do continente africano: *C. arabica* ocorre espontaneamente nos sub-bosques das florestas de altitude nas regiões altas da Etiópia, onde o clima é ameno e com alta umidade relativa durante o ano todo; *C. canephora* é originária das planícies equatoriais da bacia do rio Congo, onde a temperatura é superior a 20°C e a precipitação ultrapassa 2000 mm por ano. No Brasil, a espécie *C. arabica* é cultivada principalmente nos estados de Minas Gerais, São Paulo e Paraná, enquanto que o cultivo da espécie *C. canéfora* se concentra nos estados da Bahia, Espírito Santo e Rondônia.

Entre as principais pragas associada à cultura do café merecem destaque: broca-do-café - *Hypothenemus hampei* (Coleoptera: Scolitidae), ácaro vermelho - *Oligonychus ilicis* (Acari: Tetranychidae) e o bicho-mineiro - *Perileucoptera coffeella* (Lepidoptera: Lyonetiidae) (EMBRAPA, 2015). A broca-do-café ataca os frutos em qualquer estágio de maturação e as infestações podem ser influenciadas por fatores climáticos, manejo, colheita, sombreamento, espaçamento e altitude (EMBRAPA, 2015). Níveis de infestação acima de 30% são prejudiciais e levam a queda de produtividade e qualidade do café. A broca-do-café perfura os frutos afetando a classificação, beneficiamento e qualidade da bebida, resultando na perda de valor comercial (EMBRAPA, 2015). O ácaro vermelho vive na parte superior das folhas e seu ataque pode causar desfolha severa e atraso no desenvolvimento de lavouras em estágio de formação (REIS et al., 1997; MATIELLO, 1998). Ele alimenta-se das folhas onde perfura as células e suga parte do conteúdo celular, resultando em redução da área foliar e perda da capacidade fotossintética devido às lesões da praga no limbo das folhas (REIS et al., 1997). Desequilíbrios causados pelo uso de inseticidas e fungicidas, assim como períodos de estiagem prolongados, promovem o aumento populacional dessa praga (COSTA et al., 2003).

O bicho-mineiro (espécie alvo deste trabalho) é de origem africana, mas colonizou outras regiões tropicais e atualmente é uma das principais pragas de importância econômica para a cultura do café no Brasil, Índia e países da América Central (GALLO et al., 1978). Isso se deve ao fato de que *L. coffeella* é exclusivamente associada às espécies do gênero *Coffea* (RAMIRO et al., 2004). A espécie é um micro lepidóptero noturno e apresenta metamorfose completa, isto é: ovo, lagarta, crisálida e mariposa (SOUZA, 1998). A duração do ciclo total de *L. coffeella* é fortemente regulada pela temperatura e pela umidade relativa do ar (SPEER, 1949). Estudos relatam que o ciclo total desse inseto em condições de temperatura controlada pode variar de 73 dias, em temperatura de 21°C (FONSECA, 1944), a 17,5 dias em temperatura de 35°C (PARRA, 1985). Além disso, sua ocorrência está relacionada aos atributos da planta do café (idade e posição da folha, conteúdo de nitrogênio) e interações bióticas (competição

intra e interespecífica, predação, parasitismo) (LOMELÍ-FLORES et al., 2009, 2010). A oviposição ocorre com maior frequência em folhas mais velhas do terceiro e quarto internódios, na epiderme superior das folhas (WALKER; QUINTANA, 1969). As lagartas possuem aparelho bucal do tipo mastigador e após a eclosão, as lagartas perfuram a cutícula da folha e penetram diretamente no parênquima paliádico onde se alimentam até a formação da crisálida (SOUZA, et al., 1998). O casulo dessa espécie possui forma de “X” e se localizam especialmente na superfície abaxial das folhas (MATOS, 2001). Além disso, o adulto é uma mariposa de coloração prateada com aproximadamente 6,5 mm de envergadura (SOUZA, et al., 1998), que possui hábito crepuscular noturno, com maior atividade de voo entre 16 e 20 horas (EVANS, 1970).

As minas construídas pelo inseto resultam na redução da fotossíntese e queda prematura de folhas (WALKER; QUINTANA, 1969). Essa diminuição é severa, sobretudo porque a incidência de minas é maior nas folhas do terceiro e quarto internódios - onde a atividade fotossintética é maior. Adicionalmente, as injurias causadas por esse inseto resultam na redução da formação dos botões florais e da área foliar, especialmente, quando as minas são feitas na região do pecíolo (GALLO et al., 2002). O bicho mineiro possui uma ampla gama de inimigos naturais, como fungos, bactérias entomopatógenos (BOBBS et al., 1976), insetos predadores e parasitoides (MENDES, 1940; TAPLEY, 1960; SOUZA et al., 1980; WALLER et al., 2007).

Os principais insetos praga associados à cafeicultura possuem ampla gama de inimigos naturais, como fungos e bactérias entomopatógenos (BOBBS et al., 1976), insetos predadores e parasitoides (MENDES, 1940; TAPLEY, 1960; SOUZA et al., 1980; WALLER et al., 2007), além de aves e morcegos (KARP et al. 2013). Apesar das espécies de interesse econômico dentro do gênero *Coffea* serem consideradas plantas autopolinizadas (REHM; ESPIG, 1991; FREE, 1993), estudos mostram que a produção de frutos aumenta quando ocorre a polinização cruzada realizada por insetos polinizadores (KLEIN et al., 2003; ROUBIK, 2002). Vespas, abelhas e sirfídeos foram utilizados para representar os insetos benéficos. As vespas e diversas espécies de sirfídeos são importantes agentes de controle biológico de insetos praga em diversas culturas agrícolas (RICHTER, 2000; ROJO et al., 2003). Abelhas e sirfídeos são importantes polinizadores em ambos os ecossistemas naturais e agrícolas (ALLEN-WARDELL et al. 1998; POTTS et al. 2016; INOUE et al. 2015; LUCAS et al. 2017; OLLERTON 2017). Além disso, vespas, abelhas e sirfídeos são considerados bioindicadores confiáveis para avaliar a perda de biodiversidade e o sucesso de projetos de conservação (TSCHARNTKE et al., 1998; KLEIN et al., 2002a; SOMMAGGIO, 1999; RICARTE et al., 2011; SOMMAGGIO; BURGIO, 2014).

A família Vespidae (Hymenoptera) possui mais de 5.000 espécies descritas e classificadas em seis subfamílias: Stenogastrinae, Euparagiinae, Masarinae, Eumeninae, Polistinae e Vespinae (CARPENTER, 1982; ROSS; MATTHEWS, 1991; PICKETT; CARPENTER, 2010). Os representantes dessa família apresentam quatro padrões principais de comportamento: solitárias, pré-sociais, eusociais facultativas (CRESPI; YANEGA, 1995), e eusociais (HUNT, 1999; ST LOUIS JAMES, 2007). Do ponto de vista do controle biológico de pragas, a subfamília Polistinae merece destaque por possuir grande diversidade de espécies, sobretudo na região Neotropical, onde mais de 900 espécies pertencentes a 26 gêneros foram registradas (ANDENA; CARPENTER, 2014). Além disso, as espécies desse grupo apresentam organização social complexa e suas colônias podem ser compostas por dezenas e até centenas de rainhas funcionais (poliginia) e milhares de operárias (CARPENTER; MARQUES, 2001; NOLL et al., 2004; NOLL; WENZEL, 2008). A subfamília Polistinae é ainda subdividida em quatro tribos: Polistini, Mischocyttarini, Ropalidiini e Epiponini (RICHARDS, 1978; CARPENTER, 1993). Todas essas tribos, com exceção de Ropalidiini, apresentam grande diversidade de espécies na região Neotropical (ANDENA; CARPENTER, 2014) e apresentam grande potencial como agentes de controle biológico de pragas agrícolas. No Brasil, estudos destacam a

relevância das vespas predadoras (Vespidae) como sendo os principais agentes de controle biológico de *L. coffeella* (TOZATTI; GRAVENA, 1988; VILLACORTA, 1980; REIS et al., 2000). As vespas sobrevoam as plantações de café a procura de plantas com lesões e, depois de localizarem as minas com lagartas de *L. coffeella*, rasgam a epiderme da folha com a mandíbula para acessar a presa - que é removida da mina e predada (SOUZA et al., 1980).

As abelhas (Hymenoptera, Aculeata) são representadas por mais de 16 mil espécies (MICHENER, 2007), distribuídas em diferentes regiões zoogeógrafas: 1 – Afrotropical, 2 – Paleártica, 3 – Neártica, 4 – Neotropical, 5 – Oriental, 6 – Australiana (RADCHENKO; PESENKO, 1994). A maior diversidade de espécies se encontra na região Neotropical com 315 gêneros e subgêneros, 48 tribos (RADCHENKO; PESENKO, 1994). Diferentemente da maioria dos grupos de plantas e animais que apresenta uma diminuição de riqueza de espécies em direção aos polos, as abelhas são mais abundantes em regiões semidesérticas temperadas do mundo (SILVEIRA et al., 2002). As abelhas se alimentam predominantemente de pólen e néctar e podem apresentar comportamento solitário, facultativamente social e eusocial (SILVEIRA et al., 2002). O pólen é a principal fonte de proteína na dieta das abelhas com exceção de algumas espécies do gênero *Trigona* que se alimentam de tecidos de animais mortos (GILLIAM et al., 1985). As abelhas usam as flores para descansar, coletar homônimos sexuais e óleos utilizados na alimentação e revestimento das células, onde as larvas se desenvolvem (RADCHENKO; PESENKO, 1994). Ainda de acordo com Radchenko e Pesenko (1994), as abelhas podem ser classificadas de acordo com o hábito de nidificação: (1) ninhos subterrâneos, (2) ninhos suspensos em plantas, (3) ninhos em cavidades naturais, (4) ninhos em superfícies expostas. A maioria das espécies de abelha se reproduz por partenogênese arrenótoca (determinação sexual) com exceção de algumas espécies que se reproduzem por partenogênese telítoca (RADCHENKO; PESENKO, 1994). A diferenciação sexual via partenogênese arrenótoca é determinada pelo tipo de alimento fornecido às formas larvais (KEER, 1997).

Os sirfídeos (Diptera, Syrphidae) possuem ocorrência mundial e compreendem mais de 6000 espécies, com três subfamílias e 202 gêneros. Desse total, aproximadamente 2000 espécies, pertencentes a 60 gêneros, ocorrem na região Neotropical (THOMPSON et al., 2010). Os adultos se alimentam de pólen e néctar (BERNHARDT; EDENS, 2004), enquanto as larvas desses insetos apresentam grande diversidade de guildas alimentares, incluindo fitófagos, micófagos, saprófagos, filtradores (aquáticos), coprófagos, mirmecófagos e zoófagos (THOMPSON 1969; SOMMAGGIO, 1999; STÅHLS et al., 2003). A maioria dessas guildas são extremamente especializadas em um ou poucos microhabitats que não são encontrados nos agroecossistemas (SPEIGHT, 2006; SCHWEIGER et al., 2007; MEYER et al., 2009). Nas paisagens agrícolas da Europa, os remanescentes florestais são considerados os habitats mais importantes para a maioria das espécies de sirfídeos, devido à alta diversidade de microhabitats larvais (SPEIGHT, 2006). Em contraste, muitas espécies zoófagas forrageiam na matriz agrícola, onde as fêmeas realizam a postura dos ovos, entretanto, a ela é feita apenas na presença da presa (SADEGHI; GILBERT, 2000; BELLIURE; MICHAUD, 2001). As larvas de espécies predadoras se alimentam com a introdução do aparelho bucal no interior do corpo da presa para a extração de substâncias líquidas, enquanto os adultos possuem adaptações fisiológicas para retirada de néctar e pólen (COLLEY; LUNA, 2000). O néctar fornece a energia necessária ao voo e o pólen é a fonte de proteína para a maturação sexual, o sucesso reprodutivo, a produção de ovos e o aumento da longevidade (GILBERT, 1986; HASLETT, 1989; HICKMAN et al., 1995).

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CHAPTER 1

FOREST COVER INCREASES NATURAL ENEMY DIVERSITY AND BIOLOGICAL CONTROL SERVICES IN BRAZILIAN SUN-COFFEE PLANTATIONS

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Submitted to the journal: *Agriculture Ecosystems & Environment*

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Resumo

A composição e a configuração da paisagem afetam diretamente a abundância e a diversidade da comunidade de insetos, os quais influenciam nos serviços e desserviços ecossistêmicos relevantes para a agricultura. Neste estudo, investigamos como as condições ambientais em nível local e de paisagem afetam insetos-praga, seus inimigos naturais e a provisão de controle biológico em plantações de café. O foco foi o inseto praga *Leucoptera coffeella* (Lepidoptera: Lyonetiidae) e seus inimigos naturais - as vespas predadoras (Vespidae: Polistinae e Eumeninae). Foram examinadas a riqueza de espécies e a abundância de vespas predadoras em 16 plantações de café e 16 fragmentos florestais adjacentes localizados ao longo de um gradiente de cobertura florestal na região sudeste do Brasil. No interior das plantações de café também foram contados o número de folhas de café minadas e o número de minas predadas, a fim de estimar a densidade da praga e o serviço de controle biológico, respectivamente. Três questões foram elaboradas: (i) Os fragmentos florestais são fontes de

vespas predadoras para plantações de café adjacentes?; (ii) O serviço de controle biológico fornecido por inimigos naturais residentes dos fragmentos florestais “transbordam” para os cafezais adjacentes ou o serviço de controle biológico é mais concentrado nas bordas?; e (iii) As pragas, inimigos naturais e o controle biológico de pragas são regulados por fatores em escala local ou de paisagem? Por um período de 13 meses, foram coletados um total de 13658 vespas predadoras, representando 82 espécies distribuídas em 26 gêneros. A sobreposição considerável entre as comunidades nos cafezais e os fragmentos florestais adjacentes sugerem que as comunidades de vespas são similares nos diferentes tipos de habitats. A predação de mina foi consistente entre a borda e o interior dos cafezais, sugerindo que os insetos predadores fornecem serviços de controle biológico, tanto na borda como no interior das plantações. A abundância de *L. coffeella* foi negativamente afetada pela cobertura florestal e se beneficiou do aumento de temperatura. A riqueza de espécies e a abundância de vespas predadoras apresentou correlação positiva com o aumento de cobertura florestal. O controle biológico foi positivamente correlacionado com a cobertura florestal e abundância de vespas predadoras. A conservação e restauração das florestas pode promover um melhor balanço entre a produção sustentável de alimentos e a biodiversidade em paisagens produtoras de café por meio do aumento da diversidade de inimigos naturais e o serviço de controle biológico no interior das plantações.

Palavras-chave: Agroecossistemas; Bicho mineiro do café; Conservação da biodiversidade; Composição e configuração da paisagem; Serviços ecossistêmicos, Vespas predadoras

Abstract

Landscape composition and configuration directly affect the abundance and diversity of insect communities, which can influence agriculturally-relevant ecosystem services and disservices. In this study we investigated how environmental conditions at local and landscape levels affect insect pests, their natural enemies and the provision of biological control services in Brazilian coffee plantations. Our study focused on the insect pest *Leucoptera coffeella* (Lepidoptera: Lyonetiidae) and their natural enemies the predatory wasps (Vespidae: Polistinae and Eumeninae). We estimated the richness and abundance of predatory wasps in 16 sun-coffee plantations and in 16 adjacent forest remnants located across a gradient of forest cover in southeast Brazil. Within coffee plantations we also recorded the number of mined coffee leaves and preyed mines to estimate pest density and biological control services, respectively. We specifically asked: (i) Are forest remnants sources of predatory wasps for adjacent coffee plantations? (ii) Do biological control services provided by forest-dwelling natural enemies 'spill-over' into coffee plantations, or are they mostly concentrated at the forest edge? and (iii) Are crop pests, natural enemies and biological control services regulated by factors at the local or landscape levels? Over a 13 month period, we collected a total of 13,658 predatory wasps representing 82 species distributed across 26 genera. Considerable overlap amongst the communities in coffee plantations and adjacent forest remnants suggested that wasp communities are similar across different habitat types. Mine predation was consistent between edge and centre of plantations suggesting that predatory insects provide biological control services well into coffee plantations. The abundance of *L. coffeella* was negatively affected by forest cover and benefitted from higher temperatures. The richness and abundance of predatory wasps increased with increasing forest cover. Biological control was positively correlated with forest cover and predatory wasp abundance. Forest conservation and restoration can promote a better balance between sustainable food production and biodiversity in coffee producing landscapes by increasing natural enemy diversity and biological control services within coffee plantations.

Keywords: Agroecosystems; Biodiversity conservation; Coffee leaf miner; Ecosystem services; Landscape composition and configuration; Predatory wasps

INTRODUCTION

Insects provide ecosystem services and disservices in agricultural landscapes with important environmental and socio-economic consequences (Klein et al., 2007; Naranjo et al., 2015). Insect pests cause economic losses for farmers both directly by damaging cultivated plants, which reduces yield or quality, and indirectly by increasing production costs through the use of chemical inputs (Oerke and Dehne, 2004; Oerke, 2006). In Brazil, it is estimated that, annual economic losses based on the damage caused by insects (pre-harvest losses), the purchase of insecticides and the coverage of medical treatment for humans poisoned by insecticides reached US\$ 17.7 billion (Oliveira et al., 2014). However, ecosystem services provided by insects (e.g., pollination and pest control) result in significant economic benefits and may compensate for these losses. Losey and Vaughan (2006) estimated that insects provide US \$7.56 billion (9.34 billion in 2018 dollars; based on inflation) annually in the United States alone.

Landscape composition and configuration directly affect the abundance and diversity of insect communities and associated ecosystem services and disservices relevant to agricultural production (Holzschuh et al., 2010; Tscharnkte et al., 2007, 2012). Wild beneficial insects, such as pollinators and natural enemies, typically move into agricultural fields to exploit resources that are limited in time and space; thus these insects strongly depend on the presence of non-crop habitats to persist in agricultural landscapes (Tscharnkte et al., 2012, 2016). Non-crop habitats are typically free of pesticides, experience relatively low rates of disturbance, and provide a more reliable supply of resources such as food and shelter (Altieri, 1999; Landis et al., 2000; Bianchi et al., 2006). These habitats are especially important when resources are not available in the crop matrix (e.g., fallow) or during disturbances such as pesticide applications, tilling and harvest (Tscharnkte et al., 2007, 2012). Complex landscapes with a large proportion of non-crop habitats provide spatio-temporal insurance for natural enemies and enhance the provision of pest control services in crop fields (Bianchi et al., 2006; Tscharnkte et al., 2012; Veres et al., 2013). Whereas natural enemies seem to benefit from the presence of non-crop habitats more than pests (Bianchi et al., 2006; Veres et al., 2013; González et al., 2017), a number of pest species such as aphids (e.g. Thies et al., 2005), planthoppers (e.g. Grilli and Bruno, 2007) and phytophagous beetles (e.g. Rusch et al., 2012) can also benefit. Therefore, the importance of non-crop habitats as a source of natural enemies and biological control in farmland can vary according to pest biology, crop management and landscape structure (Tscharnkte et al., 2016).

The effects of landscape structure on insects and associated services and disservices have been widely investigated in temperate regions at multiple spatial scales (e.g. Bianchi et al., 2006; Tscharnkte et al., 2007, 2012, 2016). However, this issue remains understudied in Neotropical regions where only a handful of studies have been reported in Chile (Grez and Prado, 2000), Argentina (González et al., 2017) and Brazil (Saturni et al., 2016; Librán-Embid et al., 2017; Hipólito et al., 2018; Nery et al., 2018).

We studied the non-native but pervasive coffee leaf miner *Leucoptera coffeella* (Lepidoptera: Lyonetiidae) and native predatory wasps (Vespidae: Polistinae and Eumeninae) as a model system. *Leucoptera coffeella* (a multivoltine insect) is a major coffee pest in Brazil, India and Central America (Gallo et al., 2002). The larvae of *L. coffeella* are oligophagous and feed exclusively on species within the genus *Coffea* (Ramiro et al., 2004). This insect pest creates necrotic mines within coffee leaves causing abscissions that reduce photosynthesis, productivity and longevity of coffee plants (Pierre, 2011). Predatory wasps are important natural enemies of *L. coffeella* in Brazilian coffee plantations (Tozatti and Gravena, 1988; Villacorta, 1980; Reis et al., 2000; Carvalho et al., 2004), but probably depend on the presence of forest remnants to find a constant supply of multiple resources and safe places for nesting

(Edwards, 1980; Matsura and Yamane, 1984). In many coffee-growing regions, coffee is produced in sun-grown plantations that are submitted to frequent pesticide applications. Moreover, most farmers remove on-site wasp nests to avoid wasp stings during harvest. However, little is known about the effect of landscape structure and local variables on both the diversity and density of these insects, as well as on the biological control services they provide.

We investigated how environmental conditions at local and landscape levels affect the occurrence of insect pests, natural enemies and the provision of biological control services in Brazilian coffee plantations. We considered microclimatic conditions and crop management as factors at the local level, and coffee cover, forest cover, forest connectivity, landscape diversity and edge density as factors at the landscape level. We specifically asked: (i) are forest remnants sources of predatory wasps to adjacent coffee plantations? (ii) Do biological control services provided by these forest-dwelling natural enemies extensively spill over into coffee plantations or are they mostly concentrated at the forest edge? and (iii) Are certain crop pests, natural enemies and biological control services mostly regulated by factors at the local or landscape level? We predicted that: i) the species composition of predatory wasps in coffee plantations and in adjacent forest remnants are similar, suggesting that most species spill over from forest remnants into adjacent coffee plantations. ii) Biological control is stronger at the forest edge compared to the centre of the plantation. iii) Coffee leaf miner abundance is affected by coffee plantation size at a local scale and coffee cover at a landscape scale because its entire life cycle depends exclusively on coffee plants. iv) Biological control services increase with increasing species richness and abundance of predatory wasps, which would indicate the relevance of predatory wasps as agents of biological control. v) Landscapes with high forest cover support lower pest densities, more diverse wasp communities and greater biological control services than structurally simple landscapes dominated by monocultures.

Material and Methods

Study area

Our study region was located along the border between the states of São Paulo and Minas Gerais in southeast Brazil (Fig. 1).

Figura 1. Location of the study area in Brazil (A), landscapes within 1000 meters from a coffee plantation represent a gradient of forest cover from 2.8 % to 59.3%. The 16 sampled landscapes (yellow circles) in the study area (C). In (C), the study region encompasses the cities of Poços de Caldas (1) and Andradas (3) in Minas Gerais State and São João da Boa Vista (2) and Espírito Santo do Pinhal (4) in São Paulo State.

This region produces approximately 25% of coffee in Brazil (Conab, 2014) and is situated in the Atlantic Forest biodiversity hotspot, a biome that supports high levels of biodiversity and endemism (Myers et al., 2000) but has been heavily fragmented with less than 16% of its original cover still remaining (Ribeiro et al., 2009). Atlantic Forest remnants in the study region are composed of secondary vegetation after intensive logging occurring mainly in the 1970s and 1980s (local farmers pers. comm.). These forest remnants are restricted to small and isolated fragments immersed in a matrix predominantly composed of sun coffee plantations with other small-scale land uses such as pasture, eucalyptus and sugar cane production (Librán-Embí et al., 2017).

The study region encompasses mountainous relief in the north that becomes flatter towards the south. In the north coffee is typically cultivated without mechanization by small- and medium-scale producers in hilly terrain between 850 - 1300 m.a.s.l. (Librán-Embí et al., 2017). In the south, coffee cultivation is dominated by medium and large-scale producers who predominantly employ high levels of mechanization and cultivate coffee in level terrain between 700 - 850 m.a.s.l. Most farmers adopt conventional crop management based on the use of fertilizers, insecticides, fungicides and herbicides.

Insect surveys

We sampled the predatory wasps (Vespidae: Polistinae, Eumeninae) in 16 sun-coffee plantations and adjacent forest remnants located in different crop management and landscape contexts. At each of the 16 sites, we sampled wasps in three habitats: a) interior of the coffee plantation; b) interior of the adjacent forest remnant; and c) at the coffee-forest edge (Fig. 2).

Figura 2. Sampling design used in the 16 landscapes. Yellow circles represent traps used to collect wasps. Distance between traps was 50 m and between habitats (coffee-forest-edge) was 100 m.

In each habitat (coffee, edge and forest) we simultaneously set up one Malaise trap (Townes model; Fig. 3A) and three bait traps (Fig. 3B) 50 m apart along a 200 m transect parallel to the edge to capture wasps (a total of 3 Malaise traps and 9 bait traps per site).

Figura 3. Trap models used to collect predatory wasps. A – Malaise trap model Townes and B – bait traps.

Transects within interior of coffee and forest habitats were 100 m apart from any edge. Each bait trap consisted of a 2 L PET (Polyethylene Terephthalate Bottles) bottle hung from a branch approximately 1.3 m above the ground with four 4 cm diameter holes cut midway up the height of the bottle and filled with 300 ml of orange juice (Locher et al., 2014) and 0.4 ml of propylene glycol. Traps remained open for seven consecutive days per month for 13 months between June 2016 and June 2017. For all the sampling sites we quantified both abundance and richness of wasps.

Captured wasps were preserved in 70% ethanol and identified to the lowest taxonomic level possible using identification keys available for both subfamilies: Andrena and Carpenter (2012), Richards (1978) and Santos Junior et al. (2015) for Polistinae; Bohart and Stange (1965), Giordani Soika (1978, 1990), Willink and Roigk-Alsina (1998), Carpenter and Garcete-Barrett (2002) and Grandinete et al. (2015) for Eumeninae.

Biological control

Within each coffee plantation we visually assessed 200 coffee leaves per month to estimate the number of mined leaves (pest abundance) and preyed mines (biological control). Once a month we randomly selected 10 coffee plants in the centre of each plantation and 10 coffee plants along the edge of the forest remnant. We randomly selected five branches on each coffee plant at different heights and orientations and visually assessed the third pair of leaves from the branch tip ($n = 10$ leaves per tree). The total number of mined coffee leaves and preyed mines per plantation were recorded on a monthly basis and used to estimate the percentage of mined leaves (pest abundance) and preyed mines (biological control) over 13 months. We only considered leaves with fresh mines (dark brown in colour) to estimate pest abundance. Predated mines can be readily differentiated from those in which *L. coffeella* larvae have completed development because mines attacked by predatory insects display characteristic linear cuts on the mine surface. In contrast, mines in which pest development was complete display a circular emergence opening at the margin of the mine (Pierre, 2011). After assessment, we marked each coffee plant using coloured plastic ribbons to avoid evaluating the same tree twice.

Local and landscape level variables

We used coffee plantation size, coffee variety (Catuaí or Mundo Novo), crop management (manual or mechanized), agrochemical usage (the number of applications of fertilizer, insecticide, herbicide and fungicide over the 13 months), altitude and microclimatic conditions (overall annual mean of temperature, humidity and luminosity) in both coffee plantations and forest remnants as explanatory variables related to local factors. Considering that *L. coffeella* is restricted to coffee plantations, we used microclimatic conditions within coffee plantations only to explain pest abundance and biological control patterns. We used the datalogger Instrutherm®, model HT-500 to monitor temperature and humidity and the datalogger HOBO Pendant®, model UA-002-64 to record luminosity. Both dataloggers were attached to Malaise traps at 1.3 m above the ground and microclimatic conditions were recorded every hour during insect surveys (7 days/month over 13 months). Information related to agrochemical usage was obtained by periodic interviews with farmers.

To define the extent of each landscape, we considered the dispersal of predatory wasps; however, little is known about their dispersal capacity in the Neotropics. The few studies conducted indicate some species have a dispersal range up to 300 m (Santos et al., 2000; da Cruz et al., 2006; Ribeiro et al., 2008). Based on this estimated range we built land use maps for each site at four scales from 250 m to 1000 m radii using intervals of 250 m. Maps were built using high-resolution images from ArcGIS basemap imagery, 2013–2015 Digital Globe satellites, 0.5–1 m resolution and a 1:5000 scale. Extensive ground verification was used to achieve high levels of map accuracy. We considered coffee cover, forest cover and landscape diversity for landscape composition, and edge density and forest connectivity for landscape configuration. We measured these variables within radii of 250, 500, 750 and 1000 m around the centre of each sampled coffee plantation using ArcGIS 10.3 with Patch Analyst (Rempel et al., 2012) and V-LATE (LARG, 2006) extensions. To calculate forest connectivity we used the ‘proximity index’ which is based on the proximity and size of all forest fragments within a pre-determined search radius of the focal patch (Gustafson and Parker, 1994). Landscape diversity increases with an increasing number of habitat types in the landscape and was calculated using the Shannon diversity index metric in Fragstats (McGarigal, 2015). Edge density represents the sum of the lengths (m) of all edge segments in the landscape, divided by the total landscape area (m²) (McGarigal, 2015). Coffee cover and forest cover were negatively correlated between spatial scales (Spearman correlations $r_s > 0.50$; $p < 0.01$); thus we excluded coffee cover from analyses to avoid multicollinearity. In our final analysis, forest cover and landscape diversity represented landscape composition, and edge density and forest connectivity represented landscape configuration.

Statistical analyses

We estimated the dissimilarity of predatory wasp communities among coffee plantations, adjacent forest remnants and their interface using non-metric multidimensional scaling (NMDS) with a Jaccard distance matrix (Oksanen, 2007). Analytically, NMDS is an iterative process that uses the rank orders of species to orient samples in multidimensional space with the goal of expressing the original positions of samples in a reduced number of dimensions that can be easily visualized. Stress, a measure of how well the true multivariate distance between samples is represented in a reduced-dimensional space, was high (> 0.2) for two dimensions; thus we required three dimensions to adequately represent wasp communities. The dimensional space of each habitat type was visualized by plotting convex hulls that enclosed the three different habitats (forest, coffee, edge). We conducted the NMDS in R using the vegan package (Oksanen et al., 2018) and plotted the results using ggplot2 (Wickham, 2009). Jaccard dissimilarity index was calculated using the function `vegdist` available in the vegan package (Oksanen et al., 2007). We evaluated statistical differences in species composition among habitats using permutational multivariate analysis of variance using distance matrices with the function `adonis` of the vegan package (Oksanen et al., 2007).

To determine whether biological control services spill over into coffee plantations from forest fragments, we compared the mean percentage of predated *L. coffeella* mines between the center and edge plots using a paired t-test.

We used generalized linear models to determine if local and landscape level variables explained pest abundance, species richness and abundance of predatory wasps, and to estimate how local and landscape variables and the predatory wasp community affect biological control services. Species richness and abundance of predatory wasps were fitted with Poisson error structure, whereas pest abundance (% mined leaves) and biological control (%)

preyed mines) were fitted with Gaussian error structure. For each dependent variable and spatial scale, we analyzed seven competing models (Table 1) and a null model that represented the absence of effects.

Tabela 1. List of competing models used to identify the most relevant variables to explain patterns of richness and abundance of wasps, pest abundance and biological control services within coffee plantations in southeast Brazil.

Models	Fixed effects
Landscape composition	$y \sim \text{Forest cover} + \text{Landscape diversity}$
Landscape configuration	$y \sim \text{Edge density} + \text{Forest connectivity}$
Local environment	$y \sim \text{Altitude} + \text{Crop size} + \text{Crop management} + \text{Fertilizer} + \text{Coffee variety}$
Pesticide usage	$y \sim \text{Insecticide} + \text{Herbicide} + \text{Fungicide}$
Prey abundance*	$y \sim L. coffeella \text{ abundance}$
Microclimate (forest+coffee)*	$y \sim \text{Temperature} + \text{Humidity} + \text{Luminosity}$
Microclimate (coffee plantations)**	$y \sim \text{Temperature} + \text{Humidity} + \text{Luminosity}$
Wasp community**	$y \sim \text{Species richness} + \text{Abundance}$

* Only included in the list of competing models used to explain species richness and abundance of predatory wasps.

** Only included in the list of competing models used to explain pest abundance and biological control services.

The best models were identified using the Akaike Information Criterion (AIC; Burnham and Anderson, 1998) with the small sample correction (AICc; Hurvich and Tsai, 1989). We used AICc weight (wAICc) and AICc delta (ΔAICc) to rank the models. The wAICc represents the weight of evidence in favor of a given model amongst competing models (Burnham and Anderson, 2002). The ΔAICc is the difference between the AICc of a considered model and the best model, i.e., the model with the lowest AICc value (Burnham and Anderson, 2002). The models with p-values < 0.05 (model fit), $w\text{AICc} \geq 0.1$ and $\Delta\text{AICc} \leq 2.5$ were considered equally plausible at explaining the dependent variables. All analyses were performed in R version 3.0.2 with the AICctab function of the bbmle package (Bolker, 2010) for model selection.

RESULTS

Predatory wasps, pest density and biological control

We collected 13,658 predatory wasps (Vespidae: Polistinae, Eumeninae), representing 82 species distributed across 26 genera (Appendix A). Species richness varied from 19 to 44 species per site and abundance varied from 167 to 1709 predatory wasps per landscape. The most abundant wasp species were *Agelaia vicina* (26.3% of all specimens), *Agelaia multipicta* (23.2%) and *Agelaia pallipes* (12.7%). Wasps were twice as abundant within coffee plantations (6378 specimens) compared to forest (3809 specimens) and edge (3471 specimens) habitats. The

mean percentage of mined leaves (pest abundance) and preyed mines (biological control) in coffee plantations over the 13 months surveyed ranged from 5.3 - 32.5 % and from 12.7 - 72.8 %, respectively.

Forest remnants as sources of predatory wasps

Wasp communities were adequately described using a NMDS ordination with three axes (stress = 0.170). Intermediate overlap suggests that wasp communities are not very similar among habitats (Fig. 4 A, B, C).

Figure 4. Three dimensional ordination plots (non-metric multidimensional scaling) of predatory wasp communities at coffee-forest interfaces in southeast Brazil: A) axes 1 and 2, B) axes 2 and 3 and C) axes 1 and 3. Wasp species are represented as gray points (black points indicate where species points overlap) and sampling locations as colored symbols. Samples from the same habitat type are grouped using convex hulls.

Permutational multivariate analysis of variance using distance matrices indicated that wasp communities significantly differed among coffee, forest and edge habitats ($R^2 = 0.13$, $p = 0.001$). However, when we only consider abundant species high overlap is observed (Fig. 5 A, B, C) and significant differences among habitats were not detected ($R^2 = 0.08$, $p = 0.062$).

Figure 5. Three dimensional ordination plots (non-metric multidimensional scaling) of the eight abundant predatory wasp species in coffee-forest interfaces within southeast Brazil. Wasp species are represented as gray points (black points indicate where species points overlap) and sampling locations as a colored symbols. Samples from the same habitat type are grouped using convex hulls.

We considered the eight most abundant species, which together encompassed 86.7% of all specimens collected: *Polybia punctate* (n = 377 specimens), *Polybia ignobilis* (n = 501), *Polybia occidentalis* (n = 755), *Polybia fastidiosuscula* (n = 772), *Polybia paulista* (n = 951), *Agelaia pallipes* (n = 1731), *Agelaia multipicta* (n = 3170) and *Agelaia vicina* (n = 3598).

Do biological control services spill-over into coffee plantations?

The predation rate (preyed mines) was consistent between the plantation edge and centre for all sites and months of study (Fig. 6C and 6D). Mine abundance was higher in the plantation centre than at the edge during the dry season (June – Nov. 2016; Fig. 6A), but stabilized to be non-discernible from mine abundance at the edge at the beginning of the wet season (Dec. 2016 – June 2017; Fig. 6A, 6B). During the dry season mine abundance surpassed the threshold of economic damage of 30 % of mined leaves (Souza et al., 1998) in seven coffee plantations.

Figure 6. Results of *L. coffeella* mine abundance and predation: mine abundance (a) and percentage of mines that have been predated (b) over 13 months from June 2016 to June 2017, and mean annual mine abundance (c) and percentage of mines that have been predated (d) in the centre (red) and edge (yellow) of the coffee plantations. In panels (a) and (c), the dry season is shaded gray. The economic threshold of 30% coffee leaves mined is depicted as a dashed horizontal line in (a) and (b).

The effects of local and landscape factors

Local and landscape explanatory variables varied considerably along the 16 sites. Agrochemical usage varied from 2 to 13 applications per year (fertilizers = 0 ± 3 and pesticides = 2 ± 10). Coffee plantation size varied from 2.4 to 14 hectares and altitude ranged from 720 to 1250 m.a.s.l. Forest cover within 1000 m varied from 2.8% to 59.3%, forest connectivity from 4.71 to 958.77, landscape diversity from 1.05 to 1.86 and edge density from 127 to 246.

Species richness of predatory wasps was best explained by landscape composition ($wAICc \geq 0.819$; forest cover) at all spatial scales (Table 2; Fig. 7). The abundance of predatory wasps was also correlated with landscape composition at all spatial scales; however the power of explanation of the forest cover model was much higher at 250 and 500 m compared with the larger scales ($wAICc > 0.9$ vs. $wAICc < 0.7$). The abundance of coffee leaf miners was affected by landscape composition at all scales ($wAICc \geq 0.247$; forest cover) but also by microclimatic conditions within coffee plantations ($wAICc \geq 0.448$; temperature). Biological control services were significantly correlated with landscape composition ($wAICc \geq 0.190$; forest cover) only at scales of 250 and 500 m, and with the wasp community ($wAICc \geq 0.633$; wasp abundance). None of the response variables were explained by landscape configuration or the other variables related to local factors such as pesticide usage, altitude and coffee variety.

Tabela 2. Results for the best models to explain the species richness and abundance of predatory wasps, pest occurrence and biological control in 16 coffee plantation landscapes in southern Brazil. AICc = Akaike Information Criterion with the small sample correction; wAICc = evidence weight of the model. Asterisks indicate the level of significance of each fixed effect within the models. The symbols – and + within parentheses indicate the direction of correlation between response variables and the fixed effects at all four spatial scales (250, 500, 750 and 1000 m).

Response variable	Model	Spatial scales from center of plantations				Fixed effects
		250 m	500 m	750 m	1000 m	
Wasp species richness	Landscape composition	0.0 / 0.923	0.0 / 0.819	0.0 / 0.896	0.0 / 0.903	Forest cover***(+) Landscape diversity
Wasp abundance	Landscape composition	0.0 / 0.950	0.0 / 0.927	0.0 / 0.526	0.0 / 0.671	Forest cover**(+) Landscape diversity
<i>L. coffeella</i> abundance	Landscape composition	0.0 / 0.539	1.4 / 0.321	0.3 / 0.454	2.2 / 0.247	Forest cover***(-) Landscape diversity
	Microclimate	0.4 / 0.448	0.0 / 0.660	0.0 / 0.531	0.0 / 0.731	Temperature***(+) Humidity Luminosity
Pest biological control	Landscape composition	1.1 / 0.365	2.5 / 0.190	n.s	n.s	Forest cover**(+) Landscape diversity
	Wasp community	0.0 / 0.633	0.0 / 0.810	0.0 / 0.977	0.0 / 0.971	Species richness Abundance**(+)

* P< 0.05; ** P< 0.01; *** P< 0.001

Relationships between variables found for the best models for: a) predatory wasp species richness, b) wasp abundance and c) percentage of mined leaves vs. forest cover, d) percentage of mined leaves vs. temperature and e) percentage of mines that have been predated vs. forest cover and f) vs. wasp abundance in 16 coffee plantation landscapes in southeast Brazil. The best models and spatial scales were selected based on the spatial scale with the highest model weight ($wAICc > 0.10 < 1.00$) (Table 2).

DISCUSSION

Forest remnants as sources of predatory wasps

Despite differences in species composition among habitat types, overall wasp richness and abundance as well as pest biological control increased with increasing forest cover in the surrounding landscape. Furthermore, the eight most abundant species had high densities in all habitats suggesting high spillover of predatory wasps from forest to coffee habitats. These eight species encompassed 86.7 % of total specimens collected and heavily

influenced the positive correlation between total wasp abundance and pest biological control. Social wasps are central foragers and need to move between nesting and feeding habitats repeatedly (Richter, 2000). Moreover, wasps use odor or visual cues such as leaf damage to find prey and benefit from high densities of lepidopteran pests in several agroecosystems (Richter, 2000) including *L. coffeella* in Brazilian coffee plantations (Parra et al., 1977, Gravena, 1983). Based on our observations, we argue that wasps, particularly social species build their nests in forest remnants and search for preys within adjacent coffee plantations. The opposite trend is less probable due to constant disturbance in coffee plantations. The intensive use of pesticides in many plantations along with pruning and harvest activities result in high mortality rates of individual wasps and the destruction of nests within coffee plantations. Moreover, wasp nests found in close proximity to humans (either within crops or on human-built structures) are usually removed to prevent wasp stings. In contrast, forest remnants provide undisturbed nesting habitat and a constant supply of floral resources, prey and fiber for building nests when these resources are not available in coffee plantations. Indeed, non-crop habitats such as forests, wetlands and grasslands are relatively stable and provide a variety of resources for parasitoids and predatory insects, such as prey and hosts, shelter, overwintering sites, mating sites, pollen and nectar (Altieri, 1999; Landis et al., 2000; Tscharntke et al., 2007, 2012).

Although coffee plantations are intensively managed, wasps were more than twice as abundant within coffee plantations in comparison with forest and edge habitats. These results reinforce our hypothesis that wasps use forest as nesting habitats and adjacent coffee plantations as feeding habitats. The constant disturbance within coffee plantations probably affects individual foragers searching for prey, while colonies remain intact inside adjacent forest remnants. Wasp colonies inside forest remnants seem to act as permanent sources of foragers to adjacent coffee plantations resulting in the rapid recolonization of crops after disturbance such as pesticide applications and nest removal. Therefore, forest remnants may attenuate the tradeoffs between crop management and conservative biological control within coffee plantations.

How far do biological control services spill over into coffee plantations?

Contrary to our expectation, biological control was not stronger at the forest edge compared to the centre of the plantation (100 m from any edge); the percentage of mines predated (biological control) was consistent between the plantation edge and centre. Biological control services increase with increasing wasp abundance; thus similar rates of pest control between the plantation edge and centre can be associated with a high dispersal capacity of social wasps, which heavily influenced total abundance. The few existing studies conducted in the Neotropics suggest that the scale of the effect of some Polistinae species is approximately 300 m (Santos et al., 2000; da Cruz et al., 2006; Ribeiro et al., 2008). Our results indicate that the most wasp species respond to landscape context at larger spatial scales between 500 and 1000 m; however, abundant species such as *A. vicina*, *A. multipicta* and *A. pallipes* seem to disperse up to 500 m. Therefore, predatory wasps can provide biological control services at a local scale (plantation edge and center) and at a landscape scale covering several coffee plantations, although it seems likely that coffee plantations larger than 500 m radius (~ 70 ha) will derive fewer biological control services than seen in smaller fields.

The effects of local and landscape factors

Habitat amount hypothesis predicts that species richness increase with increasing habitat amount in the surrounding landscape independent of patch size and isolation (Fahrig, 2013). This hypothesis seems to be true for wasps which were positively correlated with forest cover regardless of landscape diversity and configuration. Forest cover also overcame the influence of important local factors such as microclimate and pesticide usage. Our findings suggest that forest amount is essential for long-term persistence of wasps in coffee producing landscapes. Studies conducted in fragmented landscapes in southeast Brazil suggest that wasps use forest remnants as nesting sites (Souza et al., 2010, 2014, 2015). Therefore, wasps probably depend on forest to find suitable nesting habitats since crops provide poor nesting conditions due to the intensive management or low habitat quality (Perfecto and Vandermeer, 2002; Chacoff and Aizen, 2006).

Despite constant disturbance, agricultural land is not totally hostile and also provides important resources such as mass flowering crops (Westphal et al., 2003). However, the availability of resources in crops is limited in space and time resulting in the failure of crop-dominated landscapes to consistently provide resources required by many species, particularly beneficial insects such as natural enemies and pollinators (Tscharntke et al., 2005, 2016). In fragmented landscapes in Brazil, at least 30-35% forest cover is needed to maintain high levels of animal diversity, including birds, mammals, amphibians (Banks-Leite et al., 2014) and bees (Ferreira et al., 2015), while bats and large-sized mammals may need ~ 50% forest cover (Muylaert et al., 2016; Beca et al., 2017). Although we did not detect clear thresholds, landscapes with less than 20% forest cover supported low wasp diversity and high levels of pest densities that surpassed the economic damage threshold during the outbreak season (Fig. 4, June-November 2016). High forest cover in the landscape negatively affected *L. coffeella* by increasing predatory wasp occurrence and biological control services in coffee plantations. Additionally, high forest cover means low cover of coffee, which is the only locally-available host plant for this oligophagous leaf mining pest (Ramiro et al., 2004), thereby reducing recolonization potential between and within coffee plantations.

Microclimatic conditions also have a strong influence on the life cycle of *L. coffeella* (Speer, 1949; Parra, 1985). Temperature directly affects *L. coffeella* development and the number of generations, which can range from 4 to 12 per year (Parra et al., 1981; Reis et al., 1984; Parra et al., 1995). The *L. coffeella* life cycle development rate increases steadily as temperatures increase from 18°C to 32°C (Jaramillo, 2016); therefore, higher temperatures most likely lead to more generations per year, resulting in greater pest pressure. Moreover, Righi et al. (2013) found lower *L. coffeella* infestation in coffee agroforestry than in coffee monoculture suggesting that shade provided by trees can reduce air and foliage temperature; the resulting high foliar water content can provoke the asphyxiation of larvae inside the leaf. Such fluctuations in foliar water content mediated by temperature may also explain the high abundance of *L. coffeella* in the centre of coffee plantations during the dry season followed by accentuated decline in the wet season when foliar water content increases regardless of distance from forest edge as found by Righi et al. (2013) in shaded coffee plantations.

Implication for conservation and policies

As pointed by Duarte et al. (2018), ecosystem services such as water quality, disease control, pest control, pollination and aesthetic values are influenced by several landscape structure attributes (landscape complexity, percentage of non-crop or natural habitats, aggregation, spatial heterogeneity, landscape connectivity and habitat

fragmentation). Here we provide empirical evidence that forest remnants are sources of natural enemies of a widespread and costly pest in coffee, and that the proportion of forest cover on the landscape increases biodiversity and ecosystem services in a Neotropical region. Similarly, previous studies conducted in Brazil found that forest remnants increase the abundance and diversity of beneficial insects including bees (Saturni et al., 2016; Boscolo et al., 2017), syrphids (Medeiros et al., 2018), parasitoids (Bortolotto et al., 2016) and predatory wasps (Sousa et al., 2011) in adjacent agroecosystems. Thus, we recommend that agri-environment schemes in Brazilian agricultural landscapes should focus on the conservation of forest remnants and forest restoration in areas of low agricultural importance, abandoned crops and riparian areas at multiple spatial scales.

Forest conservation and restoration can be particularly relevant in coffee producing regions where forest cover seems to enhance pollination services (Saturni et al., 2016) and prevents *L. coffeella* outbreaks by increasing biological control services in coffee plantations. Forest conservation and restoration can also enhance other ecosystem services from water quality maintenance (Mikkelsen et al., 2013) to cultural services (Sodhi et al., 2009; Plieninger et al., 2013; Riechers et al., 2016).

Understanding the effects of non-crop habitats on insect communities and associated ecosystem services and disservices they support is an essential part of achieving more sustainable agricultural systems. The importance of these forest patches as sources of ecosystem services will vary depending on the crop, the service, the nature and extent of non-agricultural land cover, and management practices. Although the delivery of agriculturally-relevant ecosystem services will not and should not be the primary argument for conserving and restoring forested habitat in the Neotropics, results of studies like ours support that in some cases, there can be direct benefits to agricultural production derived from forested land in the wider landscape. Studies that integrate several services and disservices would be beneficial in achieving a better understanding of how landscape structure and crop management mediate tradeoffs between ecosystem services and disservices at multiple spatial and temporal scales. Such information is crucial to aid regional planners in decision-making and selection of appropriate spatial scales and policies.

ACKNOWLEDGEMENTS

We are grateful to the owners of private lands where the study sites were located. We also thank the Rufford Foundation that provided crucial financial support for field work activities (reference project: 18799-1). HRM received a research grant from the Brazilian Government Research Council (CNPq) (142147/2015-0 / 141932/2016-3) and a scholarship from the Emerging Leaders of Americas Program (ELAP) supported by the Canadian Government. PM was funded by an Isaac Walton Killam Postdoctoral Fellowship. KAH received funding from the Natural Sciences and Engineering Research Council of Canada. YCG thanks Rogério Botion Lopes who helped identify *Zethus* species. YCG also thanks Rogério Botion Lopes and Gustavo Bellini Cortes who collaborated with some species identifications and sorting of Malaise material. MCR thanks FAPESP (process #2013/50421-2), CNPq (processes # 312045/2013-1; #312292/2016-3) and PROCAD/CAPES (project # 88881.068425/2014-01) for their financial support.

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APÊNDICE A.

List of predatory wasp species recorded in 16 coffee-forest interfaces in southeast Brazil.

Sub-family	Species	Coffee	Edge	Forest
Eumeninae	<i>Alphamenes campanulatus</i> (Fabricius, 1804)	0	1	1
	<i>Alphamenes</i> sp	2	2	0
	<i>Cyphomenes anisitsii</i> (Brèthes, 1906)	1	0	0
	<i>Hypalastoroides</i> sp	0	1	0
	<i>Hypancistrocerus</i> sp1	13	0	0
	<i>Hypancistrocerus</i> sp2	2	0	0
	<i>Monobia</i> sp	0	0	1
	<i>Montezumia ferruginea</i> de Saussure, 1852	1	0	1
	<i>Montezumia petiolata</i> de Saussure, 1855	1	0	0
	<i>Montezumia</i> sp	1	0	0
	<i>Omicron gondwanianum</i> Giordani Soika, 1978	0	1	0
	<i>Omicron graculum</i> (Zavattari, 1912)	1	0	0
	<i>Omicron microscopicum</i> (de Saussure, 1852)	1	0	0
	<i>Omicron opifex</i> (Brèthes, 1909)	0	1	0
	<i>Omicron ruficollis</i> (Zavattari, 1912)	1	0	0
	<i>Omicron</i> sp1	2	1	0
	<i>Omicron</i> sp2	1	0	0
	<i>Omicron</i> sp3	1	0	0
	<i>Omicron tuberculatum</i> (Fox, 1899)	2	13	0
	<i>Pachodynerus gadulpensis</i> (de Saussure, 1853)	5	5	2
	<i>Pachodynerus nasidens</i> (Latreille, 1817)	0	1	0
	<i>Pachodynerus serrulatus</i> Brèthes, 1920	0	1	0
	<i>Pachymenes ater</i> de Saussure, 1852	5	10	13
	<i>Pachymenes bipartitus</i> (Fox, 1899)	1	1	0
	<i>Pachymenes ghilianii</i> (Spinola, 1851)	3	5	2
	<i>Pachymenes laeviventris</i> (Fox, 1899)	1	1	0
	<i>Pachymenes olympicus</i> (Zavattari, 1912)	1	1	1
	<i>Pachymenes sericeus</i> de Saussure, 1852	3	3	0
	<i>Parancistrocerus</i> sp1	1	0	0
	<i>Parancistrocerus</i> sp2	1	0	0
	<i>Pirhosigma superficiale</i> (Fox, 1899)	6	0	0
	<i>Pseudodynerus griseus</i> (Fox, 1902)	0	0	1
	<i>Stenonartonia apicipennis</i> (Fox, 1902)	1	0	0
	<i>Zeta argillaceum</i> (Linnaeus, 1758)	2	3	0
	<i>Zethus fuscus</i> (Perty, 1833)	0	0	1
	<i>Zethus</i> sp	2	0	0
Polistinae	<i>Agelaia angulata</i> (Fabricius, 1804)	3	1	5
	<i>Agelaia multipicta</i> (Haliday, 1836)	1266	893	1011
	<i>Agelaia pallipes</i> (Olivier, 1792)	894	525	312

<i>Agelaia vicina</i> (de Saussure, 1854)	1295	1027	1267
<i>Apoica pallens</i> (Fabricius, 1804)	67	23	8
<i>Brachygastera augusti</i> (de Saussure, 1854)	1	0	1
<i>Brachygastera lecheguana</i> (Latreille, 1824)	86	11	4
<i>Brachygastera mouleae</i> Richards, 1978	1	0	1
<i>Metapolybia cingulata</i> (Fabricius, 1804)	1	1	1
<i>Mischocyttarus cassununga</i> (von Ihering, 1903)	8	1	7
<i>Mischocyttarus cearensis</i> Richards, 1978	1	10	2
<i>Mischocyttarus drewseni</i> de Saussure, 1857	18	7	0
<i>Mischocyttarus rotundicollis</i> (Cameron, 1912)	0	0	1
<i>Mischocyttarus rotundicollis</i> (Cameron, 1912)	29	36	21
<i>Mischocyttarus socialis</i> (de Saussure, 1854)	6	2	0
<i>Mischocyttarus</i> sp1	2	0	0
<i>Mischocyttarus</i> sp2	0	6	0
<i>Mischocyttarus</i> sp3	0	0	1
<i>Mischocyttarus</i> sp4	0	0	1
<i>Polistes billardieri</i> Fabricius, 1804	1	0	0
<i>Polistes cinerescens</i> de Saussure, 1854	2	3	1
<i>Polistes erythrocephalus</i> Latreille, 1813	33	27	2
<i>Polistes lanio</i> (Fabricius, 1775)	4	2	0
<i>Polistes melanosoma</i> de Saussure, 1853	1	1	0
<i>Polistes pacificus</i> Fabricius, 1804	4	4	0
<i>Polistes simillimus</i> Zikán, 1851	38	18	4
<i>Polistes</i> sp1	1	0	0
<i>Polistes subsericeus</i> de Saussure, 1854	3	1	0
<i>Polistes versicolor</i> (Olivier, 1792)	116	116	27
<i>Polybia bifasciata</i> de Saussure, 1854	4	6	3
<i>Polybia chrysothotax</i> (Lichtenstein, 1796)	57	74	86
<i>Polybia dimidiata</i> (Olivier, 1792)	9	17	5
<i>Polybia fastidiosuscula</i> de Saussure, 1854	415	187	170
<i>Polybia ignobilis</i> (Haliday, 1836)	287	139	75
<i>Polybia jurinei</i> de Saussure, 1854	70	80	33
<i>Polybia minarum</i> Ducke, 1906	26	13	21
<i>Polybia ocidentalis</i> (Olivier, 1792)	396	242	117
<i>Polybia paulista</i> von Ihering, 1896	768	120	63
<i>Polybia punctate</i> du Buysson, 1908	130	89	158
<i>Polybia sericea</i> (Olivier, 1792)	146	61	29
<i>Protonectarina sylveirae</i> (de Saussure, 1854)	97	3	2
<i>Protopolybia exigua</i> (de Saussure, 1854)	4	0	0
<i>Protopolybia sedula</i> (de Saussure, 1854)	15	7	1
<i>Pseudopolybia vespiceps</i> (de Saussure, 1863)	4	3	3
<i>Synoeca cyanea</i> (Fabricius, 1775)	7	2	5

CHAPTER 2

FOREST COVER, LANDSCAPE DIVERSITY AND EDGE DENSITY SHAPE THE DIVERSITY OF BENEFICIAL INSECTS IN COFFEE PRODUCING LANDSCAPES

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Submitted to the journal: *Conservation Biology*

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Resumo

A expansão das monoculturas e o uso indiscriminado de agrotóxicos resultam na perda de insetos benéficos e no interrompimento de serviços ecossistêmicos, como a polinização e o controle biológico de pragas em paisagens agrícolas. Neste estudo, abelhas, vespas e sirfídeos foram utilizados como modelo de estudo para investigar como a estrutura da paisagem afeta a diversidade alfa e beta de diferentes grupos funcionais de insetos em paisagens agrícolas produtoras de café. A cobertura florestal, diversidade da paisagem e densidade de bordas foram utilizadas para representar a estrutura da paisagem em múltiplas escalas espaciais. Ao longo de um período de 13 meses foi registrado um total de 13.658 vespas (86 espécies; e 26 gêneros), 8.393 abelhas (116 espécies; 73 gêneros) e 4.984 sirfídeos (63 espécies; 20 gêneros). A abundância e riqueza de espécies de vespas, assim como a riqueza de espécies abelhas apresentaram correlação positiva com a cobertura florestal em todas as escalas espaciais, enquanto que o grupo dos sirfídeos não respondeu a nenhuma das variáveis explanatórias. A composição da comunidade de vespas e abelhas em paisagens com baixa cobertura florestal foi composta por subgrupos das comunidades localizadas em paisagens com alta cobertura florestal, resultando na perda de espécies em paisagens simplificadas. Esses resultados indicam que iniciativas de conservação de insetos benéficos no *hotspot* de biodiversidade Mata Atlântica devem focar na conservação e restauração florestal, uma vez que altos níveis de desmatamento resultam na perda de espécies de abelhas e vespas com potencial perda de serviços ecossistêmicos, como polinização e controle biológico de pragas nos agroecossistemas. Além disso, altos níveis de diversidade de paisagem e de densidade de bordas resultam na mudança de composição de espécies de sirfídeos, com espécies predadoras, substituindo os demais grupos funcionais em paisagens simplificadas. Como consequência, estratégias de complementação da paisagem, como cordões vegetados, diversificação de culturas e conversão das plantações em sistemas mais sustentáveis, podem beneficiar insetos não alvos. Tais estratégias devem também ser incluídas no planejamento e manejo de paisagens agrícolas.

Palavras-chave: Agroecossistemas; Diversidade de insetos; Estrutura da paisagem; Manejo agrícola; Serviços ecossistêmicos

Abstract

The expansion of monocultures and the overuse of agrochemicals have resulted in the loss of beneficial insects and disruption of ecosystem services such as pollination and biological control in agricultural landscapes. Bees, wasps and flower flies were our model groups to investigate how landscape structure attributes affect alpha and beta diversity of different beneficial insect groups in Brazilian landscapes containing coffee crops. We used forest cover, landscape diversity and edge density to represent landscape structure at four spatial extents (250, 500, 750 and 1000 m). Over a period of 13 months, we recorded a total of 13,658 wasps (86 species; 26 genera), 8,393 bees (116 species; 73 genera) and 4,984 flower flies (63 species; 20 genera). Species richness and abundance of wasps, and bee richness were positively correlated with forest cover at all spatial extents. Bee abundance, and species richness and abundance of flower flies did not respond to any landscape predictor. The community composition of wasps and bees in landscapes with low forest cover was composed of subsets of the communities located in forested landscapes, leading to species loss in structurally impoverished landscapes. High landscape diversity and edge density resulted in changes in flower fly composition, in which predatory species replaced non-predatory species found in simpler landscapes. Such results indicate that initiatives for the conservation of beneficial insects in Atlantic Forest biodiversity hotspots must focus on forest conservation and restoration, because high levels of forest loss can result in the loss of wasp and bee species with potential negative consequences for the provision of pollination and pest control services in agroecosystems. Additionally, because high landscape diversity and edge density promoted species replacement in flower fly communities, landscape complementation strategies such as flower strips along crop edges, and diversification and conversion of crops into more sustainable systems can benefit both forest and non-forest associated beneficial insects. Such complementation strategies should be combined with forest conservation and restoration in landscape planning and management.

Keywords: Agroecosystems; Natural habitats; Landscape structure; Beta diversity; Pollinators; Natural enemies; Tropical forest

Introduction

One of the key global environmental challenges is to balance sustainable food production and biodiversity conservation (Johnson et al. 2017). Agricultural practices have intensified over the centuries as a means to increase food production, which relates to the expansion of monoculture and results in high habitat loss and fragmentation at the landscape level - a process known as landscape simplification (Allen-Wardell et al. 1998; Kremen et al. 2002; Tscharntke et al. 2005; Deguines et al. 2014; Eeraerts et al. 2017). At a local level, pesticide applications heighten both mortality rates and sublethal effects in beneficial insects foraging in arable fields (Stapel et al. 2000; Geiger et al. 2010). Agricultural intensification is considered one of the main threats to biodiversity conservation (Butchart et al. 2010) and the main cause of the decline of natural enemies and pollinators (hereafter beneficial insects), which provide important ecosystem services to both natural and anthropogenic ecosystems (Tscharntke et al. 2012a; Ollerton 2017).

Ecosystem services provided by beneficial insects afford approximately US\$ 71.3 billion (2018 dollars, considering inflation) annually in the United States (Losey & Vaughan 2006). Animal pollination services are responsible for 30% of global food production (Klein et al. 2007) contributing US\$235–577 billion to global crop output (Potts et al. 2016), whereas biological control of crop pests was valued at US\$619/ha (2018 dollars) globally (Costanza et al. 1997). Despite its recognized importance, pollination and biological control are endangered ecosystem services due to the decline of beneficial insects in agricultural landscapes (Klein et al. 2007; Geiger et al. 2010; Potts et al. 2010).

Habitat loss via landscape simplification drastically reduces the availability of natural habitats (e.g. wetland, forest and grassland), which are crucial for the maintenance of biodiversity in farmland, particularly invertebrates (Landis et al. 2000; Bianchi et al. 2006). Natural and semi-natural habitats (hereafter non-crop habitats) are less affected by pesticides and provide refuge and resources for beneficial insects, especially during disturbances in crops such as pesticide application, tillage and harvest operations (Altieri 1999; Landis et al. 2000; Bianchi et al. 2006; Tscharntke et al. 2012b). Moreover, these habitats support high plant diversity, thus providing diverse and continuously available food resources from floral resources (Danner et al. 2016) to alternative preys (Landis et al. 2008). Therefore, a high amount of non-crop habitats on the landscape is crucial to provide spatio-temporal refugia for beneficial insects in farmland (Tscharntke et al. 2005, 2012b).

Landscape simplification also reduces other important elements of landscape structure such as the diversity of habitats (landscape diversity) and edge density, which can maintain a spatio-temporal refuge for biodiversity through landscape complementation and supplementation (Quin et al. 2004; Tscharntke et al. 2012b; Fahrig 2017). According to Tscharntke et al. (2012b), landscape complementation means that organisms must forage in different habitats to gather spatially separated resources that are necessary to fulfill their needs. For landscape supplementation, landscapes provide organisms with supplemental non-crop and managed habitats with high concentrations of the same type of required resources.

Studies from temperate and tropical regions indicate that complex structured landscapes with a large proportion of non-crop habitats and high habitat diversity can support greater abundance and local species richness (alpha diversity) of beneficial insects than do simpler landscapes dominated by monocultures (Meyer et al. 2009;

Mandelik et al. 2012; Kennedy et al. 2013; González et al. 2015, 2016; Kratschmer et al. 2018). However, only a few studies have been conducted in the Neotropics, such as in Brazilian agricultural landscapes (Moreira et al. 2015; Sartuni et al. 2016; Boscolo et al. 2017; Medeiros et al. 2018; Hipólito et al., 2018; Aristizabal & Metzger in press). Furthermore, most studies related to the effects of landscape simplification on biodiversity have focused on alpha diversity, while beta diversity has received much less attention (Mori et al. 2018).

According to Baselga (2010) beta diversity quantifies the differences among biological communities and reflects two different phenomena: the spatial species turnover and nestedness that represent the replacement and loss of species between communities, respectively. Beta diversity is an essential approach to elucidate processes involved with changes in community composition due to natural and anthropogenic disturbances such as biological invasions (Socolar et al. 2016; Silva & Hernández 2018) and agricultural intensification (Gabriel et al. 2006; Karp et al. 2012). Understanding how landscape features affect beta diversity is crucial to aid decision makers and conservationists in selecting appropriate indicators and spatial scales for species conservation (Clough et al. 2007). Moreover, integrating alpha and beta diversity could be a way to accommodate multiple ecosystem services at the landscape level (Frei et al. 2018; Rodríguez-Loinaz et al. 2014).

We aimed to understand how landscape structure influences alpha and beta diversity of beneficial insects. We used wasps (Insecta: Hymenoptera: Vespidae), bees (Insecta: Hymenoptera: Apoidea) and flower flies (Insecta: Diptera: Syrphidae) as a model of different groups of beneficial insects. Bees, wasps and flower flies provide important pollination services in natural and agroecosystems (Allen-Wardell et al. 1998; Potts et al. 2016; Inouye et al. 2015; Ollerton 2017; Lucas et al. 2017, 2018) including coffee plantations (Roubik 2002; De Marco & Coelho 2004; Ricketts et al. 2004; Klein et al. 2003, 2008; Vergara & Badano 2009; Saturni et al. 2016). Moreover, bees, wasps and flower flies have been used as bioindicators to assess the loss of biodiversity and the efficiency of restoration and conservation policies (Sommaggio 1999; Tscharncke et al. 2005; Ricarte et al. 2011; Sommaggio & Burgio 2014), and many wasp and flower fly species are important agents of biological control of pests in several agroecosystems (Richter 2000; Rojo et al. 2003; Schmidt et al. 2004; Nelson et al. 2012; Eckberg et al. 2015). In this context, we hypothesized that both alpha and beta diversity of wasps, bees and flower flies are more affected by forest cover (habitat amount hypothesis – Fahrig 2013) than landscape diversity and edge density. We expected that: (i) alpha diversity of all insect groups increases with increasing forest cover at multiple spatial extents suggesting that forest is a key habitat for the maintenance of high insect diversity in agricultural landscapes; (ii) forest cover shapes community composition of wasps, bees and flower flies such that communities located in crop dominated landscapes support subsets of species-rich communities in forested landscapes; and (iii) forest loss results in community homogenization with a few crop associated species replacing most species. Here we provide novel information on the effects of landscape composition and configuration on the diversity of pollinator and natural enemy insects in Brazilian farmland, where it remains unexplored with only few available studies (Saturni et al. 2016; Boscolo et al. 2017; Hipólito et al. 2018; Medeiros et al. 2018).

MATERIAL AND METHODS

Study area

The study was conducted in 16 coffee producing landscapes near the border of the states of São Paulo and Minas Gerais in southeastern Brazil (Fig. 1). Landscape area was defined by a buffer of 1 km around the centroid

of each sampling area, a subjectively determined location along the interface between forest and coffee habitats. Previous studies conducted in Brazil have indicated that these radii are suitable to encompass the dispersal range sizes of most bee, wasp and flower fly species (Santos et al. 2000; da Cruz et al. 2006; Saturni et al. 2016; Silva et al. 2017; Medeiros et al. 2018).

Figura 1. Location of study sites in southeastern Brazil: a) Minas Gerais (MG) and São Paulo (SP) states in southeastern Brazil and the study region along the border of SP and MG, b) the sampled landscapes (black points) within the study region and c) land use maps of the studied landscape. In b) letters A, B and C represent the locations of the following cities: A = Espírito Santo do Pinhal, B = São João da Boa Vista, and C = Poços de Caldas. The dark gray line in b) represents the border between MG and SP. The land use maps in c) are 1 km radius and show the gradient of forest cover from 2.8 % (landscape 9) to 59.3% (landscape 7).

The study region presents a subtropical highland climate (Köppen climate classification, Cwb) characterized by rainy summers and dry winters with an average annual rainfall and temperature of 1,478 mm and 19.9 °C, respectively (Cipriani et al. 2011; Barros et al. 2012). The study region encompasses fragments of Atlantic Forest, pasture and eucalyptus stands immersed in a matrix of sun-coffee monocultures that are conventionally managed based on agrochemical usage (fertilizers, insecticides, fungicides and herbicides). The Atlantic Forest originally extended from northeastern to southwestern Brazil and into Argentina and Paraguay, mainly along the coast (Muyllaert et al. 2018), but only 26% of those forests remains in Brazil (Rezende et al. in press). The northern part of the study region has a hilly terrain where coffee is cultivated without mechanization by small and medium-scale farmers, whereas high levels of mechanization are employed in flat areas in the south where coffee is cultivated by medium and large-scale farmers. The original vegetation of the study region is seasonal semideciduous forest,

which is considered one of the most threatened ecosystem types of the Atlantic Forest hotspot (Ribeiro et al. 2009). Most forest remnants in the study region are composed of secondary vegetation due to intensive logging in past decades (local farmers, personal communication).

Insect surveys

We sampled wasps (Hymenoptera: Vespidae: Polistinae and Eumeninae), bees (Hymenoptera: Apoidea: Andrenidae, Apidae, Colletidae, Halictidae and Megachilidae) and flower flies (Diptera: Clycorrhapha: Syrphidae) in three distinct habitats centrally located in each landscape: interior of the coffee plantation, interior of the adjacent forest remnant and at the coffee-forest edge – hereafter coffee, forest and edge habitats. In each habitat we set up one Malaise trap (Townes model) and three baited traps along a linear transect parallel to the habitat edge to capture beneficial insects (a total of three transects per landscape). Transects within the interior of forest and coffee habitats were 100 m away from any edge. The four traps were 50 m apart along each transect. Baited traps consisted of 2 L PET (Polyethylene Terephthalate) bottles hung from branches approximately 1.3 m above the ground with four circular 4 cm diameter holes cut midway and filled with 300 ml of orange juice (Locher et al. 2014) and 0.4 ml of propylene glycol. Traps remained open for seven consecutive days per month for 13 months from June 2016 to June 2017. Captured insects were preserved in 70% ethanol and identified to the lowest taxonomic level possible using available identification keys for each of the three insect groups: Michener (2007) and Silveira et al. (2002) for the bees (family level classification follows Silveira et al. (2002), whereas genus- and species-level taxonomy follows Moure et al. (2012), complemented by Almeida (2008); Aguiar and Melo (2011), Camargo and Moure (1994, 1996), Ferrari and Silveira (2015), Freitas and Silveira (2017), Nemésio and Ferrari (2011); Andena and Carpenter (2012), Richards (1978) and Santos Junior et al. (2015) for Polistinae; Bohart and Stange (1965), Giordani Soika (1978, 1990), Willink and Roigk-Alsina (1998), Carpenter and Garcete-Barrett (2002) and Grandinete et al. (2015) for Eumeninae; Thompson (1999) and Mengual et al. (2018) for genera of Syrphidae; Hull (1949), Thompson (1981, 2006), Borges and Couri (2009), and Carvalho Filho and Esposito (2009) for flower fly species of different genera.

Insect diversity

We aggregated all individuals collected in the three habitats (coffee, forest, edge) per landscape to calculate alpha and beta diversity at the landscape level, as coffee and forest are the dominant crop and non-crop habitats in the study region. Among the sampled landscapes the average area and median percentage of area covered with coffee and forest combined were 72.3 % and 78.3 %, respectively. Alpha diversity was characterized by the species richness and abundance of each insect group within each of the 16 landscapes.

We used Sorensen's dissimilarity index (β_{sor}) to estimate total beta diversity, which we partitioned into two components: turnover and nested. The Simpson dissimilarity index (β_{sim}) was used to calculate the turnover component, while difference between β_{sor} and β_{sim} estimates the nested component (β_{nes}) of beta diversity. Turnover and nested components, which refer to species replacement and the loss of species between landscapes respectively, reveal the processes involved in community assembly (Baselga 2010). Total beta diversity and its components were calculated in the R software version 3.3.2 (R Core Team 2014) using the presence-absence community matrix as input in the function `beta.pair` from the `betapart` package (Baselga & Orme 2012).

Explanatory variables

For the landscape variables, we built land use maps for each landscape using high-resolution images from ArcGIS basemap imagery, Digital Globe satellites 2013–2015, ~ 1 m resolution at a 1:5,000 scale. We mapped 10 land use types: abandoned crops, abandoned pastures, arable field, built up area, coffee, eucalyptus, forest, pasture, water body and wetland (Fig. 1c). We conducted extensive ground verification in order to guarantee high accuracy levels of the land use maps that were used to calculate the landscape explanatory variables: forest cover (%), landscape diversity and edge density at four spatial extents (250, 500, 750 and 1000 m radii). Landscape variables were calculated using ArcGIS 10.3 with Patch Analyst (Rempel et al. 2012) and V-LATE (LARG 2006) extensions. To estimate landscape diversity, we used the Shannon diversity index, which considers both the richness of land use (number of land use classes) and the proportional area of each land use type (McGarigal 2015). Edge density is the sum of all land use patch areas (m²) in the landscape divided by the square of the nearest edge-to-edge distance between the focal patch (forest-coffee interfaces) and all land use types located within a pre-determined distance from the focal patch (McGarigal 2015). We also recorded the cumulative number of applications of agrochemical usage (insecticides, herbicides, fungicides and fertilizers) in the 16 sampled coffee plantations during the 13 months of insect surveys. Agrochemical usage information was obtained by periodic interviews with farmers.

Statistical analyses

We used generalized linear mixed models (GLMMs) to determine the effect of the landscape variables on alpha diversity of the three insect groups at four spatial extents. The abundance and species richness of each insect group were fitted with Poisson error structure. The variable “agrochemical usage” was included in the GLMM models as a random effect, in order to take into account a possible influence of local crop management. For each dependent variable and spatial extent, we analyzed four competing models (Table 1) including a null model composed only of an intercept indicating no variation among landscapes.

Tabela 1. Competing models used to explain patterns of each insect group in coffee producing landscapes in southeastern Brazil. Y indicates species richness and abundance of each focal group (bees, wasps and flower flies).

Models	Fixed effects
Forest cover	$Y \sim \% \text{ Forest cover}$
Landscape diversity	$Y \sim \text{Shannon diversity index}$
Edge density	$Y \sim \text{Edge density index}$
Null	$Y \sim 1$

We used Akaike Information Criterion (AIC; Burnham & Anderson 1998) with the small sample correction (AICc; Hurvich & Tsai 1989) to rank and identify the best fitting models; AICc weight (wAICc) and AICc delta (Δ AICc) were used as criteria to rank the models (Burnham & Anderson 2002). We only considered models as plausible if they had p-values < 0.05 (model fit), wAICc ≥ 0.1 and Δ AICc ≤ 2.5 . All analyses were performed in R version 3.3.2 using the *bbmle* package (Bolker 2010) for model selection.

To test the effect of explanatory variables and spatial extents on beta diversity (total, turnover and nested) we conducted a multiple regression on the distance matrix, a multiple regression used to model multivariate response data (Lichstein 2007) with 9,999 permutations (Anderson 2001). Only explanatory variables with p-values lower than 0.05 were considered to have a significant relative contribution. To test whether agrochemical usage affected beta diversity we applied a redundancy analysis, which indicated that only the turnover component for wasps was influenced by this variable ($R^2 = 0.87$, $p = 0.01$). We used the residuals of this analysis in the multiple regression as a way to exclude the influence of agrochemical usage on beta diversity components. We used multiple regression to calculate the relative contribution of each beta diversity component by dividing each component by total beta diversity (Sorensen index). We also calculated the difference in each landscape variable for each pair of landscapes to evaluate the influence of landscape variables on alpha diversity, and on total, nested and turnover beta diversity (Medeiros et al. 2018). All analyses were conducted using the function *adonis* of the *vegan* package (Oksanen et al. 2007).

RESULTS

We recorded a total of 265 species among the 27,035 specimens sampled for this study: 13,658 wasps (Vespidae: Polistinae and Eumeninae) classified in 86 species and 26 genera; 8,393 bees in 116 species and 73 genera (Apoidea: Andrenidae, Apidae, Colletidae, Halictidae and Megachilidae); and 4,984 flower flies (Syrphidae) in 63 species and 20 genera in the 16 landscapes (Suppl. Material). Species richness varied from 19 to 44 species per landscape (wasps); 18 to 51 (bees) and 12 to 26 (flower flies), and abundance varied from 167 to 1,709 specimens (wasps); 203 to 784 (bees) and 112 to 659 (flower flies). There were two dominant species per group: *Agelaia multipicta* (Haliday, 1836) and *Agelaia vicina* (de Saussure, 1854) (23.2% and 26.3% of wasp records respectively); *Apis mellifera* (Linnaeus, 1758) and *Trigona spinipes* (Fabricius, 1793) (25.5% and 31.2% of bee records); and *Toxomerus watsoni* (Curran, 1930) and *Dioprosopa clavata* (Fabricius, 1794) (25.6% and 38.6% of flower fly records).

Landscape explanatory variables differed considerably along the 16 landscapes. Within the radius of 1,000 m forest cover varied from 2.8 to 59.3 %, landscape diversity from 1.05 to 1.86 and edge density from 127 to 246. Agrochemical usage varied from 2 to 13 applications per coffee plantation / year. Species richness and abundance of wasps and bee species richness were positively correlated with forest cover at all spatial extents (Table 2; Fig. 2). Bee abundance and species richness and abundance of flower flies were not explained by any of the explanatory variables at any of the extents that we considered.

Figura 2. The best-supported models and spatial scales of the relationship with forest cover for species richness of bee (a) and wasps (b), and abundance of wasps (c) in southeastern Brazil. Wasps and bees had similar responses at all spatial extents.

Tabela 2. Plausible models to explain species richness and abundance of wasps, bees and flower flies within coffee producing landscapes in southeastern Brazil. wAICc = weight of evidence of the models. All selected models have $\Delta\text{AICc} = 0.0$. Asterisks indicate the level of significance of the models (model fit). (+) indicates positive correlation between response variables and forest cover at all four spatial scales.

Taxon	Response variable	Model	Spatial extents (meters)			
			250	500	750	1000
Wasp	Richness	Forest cover (+)	0.937***	0.957***	0.970***	0.9613** *
	Abundance	Forest cover (+)	0.460***	0.813**	0.770**	0.945**
Bee	Richness	Forest cover (+)	0.951***	0.938***	0.815***	0.890***
	Abundance	Null	-	-	-	-
Flower flies	Richness	Null	-	-	-	-
	Abundance	Null	-	-	-	-

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

The nested components of beta diversity of bees and wasps were influenced by forest cover at all spatial extents (Table 3; Fig. 3), whereas the turnover component of both groups was not explained by any of the explanatory variables. In contrast, the turnover component of beta diversity of flower flies was explained by landscape diversity at 250 m and edge density at all spatial extents (Table 3; Fig. 3), whereas the nested component was not explained by any predictor.

Figure 3. The best-supported models and spatial scales for the nested component of beta diversity of bees (a) and wasps (b) versus the differences in forest cover (%) between paired landscapes and the turnover component of beta diversity of flower flies (c and d) versus the differences of edge density and landscape diversity between paired landscapes. Similar results were observed at all spatial extents.

Discussion

Our hypothesis that alpha and beta diversity of beneficial insects are more affected by habitat amount (forest cover) than by other landscape structure variables (landscape diversity and edge density) was supported for wasps and bees, but not for flower flies, which responded to landscape diversity and edge density.

Alpha diversity: responses of beneficial insects to landscape context

Species richness of wasps and bees and wasp abundance increased with increasing forest cover at multiple spatial extents, while bee abundance and flower fly richness and abundance were not explained by any of the explanatory variables at any spatial extends considered.

Wasps and bees forage in agroecosystems including coffee plantations, where wasps provide important pest control services (Pereira et al. 2007; Androcioni et al. 2018) and bees act as major pollinators (Roubik 2002). However, mass flowering crops, such as coffee monocultures, have short flowering periods (Corbet 2000; Westphal et al. 2003; Mandelik et al. 2012) and are constantly submitted to pesticide applications resulting in high mortality rates and sub-lethal effects in pollinators and natural enemies (Stapel et al. 2000; Geiger et al. 2010). Moreover, in our study region, wasp nests found within crops or on human-built structures are usually removed to avoid stings. In contrast, Atlantic forest remnants are relatively stable and provide nesting substrates and undisturbed nesting sites for wasps (Souza et al. 2010, 2014, 2015) and bees (Siqueira et al. 2012) compared to the intensive crop management and nest removal within coffee plantations. The long-term persistence of bees and wasps in coffee producing landscapes seems to depend on forest remnants with suitable nesting sites that are critical for nest survival, dispersion and reproductive division of bee and wasp colonies (Seppä et al. 2002; Siqueira et al. 2012). In the same study region, Saturni et al. (2016) found that forest cover positively affected richness, abundance and diversity of bees, which was responsible for an increase in coffee fruit set of 28%. Therefore, forest conservation and restoration are not only important for conserving biodiversity, but also from agriculture and ecosystem services perspectives.

Although richness of both bees and wasp were affected by forest cover, only wasp abundance was influenced within 1000 m radius, which could be related to the difference in movement capacity of these insect groups. Studies have indicated that bees and flower flies can disperse over long distances and respond to landscape features within a 0.5–2 km range (Steffan-Dewenter et al. 2002; Winfree et al. 2008; Zurbuchen et al. 2010; Boscolo et al. 2017; Medeiros et al. 2018), whereas wasps seem to have a more limited dispersal capacity of up to only 300 m (Santos et al. 2000; da Cruz et al. 2006).

Flower fly communities encompass a variety of larval functional groups (e.g., predator, phytophagous, mycophagous, saprophagous) with specific habitat and food requirements that are not found in agricultural matrix (Sommaggio 1999; Burgio & Sommaggio 2007; Jauker et al. 2009). Therefore, we expected that flower flies would depend on forest cover to find a high diversity of larval micro habitats; however, alpha diversity did not respond as expected. Similar results were obtained by Lucas et al. (2017), where the diversity of the plant community had no significant influence on the diversity or abundance of flower fly communities. The absence of effects of landscape variables on flower fly alpha diversity may be related to the fact that adult flower flies do not collect pollen and nectar for their offspring but for their own resources of carbohydrates, lipids and proteins (in contrast to wasps and bees that need to return to their nests repeatedly for foraging) and can move linearly into the landscape (Kleijn & van

Langevelde 2006; Jauker et al. 2009). Lucas et al. (2017) also concluded that flower abundance has a key influence on Syrphidae abundance and species richness, with increases in flower fly abundance and species richness with increases in flower resources (also increasing the feeding opportunities for adult flower flies). Moreover, the flower type present in the habitat, with varying nectar production or symmetry, might affect pollinators' abundance and richness (Lucas et al. 2017).

Beta diversity

Wasps and bees were affected by forest cover such that communities located in landscapes with low forest cover were composed of subsets of the communities located in forested landscapes, reflected by species loss when forest cover is reduced within impoverished landscapes. These findings suggest that forest cover moderates dissimilarity of local wasp and bee communities and overrides negative local effects of pesticide usage and other important properties of landscape structure such as landscape diversity and edge density. Crop dominated landscapes fail to provide resources required by most wasp and bee species, resulting in local extinctions and the potential disruption of pollination and pest control services within the agricultural matrix. We argue that forest is a key habitat for the long-term maintenance of high pollinator and natural enemy diversity in farmland. Forest is the dominant non-crop habitat type in the study region and probably provides a constant supply of multiple resources that are not consistently available steadily in crops.

Beta diversity of flower flies was affected by the number of all edges in the landscape (edge density) and the diversity of land uses on the landscape (landscape diversity), both of which increased compositional changes in flower fly communities. In a previous study, we found that alpha and beta diversity of flower flies in Brazilian cereal producing landscapes were affected by the amount of non-crop habitats with the exception of the dominant predatory species (flower flies of the subfamily Syrphinae), which were positively associated with the landscape matrix where adult female flies find cereal aphid colonies for laying eggs (Medeiros et al. 2018).

In contrast, the present study was conducted in coffee producing landscapes where hemipterans, the predominant prey of predatory flower fly larvae, are not considered important coffee pests (farmers communication), thus predatory flower flies probably depend on ruderal plants to find hemipteran colonies. However, intensive use of herbicides in coffee plantations and low light conditions inside forest remnants prevent the occurrence of ruderal plants, which probably depend on landscape diversity and edge density. Medeiros et al. (2016) found that species richness and abundance of ruderal plants increased with increasing landscape diversity and edge density in Brazilian agricultural landscapes. Therefore, landscape diversity and edge density probably increase the availability of micro habitats for larval development of predatory species, indicating that larval habitat is a factor structuring flower fly communities (Mueller & Dauber 2016; Lucas et al. 2017). Such an association can explain why predatory species, which accounted for 58.3 % of all specimens collected, seem to be gradually replacing non-predatory species in landscapes with a high diversity of habitats and high edge density.

Insect conservation in farmland

We suggest that initiatives for the conservation of beneficial insects in the Atlantic Forest biodiversity hotspot must focus on forest conservation and restoration since high levels of forest loss leads to the loss of wasp

and bee species with potential negative consequences for the provision of pest control and pollination services in agroecosystems. From the point of view of ecosystem services, conservation initiatives should include not only forest conservation and restoration, but also agroecological initiatives to retain crop pollination and biological control, such as sown flower strips at crop edges (Haenke et al. 2009; Campbell et al. 2017), diversified crop rotations (Bommarco et al. 2013) and conversion to organic systems (Kremen et al. 2002). Agroecological management and crop diversification make crops more friendly environments for beneficial insects, whereas forest provides multiple resources that are not available in the crop matrix from larval microhabitats for non-predatory flower flies (Speight & Castella 2015) to undisturbed nesting sites for wasps and bees (Morato & Martins 2006). The synergic adoption of these actions can promote both an increase in ecosystem services and the conservation of greater insect diversity including threatened species (Kleijn et al. 2015).

Despite the growing knowledge of ecosystem services in farmlands, research on how landscape structure and crop management affect biodiversity and associated ecosystem services is still in their infancy in the Neotropical region. Future studies should focus on understanding how organisms at multi-taxon levels and associated ecosystem services are affected by environmental changes at multiple spatio-temporal extents. We highlight that stakeholders' (e.g., farmers and regional planners) demands and perceptions are crucial to understanding interactions between biophysical and socio-economic systems and better integrating concepts of biodiversity and ecosystems services in policy and decision-making (Albert et al. 2014; Palacios-Agundez et al. 2014). Such information derived from real-world case studies is needed for the synergic implementation of sustainable agricultural practices and biodiversity conservation initiatives as well as the selection of appropriate spatial scales in landscape planning and management.

ACKNOWLEDGEMENTS

We are grateful to the owners of private lands where the study sites are located. We also thank the Rufford Foundation that provided crucial financial support for fieldwork activities (reference project: 18799-1). HRM received a research grant from Brazilian Government Research Council (CNPq) (142147/2015-0 / 141932/2016-3) and a scholarship from Emerging Leaders of Americas Program (ELAP) supported by Canadian Government. MCR thanks FAPESP (process #2013/50421-2), CNPq (processes # 312045/2013-1; #312292/2016-3) and PROCAD/CAPES (project # 88881.068425/2014-01) for their financial support; EABA is grateful for CNPq grants 459826/2014-0 and 304735/2016-7; this study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001. JPM was supported by a FAPESP grant (Interface Project, N. 2013/23457-6) and by the Brazilian Science Council (CNPq; grants 306121/2016-6, and 305484/2017-6)

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APÊNDICE B.
southeast Brazil.

List of bee, predatory wasp and flower fly species recorded in 16 coffee producing landscapes in

WASP SPECIES	N
<i>Alphamenes campanulatus</i> (Fabricius, 1804)	2
<i>Alphamenes</i> sp	4
<i>Cyphomenes anisitsii</i> (Brèthes, 1906)	1
<i>Hypalastoroides</i> sp	1
<i>Hypancistrocerus</i> sp1	13
<i>Hypancistrocerus</i> sp2	2
<i>Monobia</i> sp	1
<i>Montezumia ferruginea</i> de Saussure, 1852	2
<i>Montezumia petiolata</i> de Saussure, 1855	1
<i>Montezumia</i> sp	1
<i>Omicron gondwanianum</i> Giordani Soika, 1978	1
<i>Omicron graculum</i> (Zavattari, 1912)	1
<i>Omicron microscopicum</i> (de Saussure, 1852)	1
<i>Omicron opifex</i> (Brèthes, 1909)	1
<i>Omicron ruficollis</i> (Zavattari, 1912)	1
<i>Omicron</i> sp1	3
<i>Omicron</i> sp2	1
<i>Omicron</i> sp3	1
<i>Omicron tuberculatum</i> (Fox, 1899)	15
<i>Pachodynerus gadulpensis</i> (de Saussure, 1853)	12
<i>Pachodynerus nasidens</i> (Latreille, 1817)	1
<i>Pachodynerus serrulatus</i> Brèthes, 1920	1
<i>Pachymenes ater</i> de Saussure, 1852	28
<i>Pachymenes bipartitus</i> (Fox, 1899)	2
<i>Pachymenes ghilianii</i> (Spinola, 1851)	10
<i>Pachymenes laeviventris</i> (Fox, 1899)	2
<i>Pachymenes olympicus</i> (Zavattari, 1912)	3
<i>Pachymenes sericeus</i> de Saussure, 1852	6
<i>Parancistrocerus</i> sp1	1
<i>Parancistrocerus</i> sp2	1
<i>Pirhosigma superficiale</i> (Fox, 1899)	6
<i>Pseudodynerus griseus</i> (Fox, 1902)	1
<i>Stenonartonia apicipennis</i> (Fox, 1902)	1
<i>Zeta argillaceum</i> (Linnaeus, 1758)	5
<i>Zethus fuscus</i> (Perty, 1833)	1
<i>Zethus</i> sp	2
<i>Agelaia angulata</i> (Fabricius, 1804)	9
<i>Agelaia multipicta</i> (Haliday, 1836)	3170
<i>Agelaia pallipes</i> (Olivier, 1792)	1731
<i>Agelaia vicina</i> (de Saussure, 1854)	3589
<i>Apoica pallens</i> (Fabricius, 1804)	98
<i>Brachygastera augusti</i> (de Saussure, 1854)	2

<i>Brachygastra lecheguana</i> (Latreille, 1824)	101
<i>Brachygastra mouleae</i> Richards, 1978	2
<i>Metapolybia cingulata</i> (Fabricius, 1804)	3
<i>Mischocyttarus cassununga</i> (von Ihering, 1903)	16
<i>Mischocyttarus cearensis</i> Richards, 1978	13
<i>Mischocyttarus drewseni</i> de Saussure, 1857	25
<i>Mischocyttarus rotundicollis</i> (Cameron, 1912)	1
<i>Mischocyttarus rotundicollis</i> (Cameron, 1912)	86
<i>Mischocyttarus socialis</i> (de Saussure, 1854)	8
<i>Mischocyttarus</i> sp1	2
<i>Mischocyttarus</i> sp2	6
<i>Mischocyttarus</i> sp3	1
<i>Mischocyttarus</i> sp4	1
<i>Polistes billardieri</i> Fabricius, 1804	1
<i>Polistes cinerescens</i> de Saussure, 1854	6
<i>Polistes erythrocephalus</i> Latreille, 1813	62
<i>Polistes lanio</i> (Fabricius, 1775)	6
<i>Polistes melanosoma</i> de Saussure, 1853	2
<i>Polistes pacificus</i> Fabricius, 1804	8
<i>Polistes simillimus</i> Zikán, 1851	60
<i>Polistes</i> sp1	1
<i>Polistes subsericeus</i> de Saussure, 1854	4
<i>Polistes versicolor</i> (Olivier, 1792)	259
<i>Polybia bifasciata</i> de Saussure, 1854	13
<i>Polybia chrysothotax</i> (Lichtenstein, 1796)	217
<i>Polybia dimidiata</i> (Olivier, 1792)	31
<i>Polybia fastidiosuscula</i> de Saussure, 1854	772
<i>Polybia ignobilis</i> (Haliday, 1836)	501
<i>Polybia jurinei</i> de Saussure, 1854	183
<i>Polybia minarum</i> Ducke, 1906	60
<i>Polybia ocidentalis</i> (Olivier, 1792)	755
<i>Polybia paulista</i> von Ihering, 1896	951
<i>Polybia punctata</i> du Buysson, 1908	377
<i>Polybia sericea</i> (Olivier, 1792)	236
<i>Protonectarina sylveirae</i> (de Saussure, 1854)	102
<i>Protopolybia exigua</i> (de Saussure, 1854)	4
<i>Protopolybia sedula</i> (de Saussure, 1854)	23
<i>Pseudopolybia vespiceps</i> (de Saussure, 1863)	10
<i>Synoeca cyanea</i> (Fabricius, 1775)	14
BEE SPECIES	N
<i>Acamptopoeum prinii</i> (Holmberg, 1884)	18
<i>Alloscitetia</i> sp.1	3
<i>Ancyloscelis cf. apiformis</i> (Fabricius, 1793)	1
<i>Anthrenoides cf. meridionalis</i> (Schroettky, 1906)	180
<i>Apis mellifera</i> Linnaeus, 1758	2141
<i>Arhysoceble</i> sp.1	1

<i>Arhysoceble</i> sp.2	2
<i>Augochlora</i>	14
<i>Augochlora</i> (<i>Augochlora</i>) <i>esox</i> (Vachal, 1911)	6
<i>Augochlora</i> (<i>Augochlora</i>) sp.2	5
<i>Augochlora</i> (<i>Augochlora</i>) sp.3	2
<i>Augochlora</i> (<i>Oxystoglossella</i>) cf. <i>thalia</i> Smith, 1879	16
<i>Augochlorella</i> sp.1	2
<i>Augochloropsis</i> sp.1	12
<i>Augochloropsis</i> sp.2	1
<i>Augochloropsis</i> sp.3	58
<i>Augochloropsis</i> sp.4	1
<i>Bombus</i> cf. <i>pauloensis</i> Friese, 1913	8
<i>Caenohalictus</i> sp.1	2
<i>Centris</i> (<i>Hemisiella</i>) sp.1	1
<i>Centris</i> (<i>Hemisiella</i>) <i>tarsata</i> Smith, 1874	6
<i>Centris</i> (<i>Xanthemis</i>) sp.1	1
<i>Centris</i> sp.1	1
<i>Cephalotrigona capitata</i> (Smith, 1854)	5
<i>Ceratalictus allostictus</i> Moure, 1950	109
<i>Ceratina</i> sp.1	10
<i>Coelioxys</i> sp.1	3
<i>Colletes rugicollis</i> Friese, 1900	1
<i>Colletes</i> sp.1	1
<i>Cyphomelissa diabolica</i> (Friese, 1900)	3
<i>Diadasina</i> cf. <i>distincta</i> (Holmberg, 1903)	2
<i>Dialictus</i> sp.1	15
<i>Dialictus</i> sp.2	1
<i>Dialictus</i> sp.3	103
<i>Dialictus</i> sp.4	24
<i>Dichranthidium</i> cf. <i>gregarium</i> (Schrottky, 1905)	3
<i>Epicharis</i> (<i>Cyphepicharis</i>) <i>morio</i> Friese, 1924	1
<i>Euglossa</i> (<i>Glossura</i>) <i>imperialis</i> Cockerell, 1922	1
<i>Exaerete smaragdina</i> (Guérin, 1844)	1
<i>Exomalopsis</i> (<i>Exomalopsis</i>) <i> analis</i> Spinola, 1853	23
<i>Exomalopsis</i> (<i>Exomalopsis</i>) <i>auropilosa</i> Spinola, 1853	44
<i>Exomalopsis</i> sp.	51
<i>Friesella schrottky</i> (Friese, 1900)	9
<i>Geotrigona subterranea</i> (Friese, 1901)	33
<i>Habralictus</i> sp.1	7
<i>Hopliphora velutina</i> (Lepeletier & Serville, 1825)	1
<i>Megachile</i> sp.1	4
<i>Melipona</i> (<i>Eomelipona</i>) <i>bicolor</i> Lepeletier, 1836	10
<i>Melipona</i> (<i>Melipona</i>) <i>quadrifasciata</i> Lepeletier, 1836	33
<i>Melissodes</i> sp.1	1
<i>Melissoptila</i> cf. <i>minarum</i> (Bertoni & Schrottky, 1910)	2
<i>Melissoptila</i> sp.1	2

<i>Melissoptila</i> sp.2	2
<i>Melissoptila</i> sp.3	6
<i>Melitoma segmentaria</i> (Fabricius, 1804)	1
<i>Mesocheira</i> sp.1	1
<i>Mesoplia</i> cf. <i>rufipes</i> (Perty, 1833)	3
<i>Monoeca</i> sp.1	1
<i>Nannotrigona testaceicornis</i> (Lepeletier, 1836)	15
<i>Neocorynura</i> cf. <i>norops</i> (Vachal, 1904)	10
<i>Nomada</i> sp.1	1
<i>Nomada</i> sp.2	1
<i>Nomada</i> sp.3	2
<i>Osiris</i> sp.1	8
<i>Oxaea flavescens</i> Klug, 1807	11
<i>Oxytrigona tataira</i> (Smith, 1863)	24
<i>Paratetrapedia connexa</i> (Vachal, 1909)	0
<i>Paratetrapedia flaveola</i> Aguiar & Melo, 2011	1
<i>Paratetrapedia</i> sp.1	13
<i>Paratetrapedia</i> sp.2	3
<i>Paratetrapedia</i> sp.3	2
<i>Paratetrapedia</i> sp.4	2
<i>Paratrigona lineata</i> (Lepeletier, 1836)	704
<i>Paratrigona subnuda</i> Moure, 1947	89
<i>Paroxystoglossa</i> sp.1	1
<i>Partamona</i> sp.1	5
<i>Peponapis fervens</i> (Smith, 1879)	1
<i>Pereirapis</i> sp.1	1
<i>Plebeia droryana</i> (Friesse, 1900)	300
<i>Plebeia remota</i> (Holmberg, 1903)	22
<i>Psaenythia</i> sp.1	28
<i>Pseudagapostemon</i> (<i>Pseudagapostemon</i>) <i>pissisi</i> (Vachal, 1903)	2
<i>Pseudaugochlora callaina</i> Almeida, 2008	3
<i>Pseudaugochlora graminea</i> (Fabricius, 1804)	1
<i>Pseudaugochlora indistincta</i> Almeida, 2008	5
<i>Ptiloglossa</i> sp.1	1
<i>Rhopitulus</i> sp.1	22
<i>Rhynocorynura</i> sp.	3
<i>Scaptotrigona</i> cf. <i>bipunctata</i> (Lepeletier, 1836)	16
<i>Scaptotrigona</i> sp.1	14
<i>Schwarziana quadripunctata</i> (Lepeletier, 1836)	46
<i>Sphecodes</i> sp.	3
<i>Tapinotaspidini</i> sp.1	12
<i>Tapinotaspoides serraticornis</i> (Friesse, 1899)	5
<i>Temnosoma metallicum</i> Smith, 1853	6
<i>Tetragona elongata</i> (Lepeletier, 1828)	23
<i>Tetragonisca angustula</i> (Latreille, 1811)	52
<i>Tetrapedia</i> sp.1	2

<i>Thygater (Thygater) analis</i> (Lepeletier, 1841)	14
<i>Trichocerapis mirabilis</i> (Smith, 1865)	1
<i>Trigona braueri</i> Friese, 1900	74
<i>Trigona cf. fuscipennis</i> Friese, 1900	191
<i>Trigona hyalinata</i> (Lepeletier, 1836)	893
<i>Trigona spinipes</i> (Fabricius, 1793)	2616
<i>Trigona truculenta</i> Almeida, 1984	96
<i>Trigonisca intermedia</i> Moure, 1990	1
<i>Trigonopedia</i> sp.1	31
<i>Trigonopedia</i> sp.2	1
<i>Trophocleptia</i> sp.1	4
<i>Tropidopedia</i> sp.1	2
<i>Tropidopedia</i> sp.2	1
<i>Xanthopedia</i> sp.1	2
<i>Xylocopa (Neoxylocopa) frontalis</i> (Olivier, 1789)	1
<i>Xylocopa (Neoxylocopa)</i> sp.1	2
<i>Xylocopa (Schonherria) varians</i> Smith, 1874	3
<i>Xylocopa</i> sp.2	1

FLOWER FLY SPECIES	N
<i>Allograpta exotica</i>	131
<i>Allograpta hastata</i>	16
<i>Allograpta neotropica</i>	2
<i>Allograpta obliqua</i>	5
<i>Argentinomyia longicornis</i>	4
<i>Argentinomyia neotropica</i>	1
<i>Copestylum lanei</i>	1
<i>Copestylum</i> sp1	1
<i>Copestylum</i> sp2	1
<i>Dioprosopa clavata</i>	1955
<i>Fazia alta</i>	1
<i>Fazia similis</i>	6
<i>Hybobathus cf. norina</i>	6
<i>Hybobathus cf. vampyrus</i>	5
<i>Leucopodella bigoti</i>	1
<i>Leucopodella gracilis</i>	45
<i>Leucopodella n.sp.</i>	1
<i>Meromacrus nectarinoides</i>	1
<i>Mimocalla erebus</i>	1
<i>Ocyptamus</i> sp1	1
<i>Ocyptamus antiphates</i>	223
<i>Ocyptamus argentinus</i>	11
<i>Ocyptamus cf. titania</i>	16
<i>Ocyptamus dimidiatus</i>	11
<i>Ocyptamus funebris</i>	23
<i>Ocyptamus gastrostactus</i>	6
<i>Ocyptamus lepidus-grp</i> sp1	1

<i>Ocyptamus lepidus</i> -grp sp2	15
<i>Ocyptamus lepidus</i> -grp sp3	6
<i>Ocyptamus lepidus</i> -grp sp4	1
<i>Ocyptamus lepidus</i> -grp sp5	2
<i>Ocyptamus lepidus</i> -grp sp6	1
<i>Ocyptamus stenogaster</i> -grp sp1	1
<i>Ornidia therezinhae</i>	5
<i>Palpada urotaenia</i>	1
<i>Pelecinobaccha summa</i>	4
<i>Pseudoscaeva meridionalis</i>	1
<i>Relictanum adpersitum</i>	3
<i>Relictanum aff. schwarzi</i>	1
<i>Rhopalosyrphus australis</i>	1
<i>Salpingogaster nigra</i>	10
<i>Salpingogaster</i> sp1	20
<i>Syritta flaviventris</i>	1
<i>Syrphus phaeostigma</i>	12
<i>Toxomerus aquilinus</i>	2
<i>Toxomerus basalis</i>	6
<i>Toxomerus croesus</i>	10
<i>Toxomerus difficilis</i>	23
<i>Toxomerus dispar</i>	396
<i>Toxomerus duplicatus</i>	126
<i>Toxomerus floralis</i>	12
<i>Toxomerus idalius</i>	21
<i>Toxomerus lacrymosus</i>	75
<i>Toxomerus laenas</i>	76
<i>Toxomerus musicus</i>	4
<i>Toxomerus pictus</i>	10
<i>Toxomerus politus</i>	35
<i>Toxomerus procrastinatus</i>	30
<i>Toxomerus purus</i>	7
<i>Toxomerus sylvaticus</i>	6
<i>Toxomerus tibicen</i>	26
<i>Toxomerus virgulatus</i>	281
<i>Toxomerus watsoni</i>	1277

CONCLUSÃO GERAL

O presente trabalho fornece importantes *insights* em relação aos efeitos moderadores da estrutura da paisagem sobre a ocorrência e diversidade de insetos benéficos e a provisão do serviço ecossistêmico de controle biológico de pragas em paisagens agrícolas na região Sudeste do Brasil. Entre os principais resultados podemos destacar que o incremento de cobertura florestal resultou na diminuição das populações da praga (*Leucoptera coffeella*) e no aumento do serviço de controle biológico, assim como de riqueza e abundância de vespas e abelhas. Ademais, a composição e configuração da paisagem afetaram a estrutura das comunidades de abelhas, vespas e sirfídeos. A diminuição de cobertura florestal resultou na perda de espécies de abelhas e vespas, enquanto que o aumento na diversidade da paisagem e densidade de borda implicou na substituição de espécies de sirfídeos.

Os remanescentes florestais existentes nas paisagens estudadas parecem atenuar dois *tradeoffs* entre a produção agrícola e a conservação da biodiversidade: 1 - os ninhos de abelhas e vespas protegidos no interior dos remanescentes florestais atuam como fontes perenes de insetos benéficos para lavouras adjacentes, reduzindo os efeitos negativos do manejo agrícola; e 2 – o acréscimo de cobertura florestal afetou negativamente a população de *L. coffeella* devido ao aumento do serviço de controle biológico. De maneira similar, estudos conduzidos em regiões produtoras de café nos Estados de São Paulo, Minas Gerais e Bahia observaram que o acréscimo de cobertura florestal no entorno de plantações de café resultou no aumento de diversidade de polinizadores e do serviço de polinização, resultando no aumento de produtividade. Nesse contexto, entendemos que iniciativas voltadas para a conservação de insetos benéficos e maximização de seus serviços ecossistêmicos em paisagens agrícolas devem concentrar esforços na conservação e restauração florestal. Além disso, ações voltadas para a conservação da vegetação remanescente são indicadas para paisagens com alta cobertura florestal, enquanto que a restauração florestal deve ser a principal estratégia em paisagens simplificadas dominadas por monoculturas. Dentre as áreas prioritárias para a restauração florestal em paisagens simplificadas, podemos destacar àquelas de baixo potencial agrícola, como plantações e pastagens abandonadas, assim como zonas ripárias e áreas de encosta e de várzea degradadas. De maneira complementar, iniciativas agroecológicas tais como maior diversificação da matriz agrícola, ampla conversão de sistemas convencionais em sistemas orgânicos e agroflorestais e o plantio de flores nas bordas das plantações podem tornar a matriz agrícola menos hostil para insetos benéficos, resultando na retenção de seus serviços - como o controle biológico de pragas e a polinização no interior das plantações. Iniciativas combinadas de agroecologia e de conservação e restauração florestal possuem grande potencial para conciliar produção e conservação da biodiversidade em regiões produtoras de café no Brasil.

Os efeitos moderadores da estrutura da paisagem sobre a comunidade de abelhas, vespas e sirfídeos foram observados em múltiplas escalas espaciais, portanto a adoção sinérgica de iniciativas agroecológicas, de conservação e restauração florestal devem ser aplicadas em escala de paisagem. Não foi possível detectar um limiar de cobertura florestal crítico para a manutenção de alta diversidade de abelhas e vespas, mas paisagens com menos de 20% de cobertura florestal em um raio de 1000 metros apresentaram apenas subconjuntos das espécies encontradas em paisagens com alta cobertura florestal.

Por fim, vale destacar que os efeitos dos habitats naturais e de outros elementos da estrutura da paisagem sobre a biodiversidade e seus serviços ecossistêmicos dependem de múltiplos fatores e podem variar de acordo com a região de estudo, planta cultivada, biologia e ecologia das pragas e seus inimigos naturais, assim como o tipo e intensidade de manejo. Os resultados e sugestões existentes no presente trabalho podem auxiliar produtores e tomadores de decisão na definição de escalas espaciais, seleção de áreas prioritárias e de estratégias voltadas para

conservação da biodiversidade, maximização de serviços ecossistêmicos e a produção sustentável em paisagens agrícolas.