**Universidade de São Paulo
Instituto de Biociências**

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**Efeitos da estrutura da paisagem sobre o controle biológico do
bicho-mineiro-do-cafeeiro (*Leucoptera coffeella*, Lepidoptera:
Lyonetiidae) provido por aves e morcegos**

**Landscape structure effects on the biological control of the coffee-
leaf-miner (*Leucoptera coffeella*, Lepidoptera: Lyonetiidae)
provided by birds and bats**

Versão corrigida

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Orientador: Dr. Jean Paul Walter Metzger

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Epígrafe

*La primavera está en todo su esplendor
brillante la luz del sol
El jardín ha estrenado sus nuevos vestidos verdes
y entre unas matas erguidas y frondosas
surge brillante
todos los años en este mismo día
una hermosa y cautivante flor,
la flor de la Esperanza
para mi
Esa flor eres tú*

Aurelio Embid

Resumo

O controle biológico de pragas agrícolas é um dos serviços ecossistêmicos mais valorizados, dada sua importância para a produção agrícola. Embora vários estudos tenham demonstrado que a abundância e riqueza de predadores aumentam com a quantidade de floresta nativa, os mecanismos subjacentes que modulam a relação entre a cobertura florestal e provisão de controle biológico em diferentes escalas espaciais são ainda pouco conhecidos. Neste trabalho, utilizamos experimentos de exclusão de vertebrados voadores em oito paisagens cafeeiras na Mata Atlântica, num gradiente de cobertura florestal, e quantificamos as consequências para a perda foliar por herbivoria e para a frutificação. A perda foliar mostrou uma relação negativa com a cobertura florestal em paisagens com 2 km de raio, indicando que a herbivoria é melhor controlada em paisagens com alta cobertura florestal, especialmente na presença de aves e morcegos. No entanto, no nível local, 300 m ao redor das plantas de café, a perda foliar e a frutificação responderam diferentemente à cobertura florestal. Em unidades com baixa cobertura florestal local, a exclusão de aves e morcegos aumentou a perda foliar e diminuiu a frutificação em uma média de 13%. Por outro lado, em unidades com alta cobertura florestal local, a exclusão de aves e morcegos não teve efeitos significativos nem na perda foliar, nem na frutificação. Concluímos que os efeitos da exclusão de aves e morcegos na perda foliar e frutificação são modulados por diferentes processos que ocorrem no nível local e da paisagem. Sugerimos que quando a cobertura florestal local é alta (geralmente perto de fragmentos florestais), as aves e os morcegos não se alimentam apenas de herbívoros, mas também de mesopredadores. No entanto, quando a cobertura florestal local é baixa (e.g. longe de fragmentos florestais), os mesopredadores não ocorrem e aves e morcegos passam a prover serviço de controle biológico de pragas, alimentando-se principalmente de herbívoros. Destacamos a importância de empregar uma análise multiescalar em sistemas onde espécies com diferentes capacidades de dispersão proveem um serviço ecossistêmico.

Abstract

Biological control of agricultural pests is one of the most important ecosystem services given its key role for agricultural production. Although several studies have shown that the abundance and richness of predators increase with the amount of native forest in the landscape, the underlying mechanisms relating forest cover at different spatial scales with the provision of biological control are still poorly understood. We experimentally excluded flying vertebrates (birds and bats) in eight coffee landscapes in the Brazilian Atlantic Forest, encompassing a gradient of forest cover and quantified the consequences for coffee leaf loss by herbivory and fruit set. Leaf loss showed a negative relation with forest cover at landscape level, in landscapes with 2 km radius, indicating that herbivory is better controlled in landscapes with high forest cover, especially in the presence of birds and bats. However, at local level (defined as 300 m around coffee plants), leaf loss and fruit set responded to forest cover differently. In units with low local forest cover, bird and bat exclusion was associated with increased leaf loss and reduced fruit set by 13%. However, under high local forest cover, bird and bat exclusion had no significant effect on leaf loss or fruit set. We conclude that the effects of bird and bat exclusion on leaf loss and fruit set are modulated by different processes occurring at landscape and local levels. We posit that when local forest cover is high (e.g. near remnant forest fragments) birds and bats are not only controlling herbivores but may also be reducing mesopredators. In contrast, when local forest cover is low (e.g. far from forest fragments), mesopredators occur in lower abundance, and birds and bats provide biological control by feeding mainly on herbivores. We highlight the importance of employing a multi-scale analysis in systems where species with different dispersal abilities are providing an ecosystem service.

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Introdução Geral

Nos últimos 50 anos, a civilização humana transformou os ecossistemas naturais mais rápida e extensivamente que em qualquer intervalo de tempo equivalente na história da humanidade. A principal causa dessa transformação tem sido a expansão das culturas agrícolas e pastagens para suprir a demanda crescente por comida, madeira, fibra e combustível (Barnosky et al. 2012; Foley et al. 2005; MEA 2005). No entanto, um imenso número de serviços que suportam a vida e que são fundamentais para o bem-estar humano, como purificação da água, ciclagem de nutrientes e regulação do clima, são providos exclusivamente pelos ecossistemas naturais (Costanza et al. 1997; Daily 1997). Além disso, a produção pelos ecossistemas agrícolas de bens, como comida e fibra, depende de uma rede de serviços de suporte e regulação também providos por ecossistemas naturais (Zhang et al. 2007). Estes “serviços ecossistêmicos” foram definidos como as contribuições diretas e indiretas dos ecossistemas para o bem-estar humano (TEEB 2010) e atualmente são considerados peças fundamentais para atingir as metas globais referentes a desenvolvimento sustentável (MEA 2005).

Dentre esses serviços ecossistêmicos, o controle biológico de pragas agrícolas é um dos mais importantes (Bianchi et al. 2006), dado que aproximadamente 10% da produção agrícola mundial é perdida pela ação de pragas (Oerke 2006). Plantações de milho, café ou algodão, por exemplo, beneficiam-se significativamente do controle biológico das pragas que é fornecido por diversos organismos que habitam os ecossistemas naturais (Boyles et al. 2011; Cleveland et al. 2006; Karp et al. 2013). Porém, quando degradados, os ecossistemas naturais perdem sua capacidade para fornecer serviços ecossistêmicos, o que acaba por comprometer a sustentabilidade na produção de bens (Foley et al. 2005; MEA 2005).

Em paisagens dominadas por agricultura, a riqueza de espécies animais tende a aumentar com o aumento na proporção de áreas de habitat nativo (Aviron et al. 2005; Billeter et al. 2008; Tscharrntke et al. 2005). Os fragmentos de habitat nativo atuam como habitats-fonte, a partir dos quais as plantações agrícolas, menos favoráveis, são invadidas. Esse fenômeno é conhecido como efeito de “cross-habitat spillover” ou “transbordamento entre habitats”, definido como o movimento de um organismo desde seu habitat de origem a outro. Quando esses organismos realizam uma função ecológica, como forrageio, herbivoria ou polinização, num habitat vizinho ao seu de origem ocorre o chamado *spillover* funcional. É através deste processo ecológico que muitos serviços ecossistêmicos, incluindo o controle biológico de pragas, são prestados por espécies nativas que ocorrem em manchas de habitat remanescentes. As áreas naturais e semi-naturais provêm fontes energéticas alternativas, assim como habitats de nidificação, para espécies predadoras de pragas promovendo assim a atuação desses inimigos nas áreas agrícolas (Bianchi et al. 2006; Rusch et al. 2010; Tscharrntke et al. 2005).

No Brasil, o manejo agrícola sustentável não é só desejável, mas fundamental (Ferreira et al. 2012), tendo em vista que tratar-se de um país mega-diverso (Lewinsohn and Prado 2005) e um dos maiores produtores de alimentos para o mundo (FAOSTAT 2013). Para o desenvolvimento de sistemas agrícolas produtivos e sustentáveis que promovam ao mesmo tempo condições favoráveis para a biodiversidade nativa e para a produção agrícola, é fundamental que os produtores rurais conheçam como maximizar os serviços ecossistêmicos (Bianchi et al. 2006). Neste sentido, a ecologia de paisagens pode ajudar no entendimento das relações entre os padrões espaciais e os processos ecológicos que sustentam a provisão de serviços ecossistêmicos (Metzger 2001; Turner et al. 2013), trazendo assim importantes contribuições para o desenho de paisagens sustentáveis (Grimaldi et al. 2014; Mitchell et al. 2014).

A Mata Atlântica, um dos biomas mais biodiversos do mundo, é também um dos mais ameaçados como consequência da fragmentação e redução de habitats causada pela expansão agrícola (Myers et al. 2000; Ribeiro et al. 2009). Sua estrutura atual é composta por um mosaico de fragmentos de floresta nativa rodeados por plantações de diversas culturas agrícolas. Dentre estas, o café é uma das principais, sendo que várias das regiões cafeeiras mais tradicionais do Brasil situam-se em áreas antes ocupadas pela Mata Atlântica (Joly et al. 2014). Em 2014, o Brasil exportou 36,73 milhões de sacas de 60 kg, mantendo-se como o maior produtor e exportador de café no mundo (FAOSTAT 2013; MAPA 2014).

Como outras culturas, o café é susceptível a pragas, com prejuízos da ordem de centenas de milhões de dólares por ano (Oliveira et al. 2014). Os principais insetos-praga do café no mundo são o bicho-mineiro (*Leucoptera coffeella*) e a broca-do-café (*Hypothenemus hampei*). No Brasil, o bicho-mineiro-do-café é especialmente danoso, sendo responsável, em alguns casos, por quedas na produção de mais de 50% (Pierre 2011). Trata-se de um microlepidóptero de hábitos crepusculares, específico do gênero *Coffea*. Durante a fase larval, esta praga causa a diminuição da área fotossintética devido a lesões nas folhas e queda precoce destas, afetando a produtividade, o rendimento do café e a longevidade das plantas (Pierre 2011). O controle químico, com caros e nocivos inseticidas, tem sido o método mais utilizado no controle dessas pragas (Waller et al. 2007). No entanto, esse método de controle é econômica e ecologicamente insustentável, o que torna o estudo de mecanismos de controle biológico particularmente relevante para desenvolver formas alternativas ou auxiliares de controle de pragas (Chaplin-Kramer et al. 2011).

O controle biológico pode ser fornecido por uma ampla gama de espécies, incluindo aves, morcegos e invertebrados.

As aves têm um grande potencial na provisão do serviço de controle de insetos danosos à agricultura, dado que a maior parte das espécies de aves é predominantemente insetívora (Sekercioglu 2006). O hábito arbustivo do cafeeiro propicia um ambiente sombreado, que

torna as plantações atrativas para diversas espécies de aves insetívoras que forrageiam e também se refugiam entre seus galhos (Johnson et al. 2006; Tejeda-Cruz and Sutherland 2004). Estudos na Jamaica e Costa Rica conseguiram demonstrar o serviço do controle específico para a broca-do-café (*H. hampei*), além de quantificar o aumento de produção de frutos comercializáveis, bem como o incremento na renda dos produtores (Johnson et al. 2010; Karp et al. 2013; Kellermann et al. 2008).

Os morcegos têm também grande capacidade para prestar vários serviços ecossistêmicos, incluindo controle de pragas (Kunz et al. 2011), com relevante benefício econômico na produção agrícola (Boyles et al. 2011; Cleveland et al. 2006; Gandara Fierro et al. 2006). No caso do café, um estudo no México demonstrou que a atividade dos morcegos insetívoros reduziu em 84% a presença de artrópodes no cafezal (Williams-Guillen et al. 2008).

Invertebrados também são importantes no controle de pragas do café, com destaque para vespas e formigas. As vespas sociais predadoras são consideradas os agentes mais eficazes no controle biológico do bicho-mineiro (Carvalho et al. 2004; Melo et al. 2007; Reis 1999). Estudos já encontraram altos níveis de predação por vespas, de até 70% (Gravena 1984). Vários trabalhos sugerem que pode haver uma forte correlação entre as áreas de vegetação nativa próximas aos cafezais e as populações de vespas que estariam fornecendo um importante serviço de controle biológico do bicho mineiro em escala local (Amaral et al. 2010; Melo et al. 2007; Pierre 2011). No caso das formigas, já foi demonstrado no México o controle tanto da broca-do-café quanto do bicho-mineiro (Lomeli-Flores et al. 2009; Vandermeer et al. 2010).

Morcegos, aves, vespas e formigas são considerados os principais prestadores do serviço de controle de pragas em plantações de café e todos eles são afetados pela estrutura da paisagem (Gorresen and Willig 2004; Martensen et al. 2012; Perfecto et al. 2014; Steffan-Dewenter 2003). Embora muitos trabalhos tenham estudado os efeitos da composição da paisagem e proximidade às bordas sobre a abundância, composição e diversidade de inimigos naturais de pragas, poucos estudos têm, de fato, avaliado as implicações funcionais da atividade desses inimigos naturais, por exemplo, através da supressão de pragas e nível de dano nos cultivos (Bianchi et al. 2006). Portanto, para entender como manter e maximizar este serviço em plantações de café é preciso uma abordagem de paisagem que considere o impacto das pragas na produção (Chaplin-Kramer et al. 2011).

Dado que a intensificação da agricultura é considerada uma das principais causas da perda de biodiversidade, estudos anteriores mediram a eficiência do controle biológico de pragas em diferentes sistemas de produção de café, principalmente comparando o sistema "sombreado" com o "de sol" (Avelino et al. 2012; Classen et al. 2014; Karp et al. 2013). No entanto, as plantações de café "de sol" nestes estudos diferem muito das plantações brasileiras, que geralmente são associadas apenas a bananeiras (*Musa* spp.), usadas

principalmente como corta-vento. Como o café de sol brasileiro representa 89% de todo o café cultivado no país (Jha et al. 2014) e considerando que o Brasil é responsável por aproximadamente 35% da produção mundial de café (FAOSTAT 2013), é fundamental estudar como podemos desenvolver paisagens agrícolas sustentáveis e manter os serviços dos ecossistemas sob esta realidade.

Em este estudo, usamos uma abordagem experimental em oito paisagens cafeeiras na Mata Atlântica da região Mogiana (São Paulo) e Sul de Minas Gerais, a principal região cafeeira do Brasil (Conab 2014), para responder se: (1) as aves e os morcegos afetam os níveis de perda foliar por herbivoria e frutificação em plantações de café; e (2) se a estrutura da paisagem modula esse serviço ecossistêmico. As nossas hipóteses são que: (1) a presença de aves e morcegos reduz a perda foliar e aumenta a frutificação do café; e (2) que esse processo é mais intenso quanto maior a quantidade de floresta nativa na paisagem do entorno.

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Chapter 1

Opposing effects of forest cover on coffee leaf loss and fruit set at local and landscape levels

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Abstract Biological control of agricultural pests is one of the most important ecosystem services given its key role for agricultural production. Although several studies have shown that the abundance and richness of predators increase with the amount of native forest in the landscape, the underlying mechanisms relating forest cover at different spatial scales with the provision of biological control are still poorly understood. We experimentally excluded flying vertebrates (birds and bats) in eight coffee landscapes in the Brazilian Atlantic Forest, encompassing a gradient of forest cover and quantified the consequences for coffee leaf loss by herbivory and fruit set. Leaf loss showed a negative relation with forest cover at landscape level, in landscapes with 2 km radius, indicating that herbivory is better controlled in landscapes with high forest cover, especially in the presence of birds and bats. However, at local level (defined as 300 m around coffee plants), leaf loss and fruit set responded to forest cover differently. In units with low local forest cover, bird and bat exclusion was associated with increased leaf loss and reduced fruit set by 13%. However, under high local forest cover, bird and bat exclusion had no significant effect on leaf loss or fruit set. We conclude that the effects of bird and bat exclusion on leaf loss and fruit set are modulated by different processes occurring at landscape and local levels. We posit that when local forest cover is high (e.g. near remnant forest fragments) birds and bats are not only controlling herbivores but may also be reducing mesopredators. In contrast, when local forest cover is low (e.g. far from forest fragments), mesopredators occur in lower abundance, and birds and bats provide biological control by feeding mainly on herbivores. We highlight the importance of employing a multi-scale analysis in systems where species with different dispersal abilities are providing an ecosystem service.

Keywords: Brazilian Atlantic Forest, *Coffea arabica*, Ecosystem services, Landscape Ecology, Pest control

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Introduction

Biological pest control is an increasingly studied ecosystem service because of its potential to enable the development of productive and sustainable agricultural systems (Bianchi et al. 2006). Many studies have demonstrated that richness and abundance of predators in agricultural areas is related to the amount and proximity of natural and semi-natural vegetation (Aviron et al. 2005; Billeter et al. 2008; Tscharntke et al. 2005). Also, the potential of birds and bats to suppress arthropods (Kalka et al. 2008; Mooney et al. 2010; Van Bael et al. 2008; Williams-Guillen et al. 2008), including agricultural pests (Cleveland et al. 2006; Johnson et al. 2010), is already well established, with positive effects over yield and income in some economically important crops, such as coffee and cacao (Classen et al. 2014; Karp et al. 2013; Maas et al. 2013).

However, we still poorly understand how the landscape structure acts modulating the provision of biological pest control by regulating the occurrence, abundance and dispersal movement of pests and their predators (Bianchi et al. 2006; Chaplin-Kramer et al. 2011). *In situ* cage experiments are useful to isolate the impact of landscape-mediated natural enemy increases on crop damage and yield, allowing to assess not only crop damage but also avoided crop damage, however very few studies have done this across landscape gradients (Chaplin-Kramer et al. 2011). Moreover, the presence of predators, their interactions and, consequently, pest control services in agricultural systems can be affected by the landscape structure at different spatial scales given the distinct dispersal ability of different predators (Tscharntke et al. 2005). In this context, a landscape ecology perspective can be useful to understand how land use and land cover pattern affects, at different spatial scales, the ecological processes involved in pest control (Turner et al. 2013). This approach may have important economic implications when applied to dominant agricultural crops, such as coffee plantations.

In Brazil, the largest producer and exporter of coffee in the world (FAOSTAT 2013), coffee pests lead to the loss of hundreds of millions of dollars per year (Oliveira et al. 2014). One of the main insect pest related to coffee is the “coffee leaf miner” (*Leucoptera coffeella*), which has the potential to reduce yield in more than 50% through coffee defoliation (Pierre 2011). The coffee-leaf-miner is a micro-Lepidopteran, with a crepuscular nocturnal habit that feeds on coffee leaves during the caterpillar phase. The necrosed leaf surface reduces photosynthesis; nevertheless, the loss in production is mainly due to leaf loss, provoked by the increase in the level of ethylene in attacked coffee leaves (Souza et al. 1998). This process can cause severe defoliation, affecting productivity and plants longevity (Pierre 2011). Chemical control, with expensive and harmful insecticides, has been the commonest method to control this pest (Waller et al. 2007), but its use is not economically nor ecologically sustainable. Predator and parasitoid wasps are well-known predators of the miner (Carvalho et al. 2004; Melo et al. 2007; Reis 1999) and many studies suggest that they provide an important pest control service (Amaral et al. 2010; Melo et al. 2007; Pierre 2011).

However, the role of insectivorous bats and birds over the coffee-leaf-miner is not documented. Birds and bats can have negative effects on pest control, by feeding on predaceous arthropods and then releasing herbivores (Martin et al. 2013), but also positive effects, by feeding on herbivores and thus reducing plant damage and increasing plant biomass (Maas et al. 2013; Mooney et al. 2010).

These different outcomes could be explained by the scale at which ecological research was conducted (Wheatley and Johnson 2009; Wiens 1989). Given differences in flying capacity related to body size and trophic level, birds and bats tend to respond to percentage of natural or semi-natural habitat at greater scales than, for example, predator arthropods as wasps (Jackson and Fahrig 2015). If both guilds are important predators, restricting the analysis at only one scale could mask important underlying processes.

Here we take an experimental approach to explore whether bird and bat exclusion affects coffee leaf loss and fruit set as indicators of pest control, and whether this service is consistent at different spatial scales. To our knowledge this is the first study regarding the effects of landscape structure over coffee leaf loss and fruit set at different scales. More specifically, we tested the hypotheses that (1) the presence of birds and bats decreases leaf loss and raises fruit set, and (2) that these effects augment with increasing amount of forest cover at landscape and local levels (Fig.1).

Methods

Study area

The study was conducted in the largest coffee producing region of Brazil, responsible for approximately 25% of the total production in the country (Conab 2014), known as Mogiana and Sul de Minas region (Fig. 2). This region is situated in the Brazilian Atlantic Forest biome (Galindo Leal and Câmara 2003), one of the most biodiverse and endangered biomes in the world (Myers et al. 2000; Ribeiro et al. 2009), where coffee plantations were one of the most important historical drivers of deforestation. Given that the Brazilian law demands land owners to conserve 20% of native forest in this biome (Metzger 2010), agricultural coffee landscapes in the Atlantic Forest are essentially composed of heterogeneous mosaics made of patches of native forest and coffee farms.

The study region has a subtropical climate, with small variation in temperatures along the year (conforms to a Köppen's type cwb with mean temperatures of 20.4°C-13.6°C) and some seasonality in rainfall (average annual rainfall of 1695 mm), with rainy summers and dry winters (Pompeu et al. 2009). The summer 2013-2014 was very atypical, though, with higher mean temperatures and lower mean rainfalls compared to the historical record (Procafé 2014).

The coffee in this mountainous region is managed by small to medium producers, mostly without mechanization given that plantations are in hilly terrains, between 950-1300 m.a.s.l.

The dominant agricultural matrix is primarily made up of coffee plantations with some areas of pastures, eucalyptus and sugar cane. Coffee plantations are usually adjacent to native forest patches of different shapes and sizes. Brazilian coffee cultivation is mostly intensive, with varying crop densities (2000-8000 coffee plants/ha) and no shade tree cover. Most farms use herbicides, fertilizers and pesticides, but these techniques are applied by producers to a different extent depending on their knowledge, investment capacity, environmental conditions and pest infestation rates. As these applications can affect pest densities, we registered the usage during 2014 through interviews with farmers.

Landscape selection and metrics

We conducted a 10-month study in eight landscapes starting in June 2014 through March 2015. Experimental landscapes were circular spatial samples with 2 km radius, set to represent a gradient of forest cover (11% to 42%), and at the same time controlling for major differences in altitude, relief and practice (mostly not mechanized hilly regions). We chose a minimum distance between landscape centers of 6 km to consider landscapes independent from each other (Fig. 2).

Forest, coffee and other land uses were mapped using high-resolution images (ArcGis 10.3 basemap imagery, DigitalGlobe satellites 2010-2011, 0,5-1 m² resolution) with a reference scale of 1:5.000. Mapping accuracy was extensively validated in the field in 2014, and all interpretation errors or landscape changes between 2011 and 2014 were edited. For data analysis, we used native forest percent at two different organizational levels: the landscape level, considering percent of forest cover at 2 km radius from the center of the studied landscapes; and the local level, considering percent of forest cover at 300 m around each experimental unit (Table S1). The 2 km radius was selected to approximate to the scale of effect (*sensu* Jackson and Fahrig 2015) of birds (Smith et al. 2011) and the 300 m radius was selected to represent the scale of effect of predatory arthropods, mainly predatory wasps of the miner (Bichara et al. 2010; Ribeiro et al. 2008; Santos et al. 2000). The scale of effect for bats could be bigger (Ethier and Fahrig 2011; Gorresen et al. 2005; Klingbeil and Willig 2009) but we suppose that they should forage more intensively in lower scales, similarly to birds. Local level was also selected in order to have comparable data with the other few studies analyzing ecosystem services provision with a landscape perspective in a replicated design (Martin et al. 2013; Saturni 2015). Forest cover at landscape and local levels were uncorrelated (Spearman's Rho = -0.05; P = 0.51). Landscape metrics were calculated using ArcGis 10.0.

Field experiment

In the central circle of 1 km of each landscape we installed four experimental units (Fig. 2). All units were located in the same coffee varieties, Catuai or Catucaí, which have very similar physiological characteristics. Units were also placed in order to be at least 100 m apart from each other (in average they were 414 m apart from each other, Table S2) and to vary in the

local forest amount surrounding them. Each unit consisted of a bamboo-frame mesh cage structure covering four coffee plants and four coffee plants acting as control (Fig. S1). We used commercial nylon monofilament with mesh size of 2.5 x 2.5 cm; small enough to exclude birds and bats, but large enough to allow arthropods to enter.

We selected randomly (at different heights) nine branches per plant and marked four leaves in each branch ($n=36$ leaves/plant). We visited experimental units every 30-45 days to count the number of remaining leaves in each coffee plant during the six peak months of infestation (June-November) (Fig. S2). Finally, we also counted the number of flowers, young coffee berries (early fruits) and green coffee berries (late fruits) for all marked branches. Data of mature coffee berries (harvestable fruits) was also collected but just for six branches per unit. Flowers were counted during the main blossoming event and remaining buds were not removed. The main blossoming event in the study region occurs in September, berries grow from October to April and harvest begins in May.

Statistical analysis

We examined the effects of bird and bat exclusion on leaf loss and fruit set using generalized linear mixed models with binomial distribution (GLMMs; Zuur 2009). Leaf loss was calculated as the proportion of fallen leaves respect to those initially marked at each sampled time and fruit set was calculated as the proportion of early fruits turned into harvestable fruits. We did not use the proportion of flowers turned into harvestable fruits as we only had the number of flowers at the main blossoming event.

To account for the fact that there were four experimental units per landscape, we included experimental unit nested within landscape as random effect. Overdispersion of the data was corrected by adding an observation-level random effect (Zuur 2009). Exclusion treatment, pesticide (used or not), forest cover at local level (300 m) and forest cover at landscape level (2 km) were included as fixed effects in the full models for leaf loss and fruit set (Table 1). Full models were later simplified using maximum likelihood ratio tests. All interactions and single explanatory variables that did not reach statistical significance ($P < 0.05$) in the tests were removed sequentially.

In a *post hoc* analysis, we divided our 32 experimental units in two groups, in order to simplify results, considering the two units with highest and the two units with lowest local forest cover in each landscape. The High local forest cover group included units with 11%-42% local forest cover (mean = 24.6%), and the Low local forest cover group included units with 1.5%-30.4% local forest cover (mean = 11.7%). All analyses were conducted in R using the 'lme4' package (R Development Core Team 2014).

Results

For leaf loss assessment, we followed 9216 leaves in 32 experimental units divided in eight landscapes. We found a significant interaction ($P = 0.044$) between landscape cover, local

cover and treatment (Table 1, Fig 3). Leaf loss decreased with higher landscape forest cover in all cases ($P = 0.04$; Fig.3), but the slope of this relation was significantly different between treatment and control plants in low local forest cover units, with respect to high local forest cover units ($P = 0.01$; Fig. 3). Leaf loss was significantly higher when birds and bats were excluded relative to open controls in low local forest cover units ($P = 0.022$) but not in high local forest cover units ($P = 0.17$; Fig. 3).

For fruit set assessment, we counted 7931 early fruits, 6218 late fruits and 5659 harvestable fruits (Table 2). Mean number of flowers per branch was not affected by treatment; however mean number of harvestable fruits per branch was 15% lower in exclusion plants respect to controls (Table 2 and Fig. S4). We found a significant interaction between treatment and local forest cover ($P = 0.0044$) (Table 1 and Fig. 4). While fruit set in control plants was not significantly affected by local forest cover ($P = 0.16$), exclusion treatments showed a positive relation with it ($P = 0.04$). The exclusion of birds and bats tended to have a negative effect on fruit set in experimental units with low proportion of local forest cover ($P = 0.05$), though not in units high local forest ($P = 0.16$; Fig. 4). Mean fruit set per branch was 13% lower in treatment plants respect to control in low local forest units, however accounting for all units independent of local forest amount this reduction was just 3% and not significant.

Discussion

We found that pest control service in coffee plantations in the Atlantic Forest is strongly modulated by landscape structure. Leaf loss in coffee plants was significantly reduced with increasing percentage of forest cover at landscape level. Interestingly, the slope of this relation was determined by bats and birds exclusion and by local forest percentage. On the other hand, fruit set did not respond to landscape forest cover but showed a positive effect in vertebrate exclusion treatments with local forest cover. In addition, in units with low local forest cover fruit set was significantly lower when vertebrates were excluded relative to open controls, however no significant differences were observed between them in units with high local forest cover.

Opposing effects at local and landscape levels

In line with our hypotheses, leaf loss decreased with landscape forest cover in open controls suggesting a more intense provision of pest control service in high forested landscapes. Interestingly, exclusion treatments presented the same trend, which suggests that both vertebrate and arthropod predators are present in our system (Bianchi et al. 2006; Chaplin-Kramer et al. 2011). Furthermore, we found that the slopes of these curves were dependent on local forest cover. In experimental units with low local forest cover, there was a strong decrease in leaf loss with increasing landscape forest cover in open controls and almost no effect when birds and bats were excluded, as we had proposed in our hypotheses (Fig. 3, Fig. 1). Though, in experimental units with high local forest cover leaf loss decreased as much in

exclusion treatments as in open controls, and thus they were not significantly different (Fig. 3). With respect to fruit set, in experimental units with low local forest cover, open controls produced more fruits than treatments, suggesting a positive effect of birds and bats on coffee production. However, contrary to expectations, in experimental units with high local forest cover we did not find significant differences (Fig. 4).

Our results might reveal the effects of the interaction between vertebrate and arthropod predators. Predatory social wasps, which are effective predators of the coffee leaf miner, have low flying ranges, varying between 25-150 m (Bichara et al. 2010; da Cruz et al. 2006; Prezoto and Gobbi 2005; Ribeiro et al. 2008), therefore it is possible that they are mostly present just close to forest fragments, in areas that will usually present relatively high local forest cover. In fact presence of predatory wasps of the coffee leaf miner is associated with native forest fragments within or next to plantations (Pierre 2011). On the other hand, more generalist insectivorous birds and bats species, that present higher dispersal abilities, may be present across the whole landscape (Fig. 5). We suggest that in high local forest sites, flying vertebrates may be feeding on herbivores as well as on wasps (and other mesopredators), hence reducing the pest control regulation provided by wasps. On the contrary, when only flying vertebrates occur (in low local forest cover areas), birds and bats would feed just on herbivores, thus providing pest control services (Fig. 5). New experiments are needed to confirm if this mechanism is occurring in coffee plantations and to understand how it is modulated in more detail.

The trend we are proposing for coffee plantations was partially described by Martin et al. (2013) in cabbage plantations in South Korea. However these researchers lacked a multi-scale analysis (they used only local forest cover around experiments) and therefore their conclusions missed the fundamental effect of landscape forest cover. Here we demonstrate that local effects are subordinated to landscape level effects and that when accounting for them together we can affirm that overall forest cover increases pest control services, reducing leaf loss and increasing fruit set. We highlight thus the importance of taking into account more than one spatial scale of analysis in systems when more than one group of organisms with different dispersal abilities is providing an ecosystem service.

Landscape forest cover affected fruit set and leaf loss differently, while leaf loss showed a negative relation with landscape forest cover, fruit set was not significantly affected for it. On the other hand, we did find a relation between leaf loss and fruit set with local forest cover (Fig. 4, Fig. S3). In units with low local forest cover exclusion of birds and bats produced higher herbivory and lower fruit set respect to open controls. On the contrary in units with high local forest cover we found an opposite trend which was not significant. These results suggest that fruit set could be just partially determined by leaf loss and that other biological processes are probably occurring. The absence of birds and bats increases the abundance of many arthropods including invertebrate predators such as ants, spiders and wasps (Karp and Daily 2014; Maas et al. 2013). This release could be explaining fruit set

increase in treatments with increasing local forest cover as arthropod predators could be controlling other coffee pests besides the coffee leaf miner such as flower-fruit herbivores.

Even though the goal of this study was not to test pesticide effects, specific pesticide for the coffee leaf miner was used in 10 from our 32 experimental units. Interestingly we did not find evidence for effective leaf loss reduction but we found a negative trend between application and fruit set (Table 1, Fig. S5). This is the opposite of what farmers expect. We highlight the importance of avoiding unnecessary applications of pesticide, once pesticides for the miner are also toxic for wasps (Fernandes et al. 2014) and other arthropods that contribute to control the coffee leaf miner. Farmers would be doing a bad investment firstly spending money in ineffective pesticide and secondly losing money with lower fruit set.

Future perspectives

For nearly 30 years researchers from around the world have debated about the effect of vertebrate predators (mainly birds and bats) on herbivory. This discussion is summarized in the revision done by Mooney and collaborators (Mooney et al. 2010). Many studies have found contrasting effects regarding the exclusion of birds and bats, including positive effects, negative effects and no effect. This also applies for agricultural systems, including coffee plantations. Surprisingly to our knowledge no study until now has used a multi-scale analysis to answer this question. Here we demonstrate that depending on the scale of analysis we can obtain positive, negative or neutral effects of birds and bats on herbivory, which should depend on the different interactions between vertebrate predators and mesopredators at different spatial scales.

Unfortunately, the interactions between vertebrate and invertebrate predators behind biological pest control in coffee agroecosystems can be really complex (Perfecto et al. 2014), and hence, the understanding of the biological mechanisms behind the control of each target pest will demand much more data. Although some studies have identified predatory birds controlling pests in coffee and cacao plantations (Karp et al. 2013; Maas et al. 2015), more studies are needed to identify the vertebrate predators that provide pest control services in coffee plantations in Brazil. Also basic biological information regarding the potential negative interactions between vertebrate and arthropod predators in coffee plantations is needed to understand how to maximize this service. For the coffee-leaf-miner, in particular, conducting separated exclusion of birds and bats could be especially helpful. We argue that, given the crepuscular activity of the miner bats should have a greater role as predators of this pest compared to birds, and also less probability to interfere with other predators such as wasps. Therefore, we believe that bats have more potential to control the miner than birds.

The climate abnormalities that characterised our study region during 2014 could have favoured the leaf miner reproduction and survivorship, once high temperatures and low relative humidity shorten the larval phase of this pest (Pierre 2011). As a result, the patterns

described in this study could have been slightly different than in a normal year. Despite this, coffee-leaf-miner infestation was not much higher than the historical records for the region. Longer assessments, encompassing several years, would be desirable to overcome this kind of annual fluctuations.

In this study we used forest cover as a proxy for predators and pest control increase. Nevertheless, we are conscious that besides forest amount, forest quality can also determine the composition of species that a certain fragment can support, thus affecting biological control. A quick assessment of quality of fragments (Meyer et al. 2015) can help to resolve this limitations, mostly in small to medium scale studies.

Finally, coffee weight is another important factor in determining final yield and income in coffee plantations that we did not consider. Classen et al. (2014) conducted exclusion experiments in coffee plantations in a previous study and concluded that birds and bats had an effect on fruit set but not in fruit weight, though. Moreover, these researchers reported fruit set reductions of 9% on average when birds and bats were excluded, comparable to the 13% reduction we registered in units with low local forest cover.

Given that other important ecosystem services, such as pollination, are also modulated by landscape structure (Saturni 2015), improving landscape structure to optimize multiple ecosystems services provision should be done carefully. In particular, it is fundamental to consider possible synergies (Lundin et al. 2013) and tradeoffs, to avoid suboptimal ecosystem service provision. This will be one of the main challenges of the next decades given the importance of ecosystem services for sustainable food supply and for biodiversity conservation.

Conclusion

This study provided the first empirical evidence of how landscape can modulate leaf loss and fruit set in coffee plantations by affecting vertebrate predators. Also our data suggests that pressure over herbivores depends on the interactions of different vertebrate and invertebrate predators, which can vary at different spatial scales. Finally, we conclude that pest control service in coffee agroecosystems is strongly modulated by landscape and local forest cover, and that only a multi-scale analysis is able to capture the complex biological interactions between the predators which provide it. Our results can be considered as a first contribution towards an optimal design of coffee agricultural landscapes, which can support coffee production, and also maintain a considerable part of native biodiversity.

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Figures

Figure 1. Expected relationships of leaf loss and fruit set with forest cover inside and outside cage experiments. Forest cover can be considered at different spatial scales. Differences between open controls (outside cages) and birds/bats exclusion (inside cages) is expected to increase with forest cover due to the increase in pest control service provided by forest species. These relationships can be linear, as represented here, but thresholds could be expected if species that provide the service disappear suddenly with forest loss. According to Pierre (2011) we consider slight variations in exclusion treatments to account for the effect of arthropod predators.

Figure 2. A. Spatial location of the coffee studied region (Mogiana and Sul de Minas) in Brazil. B. Map showing the eight experimental landscapes with 2 km radius. C. Land use and land cover maps for the landscapes with the lowest and the highest forest cover and location of experimental units.

A) Units with low local forest cover

B) Units with high local forest cover

Figure 3. Influence of landscape forest cover on leaf loss in experimental units with (A) low and (B) high local forest cover. Response variables are detrended, showing the relationship between forest cover and leaf loss after subtracting the effect of the other predictor variables. Green lines represent open controls (outside experimental cages) and red lines represent exclusion treatments (inside experimental cages) fitted curves. The shaded area represents 95% confidence interval.

Figure 4. Influence of the local forest cover on fruit set. The green line (A) and boxes (B) represent open controls (outside experimental cages) and the red line (A) and boxes (B) represent exclusion treatment (inside experimental cages) fitted curves. The shaded area in A represents 95% confidence intervals. Response variable is detrended, showing the relationship between forest cover and leaf loss after subtracting the effect of the other predictor variables. In B, the category *Low* includes the two units with lowest local forest cover in each landscape and the category *High* includes the two units with highest local forest cover in each landscape. Middle bars represent median value, boxes are first and third quartiles, whiskers are 95% confidence intervals and dots represent outliers. Significance levels: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, † $p < 0.1$.

Figure 5. Schematic illustration of plausible biological interactions between birds, bats and wasps underpinning biological control of the coffee leaf miner in coffee plantations with different local and landscape forest cover (A), in open controls (B) and exclusion treatments (C).

Tables

Table 1. Results of generalized linear mixed effects models relating leaf loss and fruit set to explanatory variables (n= 202 and 123, respectively, in 32 plots). Significance levels:

***p<0.001, **p<0.01, *p<0.05, †p<0.1. DF = Degrees of freedom.

A) Full models

Response variable	Fixed effects	Chi ² (DF=1)	p
Leaf Loss	Week	72.57	<2e-16***
	Pesticide	0.25	0.62
	Landscape forest cover	4.16	0.041*
	Local forest cover	2.90	0.089 [†]
	Treatment	2.77	0.096 [†]
	Landscape forest cover x Local forest cover	0.12	0.73
	Landscape forest cover x Treatment	0.31	0.58
	Local forest cover x Treatment	3.03	0.082 [†]
	Landscape forest cover x Local forest cover x Treatment	4.05	0.044*
Fruit set	Pesticide	3.15	0.076 [†]
	Landscape forest cover	0.94	0.33
	Local forest cover	1.15	0.28
	Treatment	0.005	0.95
	Landscape forest cover x Local forest cover	0.065	0.80
	Landscape forest cover x Treatment	0.071	0.79
	Local forest cover x Treatment	7.80	0.005**
	Landscape forest cover x Local forest cover x Treatment	0.58	0.45

B) Simplified models

Response variable	Fixed effects	Chi ² (DF=1)	p
Leaf Loss	Week	72.71	<2e-16***
	Landscape forest cover x Local forest cover x Treatment	4.04	0.044*
Fruit set	Local forest cover x Treatment	8.11	0.0044**

Table 2. Overall number of flowers and early, late and harvestable fruits per branch for open control and exclusion treatment groups. SEM: Standard Error of the Mean.

Response variable	Mean per branch ($\pm$ SEM)	
	Control	Treatment
Flowers	36.27 $\pm$ 4.6	36.80 $\pm$ 4.7
Early Fruits	68.11 $\pm$ 4.7	60.67 $\pm$ 4.4
Late Fruits	52.83 $\pm$ 3.6	48.17 $\pm$ 3.6
Harvestable Fruits	49.65 $\pm$ 3.5	42.18 $\pm$ 3.2

Supporting Information

Figure S1. Experimental set-up showing an experimental unit. In the left the bamboo-frame mesh cage structure covering four coffee plants used to exclude birds and bats, and in the right the open control coffee plants. For illustrative purposes, we highlighted with blue rectangles three experimental branches in one coffee plant inside the exclusion cage. In total, we had 36 experimental branches inside exclusion cages (9 per plant) and 36 outside.

Figure S2. Leaf loss over time in four experimental units with low local forest cover. Green lines represent open controls (outside experimental cages) and red lines represent exclusion treatments (inside experimental cages). The shaded area represents 95% confidence interval.

Figure S3. Influence of local forest cover on leaf loss in: (a) landscapes with less than 20% of forest, (b) landscapes with 20%-30% forest, (c) landscapes with more than 30% forest and (d) all landscapes considered. Response variables are detrended, showing the relationship between forest cover and leaf loss after subtracting the effect of the other predictor variables. Green lines represent controls and red lines represent exclusion treatments fitted curves. The shaded area represents 95% confidence intervals.

Figure S5. Pesticide effect on fruit set. Response variable is detrended, showing the relationship between pesticide and fruit set after subtracting the effect of the other predictor variables on the model.

Table S1. Forest cover (in percentage) observed at two studied spatial scales. At local level (300 m), we show the range of values obtained in the four experimental units.

Landscape	300 m	2 km
São Roque	7.5 - 12.2	11.6
Mariano	15.7 – 23.9	17.2
Faisqueira	18.8 – 39.2	20.7
Matão	1.9 - 40.5	21.6
Pedro	8.3 – 27.2	25.1
Rainha	8.8 – 16.7	28.7
Toninho	7.0 – 42.0	31.8
Bocaina	1.5 – 23.1	42.4

Table S2. Distances (in meters) between exclusion experiments in each landscape.

Landscape	Minimum	Maximum	Mean
São Roque	150	600	352
Matão	125	1318	688
Pedro	137	325	222
Faisqueira	120	280	182
Toninho	100	345	205
Bocaina	160	1685	1111
Rainha	165	650	349
Mariano	130	315	204
Mean	136	690	444

Considerações finais

A motivação para desenvolver este estudo surgiu da necessidade de avançar no desenvolvimento de paisagens agrícolas sustentáveis, que sejam ao mesmo tempo produtivas, e também permitam conservar a biodiversidade. A aliança entre a ecologia de paisagens e os serviços ecossistêmicos está sendo uma das principais forças motoras desta mudança.

No Brasil, o conceito de serviços ecossistêmicos tem ganho força nos últimos cinco anos e já mostra potencial para contribuir ativamente no desenvolvimento de novas estratégias para a conservação da biodiversidade e a produção sustentável. Os serviços ecossistêmicos foram de fato concebidos no intuito de demonstrar que, em vários casos, os objetivos da conservação e o desenvolvimento agrícola não são excludentes e que existem varias estratégias para gerar situações de duplo ganho (*win-win situations*). O presente trabalho procurou contribuir nesta direção.

Neste trabalho, demostramos que, através de vertebrados predadores, a paisagem é capaz de modular o serviço de controle biológico de pragas agrícolas. O aumento na quantidade de floresta nativa na paisagem reduziu significativamente a perda foliar em plantações de café, dado que o aumento na quantidade de floresta se associa a um aumento de organismos predadores. Demonstramos também que aves e morcegos têm um efeito importante na frutificação e que utilizando uma perspectiva de paisagens é possível desenvolver estratégias para maximizar o serviço de controle de pragas. Mais ainda, mostramos que uma abordagem multiescalar é essencial para explicar o fornecimento de serviço de controle de pragas por mais de um grupo de organismos com diferentes capacidades de dispersão. Embora mais estudos sejam necessários para confirmar os mecanismos biológicos que propomos, as informações surgidas do nosso trabalho podem mostrar diretrizes para otimizar o potencial das paisagens agrícolas em termos de conservação e produção.

Este estudo demonstra pela primeira vez o efeito benéfico de aves e morcegos em plantações de café na Mata Atlântica. Instamos a futuros pesquisadores a considerar o efeito destes predadores no serviço de controle de pragas. Esperamos que as informações trazidas pelo nosso trabalho sejam uteis na elaboração de instrumentos de gestão e planos de manejo que visem maximizar a conservação da biodiversidade e a produção em paisagens agrícolas da Mata Atlântica.