



Forest cover enhances natural enemy diversity and biological control services in Brazilian sun coffee plantations

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Abstract

Landscape structure and crop management directly affect insect communities, which can influence agriculturally relevant ecosystem services and disservices. However, little is known about the effect of landscape structure and local factors on pests, natural enemies, and biological control services in the Neotropics. We investigated how environmental conditions at local and landscape levels affect *Leucoptera coffeella* (insect pest), social wasps (natural enemies), and the provision of biological control services in 16 Brazilian coffee plantations under different crop management and landscape contexts. We considered microclimatic conditions, coffee plantation size, and management intensity at the local level; and forest cover, landscape diversity, and edge density at the landscape level. Pest population, wasp communities, and biocontrol services were monitored in wet and dry seasons when *L. coffeella* outbreaks occur. We found that the amount of forest in the surrounding landscape was more important for explaining patterns than the local environment, landscape diversity, or landscape configuration. In both seasons, *L. coffeella* was negatively affected by forest cover, whereas biological control and richness and abundance of social wasps increased with increasing forest cover at multiple spatial scales. Moreover, biological control was positively correlated with wasp abundance during pest outbreaks, suggesting that social wasps are important natural enemies and provide pest control services within coffee plantations. We provide the first empirical evidence that forest cover is important for the maintenance of social wasp diversity and associated pest control services in a Brazilian coffee-producing region.

Keywords Agroecosystems · Biodiversity conservation · Coffee leaf miner · Ecosystem services · Landscape structure · Social wasps

1 Introduction

Insects provide ecosystem services and disservices in agricultural landscapes with important environmental and

socioeconomic consequences. 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 agrochemical inputs

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(Oerke 2006). It is estimated that in Brazil, annual pre-harvest losses from insect damage, the purchase of pesticides, and 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) have significant economic benefits and may compensate for these losses (Losey and Vaughan 2006).

Landscape structure and crop management directly affect the abundance and diversity of insect communities and associated ecosystem services and disservices (Tscharntke et al. 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. These insects strongly depend on the presence of non-crop habitats to persist in agricultural landscapes (Tscharntke et al. 2012, 2016). Intensive use of pesticides in farms enhances mortality rates and sublethal effects in non-target beneficial insects (Geiger et al. 2010). In contrast, non-crop habitats (e.g., forest, grassland, wetland, hedgerows) that are less subject to pesticide applications experience relatively low rates of disturbance and provide a more reliable supply of food and shelter (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 operations (Tscharntke et al. 2012). Complex landscapes with a large proportion of non-crop habitats provide spatiotemporal insurance for natural enemies and enhance the provision of pest control services into crop fields (Bianchi et al. 2006; Tscharntke et al. 2012). Although natural enemies seem to benefit more than pests from the presence of non-crop habitats, a number of pest species can also benefit from the presence of non-crop habitats (Tscharntke et al. 2016). 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 (Tscharntke et al. 2016).

The effects of landscape structure and crop management on insects and associated services and disservices have been widely investigated in temperate regions at multiple spatial scales. However, this relationship is understudied in Brazilian agricultural landscapes, where only a handful of recent studies have been reported (Sartuni et al. 2016; Librán-Embú et al. 2017; Hipólito et al. 2018; Aristizábal and Metzger 2018). Assessments in the Neotropics often rely on temperate data even though the effects of landscape elements and crop management on insects may differ between regions. Warm conditions in tropical regions associated with the overuse of pesticides allow crop production year-round—and most likely lead to more pest generations resulting in greater pest pressure due to the development of pest resistance to insecticides (Oliveira et al. 2014) and high mortality of natural enemies (Geiger et al. 2010). Moreover, the growing demand for agricultural land in the tropics and resulting intensive conversion of mega-diverse

natural habitats into monocultures are leading to species loss and more pronounced effects of agricultural intensification on biodiversity and ecosystem services.

We studied the non-native but pervasive coffee leaf miner *Leucoptera coffeella* (Lepidoptera, Lyonetiidae) and native social wasps (Vespidae, Polistinae) as a model system. *Leucoptera coffeella* is a major coffee pest in Brazil (Pereira et al. 2007). A multivoltine insect, the larvae of *L. coffeella* are oligophagous and feed exclusively on species within the genus *Coffea* (Pierre 2011). This insect pest creates necrotic mines within the coffee leaf causing abscissions that reduce photosynthesis, productivity, and longevity of coffee plants (Pierre 2011). Social wasps are important natural enemies of lepidopteran crop pests including *L. coffeella* in coffee plantations (Ritcher 2000). In Brazil, Pereira et al. (2007) found that 49.5% of *L. coffeella* mortality in a coffee plantation was associated with predation by wasps. Predatory wasps forage and deliver important biocontrol services in agroecosystems, but most wasp species probably depend on the presence of non-crop habitats to find all required resources and nesting sites that are not available in farmland. In many Brazilian coffee-growing regions, coffee is produced in sun-grown plantations that are subject to frequent pesticide applications including organophosphates and pyrethroids that are highly toxic to non-target insects (Pereira et al. 2007). Moreover, most farmers remove wasp nests on their farms to avoid wasp stings during harvest. Despite its recognized importance, little is known about the effect of landscape structure and local variables on the diversity and abundance of social wasps as well as biological control services in Brazilian coffee plantations.

We investigated how environmental conditions at local and landscape levels affect the occurrence of the insect pest *L. coffeella*, social wasps, and the provision of biological control services in Brazilian coffee plantations during the wet season when the *L. coffeella* population is low, and during the dry season when outbreaks occur. We considered microclimatic conditions and agrochemical usage as factors at the local level, and forest cover, coffee cover, landscape diversity, and edge density as factors at the landscape level. We expected that forest is the key habitat for the maintenance of wasp diversity and associated biocontrol services and that landscapes with high forest cover support lower pest densities, more diverse wasp communities, and greater biological control services than landscapes dominated by monocultures.

2 Material and methods

2.1 Study area

The study was performed in 16 sun coffee plantations located in different crop management and landscape contexts near the

border of the states of São Paulo and Minas Gerais in Southeast Brazil (Fig. 1a). This region produces approximately 25% of coffee in Brazil (Conab 2014) and is situated in the Atlantic Forest, a biome that supports high levels of biodiversity and endemism, but has been heavily fragmented (Myers et al. 2000). Atlantic Forest remnants in the study region are composed of secondary vegetation after experiencing intensive logging 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 land uses such as pasture, eucalyptus plantations, and sugar cane fields (Librán-Embid et al. 2017).

The study region encompasses mountainous relief in the north that becomes flatter in the south. Northern coffee is typically cultivated by small- and medium-scale producers without mechanization in hilly terrain at 850–1300 m.a.s.l. (Librán-Embid 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 on level terrain at 700–850 m.a.s.l. Most farmers adopt conventional crop management incorporating fertilizers, insecticides, fungicides, and herbicides.

2.2 Field surveys

In each coffee plantation, we sampled social wasps (Vespidae, Polistinae) by using one malaise trap (Townes model; Fig. 1b) and three baited traps along a linear transect located at least 100 m away from the plantation edges with traps spaced 50 m apart. Baited traps (Fig. 1c) consisted of 2000-ml PET (polyethylene terephthalate) bottles hung from branches approximately 1.3 m above the ground with four circular holes of 4-cm-diameter cut midway and filled with 300 ml of industrialized orange juice and 0.4 ml of propylene glycol. Traps

remained open for 7 consecutive days per month over 12 months from the dry season (June–November 2016) to the wet season (December–May 2017). Captured social wasps were preserved in 70% ethanol and identified to the lowest taxonomic level possible using identification keys. We estimated species richness (S) and total abundance (N) of wasps for each landscape and season, where S and N are the cumulative number of species and specimens recorded per coffee plantation, respectively. We obtained authorization from the Federal Government of Brazil to collect biological material during the entire period of this study (No. 54381-1, authentication code no. 87478664 Sisbio/IBAMA).

Within each coffee plantation, we visually assessed 200 coffee leaves per month over 12 months to estimate the number of mined leaves (pest abundance) and preyed mines (biological control) during the dry season from June to November 2016 (peak months of *L. coffeella* infestation, Librán-Embid et al. 2017) and the wet season from December 2016 to May 2017. Each month we randomly selected 10 coffee plants in the center of each plantation (> 100 m from any edge) and 10 coffee plants along the edge of each plantation. We randomly selected five branches on each coffee plant 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 was recorded on a monthly basis and used to estimate the proportion of mined leaves (pest abundance) and preyed mines (biological control) concurrent with the social wasp survey. We only considered leaves with fresh mines (dark brown in color) 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 have characteristic linear cuts on the mine surface. In contrast, mines in which pest development is complete have a circular emergence opening at the margin of the mine (Pierre 2011). After assessment,

Fig. 1 a Typical sun coffee-producing landscape in the study region. b Malaise trap. c Baited trap used to capture social wasps



we marked each coffee plant using colored plastic ribbons to avoid evaluating the same tree twice.

2.3 Local- and landscape-level variables

We used agrochemical usage (total number of fertilizer, insecticide, herbicide, and fungicide applications) and microclimatic conditions (mean of temperature, humidity, and luminosity) within coffee plantations as explanatory variables related to local factors. We used Instrutherm® (model HT-500) data loggers to monitor temperature and humidity and HOBO Pendant® (model UA-002-64) data loggers to record luminosity. In each coffee plantation, both data loggers were attached to the malaise trap 1.3 m above the ground so that microclimate conditions were recorded every hour during insect surveys (7 days/month over 12 months). The number of fertilizer and pesticide applications in each coffee plantation was obtained by interviews with farmers.

To define the extent of our landscape, we considered the dispersal of social wasps. Little is known about their dispersal capacity in the Neotropics; however, some social wasp species in this region have a dispersal range of up to 300 m (da Cruz et al. 2006; Ribeiro-Filho et al. 2008). Based on this estimated range, we built land use maps at four scales from 250 to 1000-m radii using intervals of 250 m. Maps were built using high-resolution images from ArcGIS basemap imagery, 2013–2015 DigitalGlobe satellites, 0.5–1.0-m² resolution, and a 1:5000 visual scale. Extensive ground verification was used to

Table 1 List of competing models used to identify the most relevant variables to explain patterns of pests, natural enemies, and pest control services within coffee plantations in dry and wet seasons in Southeast Brazil

Model	Fixed effects
Forest amount	$y \sim$ forest cover
Landscape diversity	$y \sim$ Shannon landscape diversity
Edge density	$y \sim$ edge density index
Fertilizer	$y \sim$ number of fertilizer applications
Insecticide	$y \sim$ number of insecticide applications
Herbicide	$y \sim$ number of herbicide applications
Fungicide	$y \sim$ number of fungicide applications
Temperature	$y \sim$ average temperature
Humidity	$y \sim$ average humidity
Luminosity	$y \sim$ average luminosity
Null	$y \sim 1$
Pest abundance*	$y \sim L. coffeella$ abundance
Wasp richness**	$y \sim$ number of species
Wasp abundance**	$y \sim$ number of individuals

*Included only in the list of competing models used to explain social wasp richness and abundance

**Used to explain biological control services

achieve a high level of map accuracy. We used forest cover, coffee cover, landscape diversity, and edge density as landscape explanatory variables. We measured these variables within the radii of 250, 500, 750, and 1000 m around the center of each sampled coffee plantation using ArcGIS 10.3.

Table 2 List of social wasp species (Vespidae: Polistinae) recorded in 16 coffee-producing landscapes in Southeast Brazil

Species	Number of individuals
<i>Agelaea angulata</i> (Fabricius, 1804)	3
<i>Agelaea multipicta</i> (Haliday, 1836)	1245
<i>Agelaea pallipes</i> (Olivier, 1792)	852
<i>Agelaea vicina</i> (de Saussure, 1854)	1196
<i>Apoica pallens</i> (Fabricius, 1804)	67
<i>Brachygastra augusti</i> (de Saussure, 1854)	1
<i>Brachygastra lecheguana</i> (Latreille, 1824)	85
<i>Brachygastra mouleae</i> Richards, 1978	1
<i>Metapolybia cingulata</i> (Fabricius, 1804)	1
<i>Mischocyttarus cassununga</i> (von Ihering, 1903)	8
<i>Mischocyttarus cearensis</i> Richards, 1978	1
<i>Mischocyttarus drewseni</i> de Saussure, 1857	18
<i>Mischocyttarus rotundicollis</i> (Cameron, 1912)	29
<i>Mischocyttarus socialis</i> (de Saussure, 1854)	6
<i>Mischocyttarus</i> sp1	2
<i>Polistes billardiieri</i> Fabricius, 1804	1
<i>Polistes cinerascens</i> de Saussure, 1854	2
<i>Polistes erythrocephalus</i> Latreille, 1813	31
<i>Polistes lanio</i> (Fabricius, 1775)	4
<i>Polistes melanosoma</i> de Saussure, 1853	1
<i>Polistes pacificus</i> Fabricius, 1804	4
<i>Polistes simillimus</i> Zikán, 1851	38
<i>Polistes</i> sp1	1
<i>Polistes subsericeus</i> de Saussure, 1854	3
<i>Polistes versicolor</i> (Olivier, 1792)	112
<i>Polybia bifasciata</i> de Saussure, 1854	4
<i>Polybia chrysothotax</i> (Lichtenstein, 1796)	54
<i>Polybia dimidiata</i> (Olivier, 1792)	9
<i>Polybia fastidiosuscula</i> de Saussure, 1854	414
<i>Polybia ignobilis</i> (Haliday, 1836)	274
<i>Polybia jurinei</i> de Saussure, 1854	64
<i>Polybia minarum</i> Ducke, 1906	26
<i>Polybia occidentalis</i> (Olivier, 1792)	393
<i>Polybia paulista</i> von Ihering, 1896	733
<i>Polybia punctata</i> du Buysson, 1908	130
<i>Polybia sericea</i> (Olivier, 1792)	146
<i>Protonectarina sylveirae</i> (de Saussure, 1854)	97
<i>Protopolybia exigua</i> (de Saussure, 1854)	4
<i>Protopolybia sedula</i> (de Saussure, 1854)	15
<i>Pseudopolybia vespiceps</i> (de Saussure, 1863)	4
<i>Synoeca cyanea</i> (Fabricius, 1775)	7

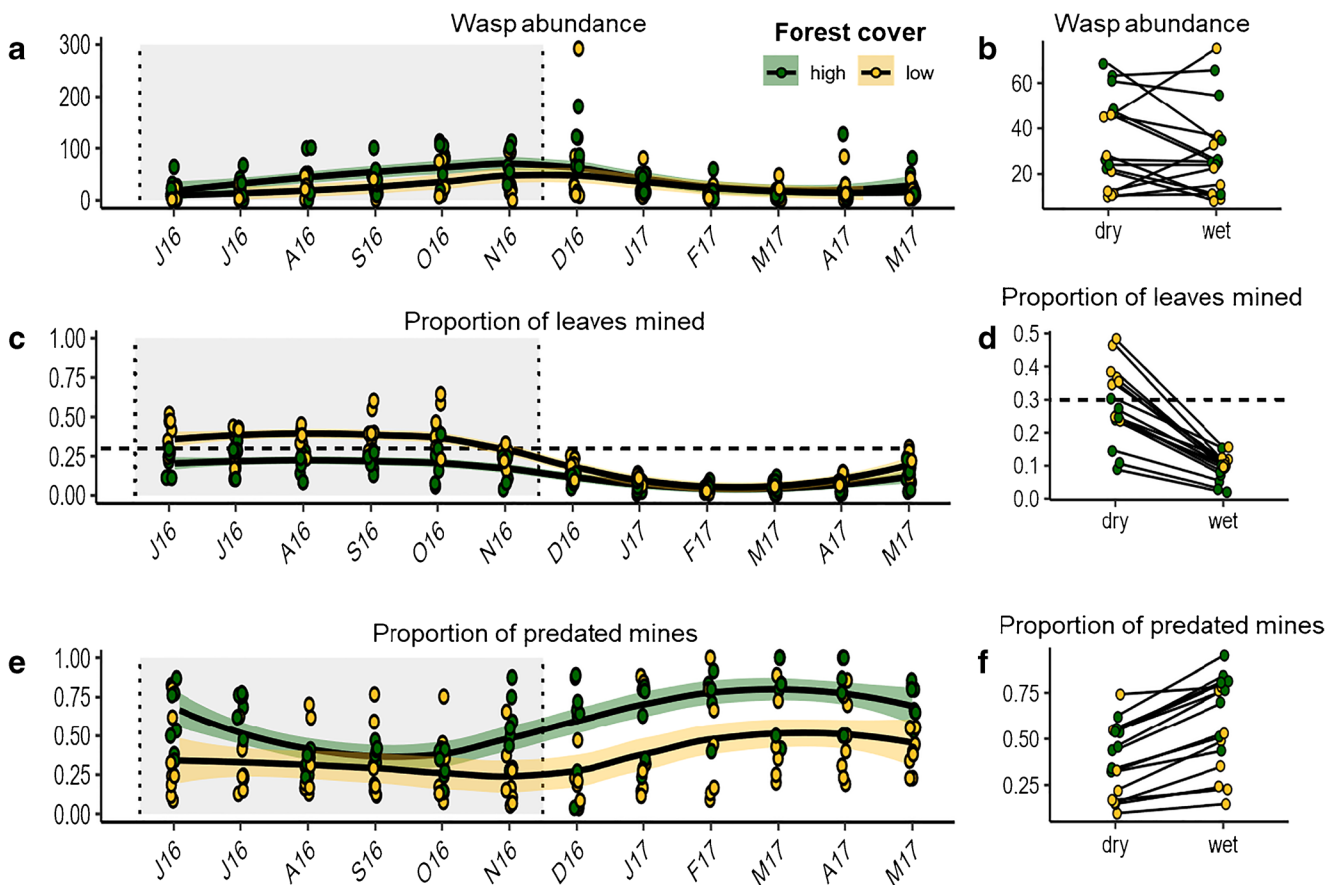


Fig. 2 Visualization of wasp abundance (a), proportion of mined leaves (*L. coffeella* abundance) (c), and proportion of preyed mines (biological control) (e) over 12 months from June 2016 (J16) to May 2017 (M17); and cumulative wasp abundance (b), *L. coffeella* abundance (d), and

biological control (f) in dry and wet seasons. Each point represents a measure taken from one of the 16 coffee plantations. In a, c, and e, the dry season is shaded in gray. The economic threshold of 30% coffee leaves mined is depicted as a dashed horizontal line in c and d

Landscape diversity, which increases with an increasing number of habitat types in the landscape, was calculated using the Shannon diversity index, which considers both the number of land use classes and proportional area of each land use type (McGarigal 2015). Edge density represents the area of all land use patches in the landscape divided by the square of the nearest edge-to-edge distance between the focal patch and all land use types located within a pre-determined distance from the focal patch (McGarigal 2015). Coffee cover and forest cover were negatively correlated (absolute Spearman's correlations $r_s > 0.60$; $P < 0.01$); thus, we excluded coffee cover from analyses to avoid multicollinearity.

2.4 Statistical analyses

We used generalized linear models to estimate the effects of local- and landscape-level variables on species richness and abundance of social wasps, which were fitted with the Poisson error structure. To estimate how local factors, landscape variables, and social wasp communities affect the proportion of mined leaves (*L. coffeella* abundance) and proportion of

preyed mines (biological control services), we used beta regressions, which are useful for models where the dependent variable is a continuous rate or proportion restricted to the standard unit interval (0, 1) (Cribari-Neto and Zeileis, 2010). For each dependent variable, spatial scale (i.e., buffer radius), and season (dry or wet), we analyzed 12 competing univariable models and a null model, which represented the absence of effects (Table 1).

The best models were identified using the Akaike information criterion (AIC; Burnham and Anderson 2002) with corrections for small samples. We used AICc weight (wAICc) and AICc delta (Δ AICc) to rank the models. The wAICc represents the weight of evidence in favor of a given model among competing models (Burnham and Anderson 2002). The Δ AICc 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). Models with significant model fit (P values < 0.05), wAICc ≥ 0.1 , and Δ AICc ≤ 2.5 were considered equally plausible at explaining the dependent variables (Medeiros et al. 2018). All analyses were performed in R version 3.5.2. We used the betareg function of the “betareg” package (Cribari-Neto and Zeileis, 2010) to fit

Table 3 Significant models to explain the species richness and abundance of social wasps, pest occurrence, and natural pest control in 16 coffee-producing landscapes in Southern Brazil in the dry and wet seasons. wAICc = evidence weight of the model. All selected models

Response variable	Season	Model	wAICc at different spatial scales (m)			
			250	500	750	1000
Wasp richness	Dry	Forest cover (+)	0.998***	0.999***	0.995***	0.997***
	Wet	Forest cover (+)	0.665**	0.625**	0.590**	0.615**
Wasp abundance	Dry	Forest cover (+)	0.997***	0.999***	0.996***	0.995***
	Wet	Forest cover (+)	0.999*	0.995*	-	-
<i>L. coffeella</i>	Dry	Forest cover (-)	0.870***	0.990***	0.902***	0.806***
	Wet	Temperature (+)	0.535**	0.563**	0.517**	0.560**
Biological control	Dry	Forest cover (+)	0.759***	0.355***	0.383***	0.413***
		Wasp abundance (+)	-	0.373***	0.357***	0.340***
	Wet	Forest cover (+)	0.921***	0.781***	0.916***	0.882***

* $P < 0.05$

** $P < 0.01$

*** $P < 0.001$

beta regression models, and the AICctab function of the bbmle package (Bolker 2010) for model selection.

3 Results and discussion

Local and landscape explanatory variables varied considerably among the 16 landscapes. There were 2–13 agrochemical applications (fertilizer, 0–3; herbicide, 0–4; fungicide, 0–4; insecticide, 0–3) per coffee plantation during the year. Forest cover within the 1000-m buffer varied from 3 to 60%, landscape diversity from 1.05 to 1.86, and edge density from 127 to 246.

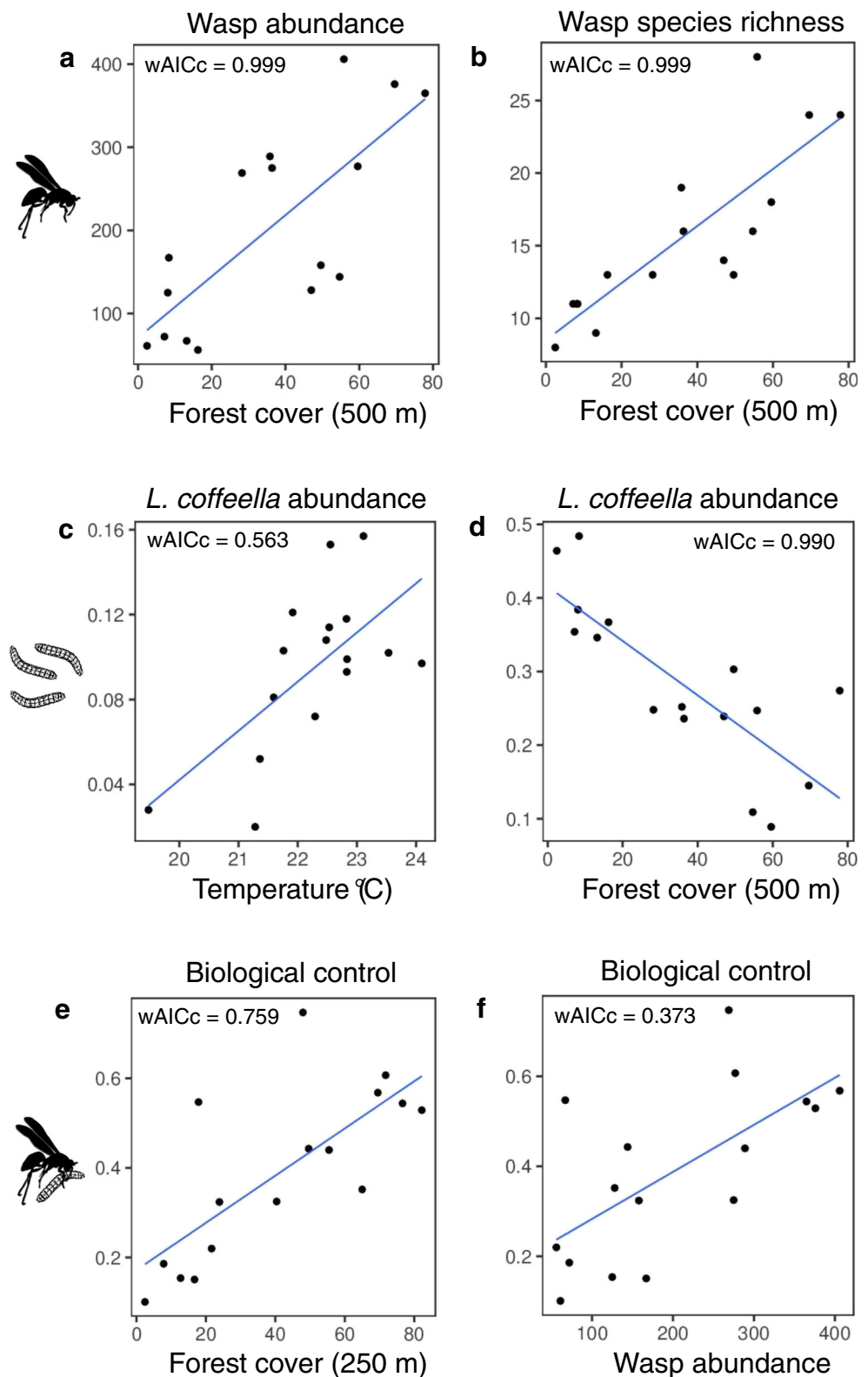
We collected a total of 6086 social wasps (Vespidae, Polistinae), representing 42 species distributed across 11 genera (Table 2). The most abundant wasp species in both seasons were *Agelaia multipicta* ($n = 1245$, 20.5% of all specimens) and *Agelaia vicina* ($n = 1197$, 19.7%). We collected 39 species and 3234 specimens of social wasps during the dry season, and 33 species and 2852 specimens during the wet season. Wasp species richness in dry and wet seasons was 9–29 and 9–21 species per landscape, respectively. Wasp abundance varied from 56 to 406 specimens during the dry season and from 49 to 458 specimens during the wet season (Fig. 2a, b). Species richness and abundance of social wasps were exclusively and positively associated with forest cover at multiple spatial scales (dry season wAICc ≥ 0.650 , wet season wAICc ≥ 0.463 ; Table 3 and Fig. 3a, b).

The habitat amount hypothesis suggests that species richness increases with increasing amount of habitat in the surrounding landscape independent of patch size and isolation (Fahrig 2013). This hypothesis seems to be true for social wasps in our study, which were positively correlated with forest cover irrespective of

had $\Delta\text{AICc} < 2.0$. The symbols – and + within parentheses indicate the direction of correlation between response variables and fixed effects at four spatial scales (250, 500, 750, and 1000 m)

landscape diversity and edge density as well as local factors such as microclimate and management intensity. Social wasps are central foragers and need to move continually between nesting and feeding habitats (Richter 2000). Wasps use odor or visual cues such as leaf damage to find prey, and benefit from high densities of Lepidoptera pests in several agroecosystems, including *L. coffeella* in Brazilian coffee plantations (Richter 2000; Pereira et al. 2007). Therefore, social wasps search for prey within coffee plantations (feeding habitats) but build their nests in forest remnants (Oliveira et al. 2017). Intensive management (e.g., pesticide applications, pruning, and harvest) in many coffee plantations results in high mortality rates of wasps and destruction of their nests within coffee plantations. Wasp nests found in close proximity to humans (either within crops or on human-built structures) are usually removed to prevent wasp stings. Moreover, coffee monocultures have a short mass flowering period, and frequent applications of herbicides prevent establishment of ruderal plants that provide floral resources and alternative prey for wasps. In contrast, forest remnants provide undisturbed nesting habitats and a constant supply of floral resources, prey, and fiber for building nests when these resources are not available in coffee plantations. Social wasps did not respond to pesticide usage, suggesting that wasp communities inside forest remnants may serve as a permanent reservoir for wasps found in adjacent coffee plantations, allowing rapid recolonization of crops after disturbance such as pesticide applications and nest removal by farmers. Indeed, monocultures often fail to provide a constant supply of resources for beneficial insects, leading biological control agents to rely heavily on adjacent non-crop habitats to obtain their ecological needs and recolonize adjacent crop matrix after disturbances (Heimoana et al. 2017).

Fig. 3 Best models and spatial scales to explain wasp abundance (a) and richness (b), *L. coffeella* abundance (c, d), and biological control (e, f) within 16 coffee plantations in southeastern Brazil during the dry season (June to November 2016) with the exception of the relationship between pest abundance and average temperature in the wet season for c. The responses of wasp richness and abundance, *L. coffeella* abundance, and biological control were similar across spatial scales in both climatic seasons. Numbers in parentheses represent spatial scales of effect in meters/radius. The best models and spatial scales were selected based on the highest evidence weight (wAICc) of the models (Table 2)



The number of mined leaves (*L. coffeella* abundance) varied considerably among the 16 landscapes and between seasons. There were 10–51% mined leaves during the dry season, which surpassed the economic threshold of 30% of mined

leaves (Reis et al. 2006) in seven coffee plantations (Fig. 2c, d). In the wet season, *L. coffeella* abundance generally declined, and only 2–16% of leaves were mined (Fig. 2c, d). The proportion of mined leaves decreased with increasing

forest cover at all spatial scales in the dry season ($wAICc \geq 0.806$; Table 3 and Fig. 3d) and increased with increasing temperature in the wet season ($wAICc \geq 0.517$; Table 3 and Fig. 3c). High forest cover means low cover of coffee, which is the only locally available host plant for this oligophagous leaf mining pest (Pierre 2011), thereby reducing recolonization potential between and within coffee plantations. Greater amounts of forest cover probably further reduce pest abundance by increasing natural enemy diversity and associated biological control services. Such generalized decline in *L. coffeella* abundance during the wet season can be associated with intense rainfall that is an important mortality factor of larvae (Pereira et al. 2007). Rainfall provokes the asphyxiation of larvae, and the positive response of *L. coffeella* to increasing temperature in the wet season can be associated with the fact that high temperatures enhance evaporation and can reduce water saturation in coffee leaves (Righi et al. 2013).

The proportion of preyed mines (biological control) ranged from 10 to 65% in the dry season and from 15 to 92% during the wet season (Fig. 2e, f). Biological control was positively associated with wasp abundance in the dry season ($wAICc \geq 0.340$; Table 3 and Fig. 3e) and with forest cover at multiple spatial scales (dry season $wAICc \geq 0.355$, Fig 3f; and wet season $wAICc \geq 0.781$, Table 3). High forest cover promoted high levels of biological control even in the wet season when wasp abundance was not correlated with the proportion of preyed mines. These findings indicate that social wasps are important natural enemies of *L. coffeella*, but not exclusive since predation marks on leaf mines are also related to other predatory insects such as ants and carabid beetles. Moreover, we probably underestimated biological control services because we did not account for parasitism that is also an important mechanism of biological control of *L. coffeella* in Brazilian coffee plantations (Pierre 2011).

Generalist natural enemies such as predatory insects affect food web dynamics in natural and agroecosystems by foraging among different habitats to exploit different resources that are spatially separated in changing landscapes (Tscharntke et al. 2012). Social wasp diversity and biological control in coffee plantations were regulated by forest cover at the landscape scale, suggesting that predatory insects are highly mobile and can provide biocontrol services at larger spatial scales covering several coffee plantations. 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). Although some previous studies detected thresholds where biological responses hinged on the amount of forest cover, our variables of interest were always linearly correlated, meaning that with more forest, there was higher wasp diversity and better provision of biological control services.

4 Conclusion

We provide the first empirical evidence that the amount of forest cover on the landscape increases social wasp diversity and biological control of a widespread economic pest in a Brazilian coffee-producing region. Thus, we recommend that agri-environment schemes in tropical 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. 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, service, nature and extent of non-agricultural land cover, and management practice (Tscharntke et al. 2016). 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 show that in some cases, there can be direct benefits to agricultural production derived from forested land in the wider landscape. A better understanding of how landscape structure and crop management mediate trade-offs between ecosystem services and disservices is crucial to aid regional planners in selecting appropriate spatial and temporal scales and policies in decision-making.

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Compliance with ethical standard

Conflict of interest The authors declare that they have no conflict of interest.

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