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Landscape structure shapes the diversity of beneficial insects in coffee producing landscapes

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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. Species richness and abundance of wasps, and bee richness were positively correlated with forest cover at multiple 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 variations in landscape diversity and edge density between landscapes resulted in flower fly species replacement suggesting that pairs of landscapes with high and low diversity of habitat types and edge density harbor different species. Such results indicate that initiatives for the conservation of beneficial insects in the Atlantic Forest biodiversity hotspot 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. Our findings can aid conservationists and policy makers to define priority actions for biodiversity conservation as well as the selection of appropriate spatial scales in landscape planning and management.

1. Introduction

Balancing sustainable food production and biodiversity conservation is one of the key global environmental challenges (Johnson et al., 2017). 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 (Klein et al., 2007; Geiger et al., 2010; Potts et al., 2010; Ollerton, 2017; Grab et al., 2018). Ecosystem services provided by beneficial insects afford approximately US$ 71.3 billion (2018 dollars, considering inflation) annually in the United States (Losey and Vaughan, 2006). Animal pollination services are responsible for 30% of global food production (Klein et al., 2007) contributing US

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$235–577 billion to global crop output (Potts et al., 2016), whereas biological control of crop pests has been valued at US$619/ha (2018 dollars) globally (Costanza et al., 1997).

Agricultural intensification encompasses the overuse of agrochemicals and the conversion of natural and semi-natural habitats (e.g., grasslands, forests, hedgerows, abandoned pastures) into expansive monocultures – a process known as landscape simplification (Meehan et al., 2011). Pesticide applications heighten both mortality rates and sublethal effects on insect physiology and behavior such as foraging, fecundity, sex ratio, and learning performance (Stapel et al., 2000; Desneux et al., 2007; Geiger et al., 2010). Landscape simplification negatively affects the capacity of a landscape to provide spatio-temporal insurance through landscape complementation and supplementation (Ouin et al., 2004; Tscharntke et al., 2012; Fahrig, 2017). According to Tscharntke et al. (2012), 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.

Landscape simplification reduces the amount and diversity of land cover types (compositional heterogeneity) including natural and semi-natural habitats (hereafter non-crop habitats) that play a key role for the maintenance of biodiversity in farmland, particularly invertebrates (Landis et al., 2000; Bianchi et al., 2006). 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., 2012). Moreover, non-crop 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). Landscape simplification also alters the spatial arrangement of crop and non-crop habitats in the landscape (configurational heterogeneity) resulting in low connectivity and spill-over opportunities between complementary habitats (Tscharntke et al., 2012; Gámez-Virués et al., 2015). Therefore, habitat loss and fragmentation reduce compositional and configurational landscape heterogeneity leading to the biotic homogenization, species loss and deterioration of ecosystem services (Tscharntke et al., 2012; Gámez-Virués et al., 2015).

The land sharing/land sparing dichotomy has stimulated debate on how to attenuate agricultural intensification in order to conciliate food production and conservation, but sharing/sparing strategies are not mutually exclusive and should work synergistically to avoid undesirable consequences for biodiversity (Fischer et al., 2014; Kremen, 2015). Only a combination of large protected areas (land sparing) surrounded by agroecological wildlife-friendly matrix (land sharing) can improve landscape heterogeneity resulting in high recolonization rates and recovery of degraded ecosystem functioning (Tscharntke et al., 2012; Kremen, 2015).

Studies from temperate and tropical regions indicate that agricultural landscapes with high compositional and configurational heterogeneity can support greater 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 Brazilian agricultural landscapes (Moreira et al., 2015; Saturni et al., 2016; Boscolo et al., 2017; Medeiros et al., 2018; Hipólito et al., 2018; Aristizabal and Metzger, 2019). Furthermore, most studies related to the effects of landscape simplification on biodiversity have focused on alpha diversity, whereas 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: spatial species turnover and nestedness, which 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 and Hernández, 2018) and agricultural intensification (Gabriel et al., 2006; Karp et al., 2012). Local-field scale studies (alpha diversity) identify only a subset of diversity, whereas beta diversity is a useful tool to quantify all components of diversity at multiple spatial scales (Gabriel et al., 2006). Integrating alpha and beta diversity could accommodate multiple ecosystem services at the landscape level (Frei et al., 2018; Rodríguez-Loinaz et al., 2014) and can aid decision makers and conservationists in selecting appropriate indicators and spatial scales for species conservation (Clough et al., 2007).

We aimed to understand how compositional and configurational landscape heterogeneity influences the diversity of beneficial insects in Brazilian coffee farms. Specifically, we tested whether alpha and beta diversity of beneficial insects change with forest cover and landscape diversity (compositional heterogeneity) and edge density (configurational heterogeneity). 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; Ricketts et al., 2004; Klein et al., 2003, 2008; Vergara and Badano, 2009; Saturni et al., 2016; Hipólito et al., 2018). 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; Tscharntke et al., 2005; Ricarte et al., 2011; Sommaggio and 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).

We expected that forest cover, landscape diversity and edge density regulate community composition of beneficial insects such that communities located in coffee monocultural landscapes support subsets of species-rich communities in more heterogeneous landscapes. We also expected that low levels of compositional and configurational heterogeneity result in community homogenization with a few crop-associated species replacing most species. Atlantic Forest is the dominant non-crop habitat in the study region and provides undisturbed nesting habitats for wasps (Souza et al., 2010, 2014, 2015) and bees (Samejima et al., 2004; Siqueira et al., 2012), and specific larval micro habitats for several flower fly species (Medeiros et al., 2018). Bees, wasps and flower flies can be found in both crop and non-crop habitats; consequently, high landscape diversity and edge density may improve the capacity of landscapes to provide multiple resources for beneficial insects via landscape complementation and supplementation. We provide novel information on the effects of landscape composition and configuration on the diversity of pollinator and natural enemy insects in Brazilian farmland.

2. Material and methods

2.1. 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 the 1 km radius is 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).

The study region experiences a subtropical highland climate

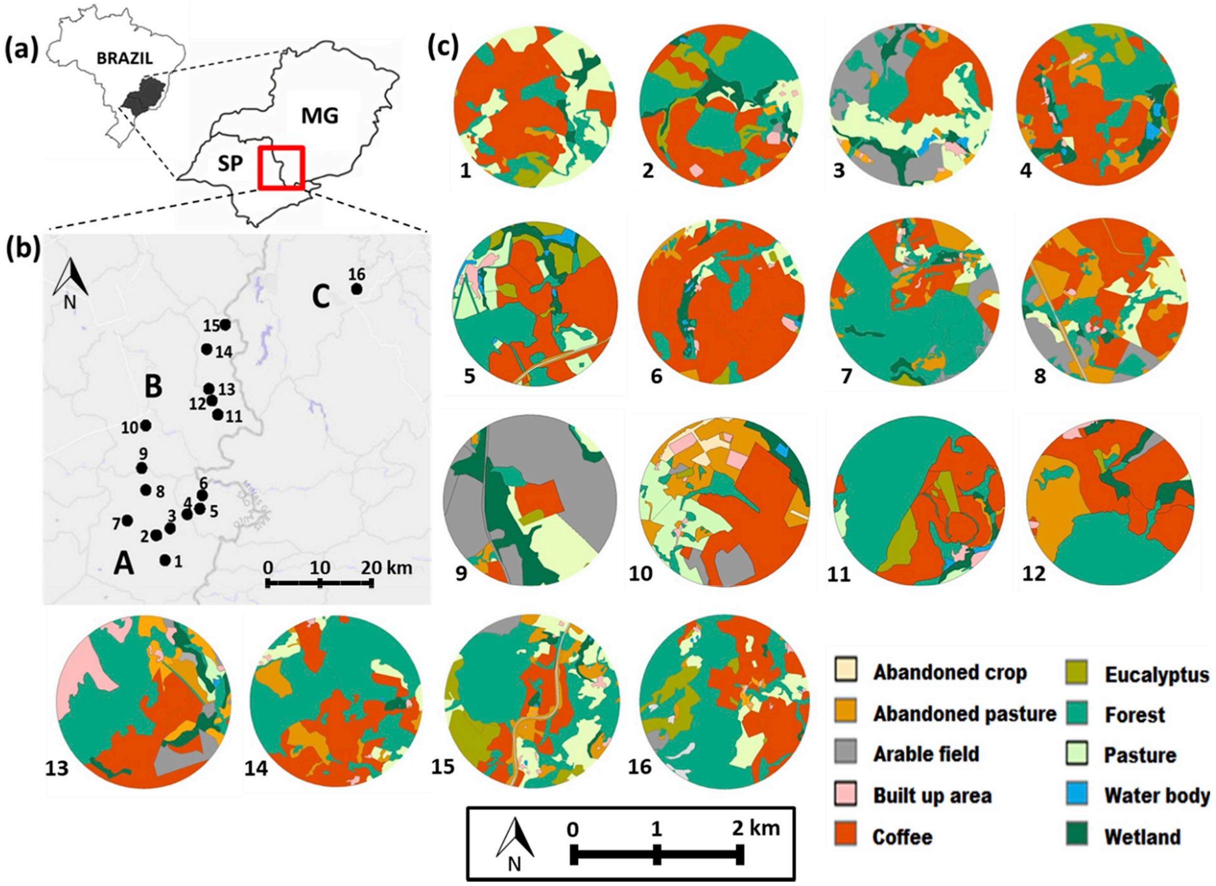

Fig. 1. Location of study sites in southeastern Brazil: a) Minas Gerais (MG) and São Paulo (SP) states in southeastern Brazil and the study region along the border of SP and MG, b) the sampled landscapes (black points) within the study region and c) land use maps of the studied landscape. In b) letters 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).

(Köppen climate classification, Cwb) characterized by rainy summers and dry winters with an average annual rainfall and temperature of 1478 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 (Muylaert et al., 2018), but only 26% remains in Brazil (Rezende et al., 2018). 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 small and isolated fragments composed of secondary vegetation due to intensive logging in past decades (local farmers, personal communication).

2.2. *Insect surveys*

We sampled wasps (Hymenoptera: Vespidae: Polistinae and Eumeninae), bees (Hymenoptera: Apoidea: Andrenidae, Apidae, Colletidae, Halictidae and Megachilidae) and flower flies (Diptera: Clyclorrhapha: 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 (see Supplementary material).

2.3. *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 proportion 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 (βsor) to estimate total beta diversity, which we partitioned into two components: turnover and nested. The Simpson dissimilarity index (βsim) was used to calculate the turnover component, while the difference between βsor and βsim estimated the nested component (βnes) 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 and Orme, 2012).

2.4. 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 1:5000 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 and landscape diversity (compositional heterogeneity) and edge density (configurational heterogeneity) 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 cover types) and the proportional area of each land cover type (McGarigal, 2015). Edge density is the sum of the lengths (m) of all true edge segments (boundaries between different land cover types) in the landscape, divided by the total landscape area (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.

2.5. Statistical analyses

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

Table 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 ~ % Forest cover
Landscape diversity	Y ~ Shannon diversity index
Edge density	Y ~ Edge density index
Null	Y ~ 1

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 9999 permutations (Anderson, 2017). 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 regressions as a way to exclude the influence of agrochemical usage on beta diversity components. We used multiple regressions 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).

3. 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; 8393 bees in 116 species and 73 genera (Apoidea: Andrenidae, Apidae, Colletidae, Halictidae and Megachilidae); and 4984 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 for wasps; 18 to 51 for bees and 12 to 26 for flower flies, and abundance varied from 167 to 1709 specimens for wasps; 203 to 784 for bees and 112 to 659 for 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) (Fig. 2); *Apis mellifera* Linnaeus, 1758 and *Trigona spinipes* (Fabricius, 1793) (25.5% and 31.2% of bee records) (Fig. 3); and *Toxomerus watsoni* (Curran, 1930) and *Dioprosopa clavata* (Fabricius, 1794) (25.6% and 38.6% of flower fly records) (Fig. 4).

Landscape explanatory variables differed considerably along the 16 landscapes. Within the radius of 1000 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. 5). 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.

Similarly to the alpha diversity, beta diversity, specifically the nested component of bees and wasps was influenced by forest cover at all spatial extents (Table 3; Fig. 6), wherein low forest cover resulted in species loss. 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. 6) suggesting that high variation in landscape diversity and edge density between landscapes resulted in species replacement. In contrast, the turnover component of bees and wasp, as well as nested component of flies were not explained by any predictor.

4. Discussion

Our hypotheses that low levels of forest cover, landscape diversity and edge density lead to both species loss and community homogenization was supported for bees, wasps and flower flies. However, these insect groups were not equally affected by compositional and configurational landscape heterogeneity suggesting that bees, wasps

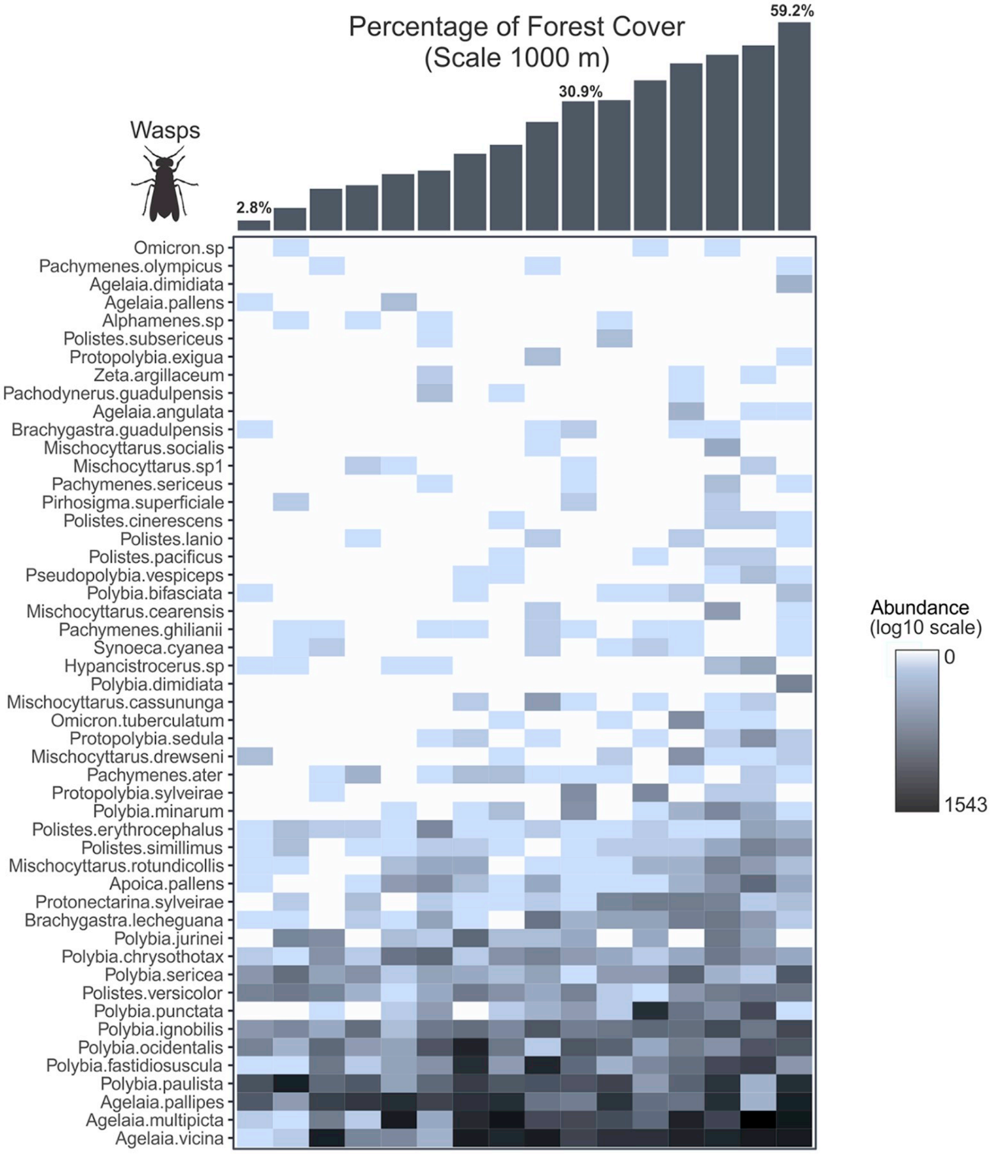

Fig. 2. Abundance of the 50 most abundant wasp species in coffee producing landscapes across the gradient of forest cover at the 1000 m scale. Species were sorted by abundance, which was log-transformed to improve visualization.

and flower flies perceive landscape structure differently. Moreover, beta diversity revealed important landscape effects on flower flies that were not detected by alpha diversity highlighting the relevance of a beta diversity approach to better understand the effects of landscape structure on community composition of beneficial insects in farmland.

4.1. *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 multiple agroecosystems including coffee plantations, where wasps provide important pest control services (Pereira et al., 2007; Androcioli et al., 2018) and bees act as major pollinators (Roubik, 2002). However, coffee monocultures present short mass-flowering periods and are constantly submitted to pesticide applications resulting in high mortality rates and sub-lethal effects (Stapel et al., 2000; Desneux et al., 2007; Geiger et al., 2010). In our study region, wasp nests found within coffee plantations or on human-built structures are usually removed to avoid stings. In contrast, Atlantic Forest remnants support high plant diversity (Murray-Smith et al., 2009) and act as an important perennial source of floral resources for beneficial insects including bees (Ramalho, 2004) and flower flies (de Sousa et al., 2014). Atlantic Forest remnants are also 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. Therefore, the long-term persistence of bees and wasps in coffee producing landscapes seems to depend on forest remnants with suitable nesting sites and floral resources that are critical for nest survival, dispersal 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 were responsible for an increase in coffee fruit set of 28%. Therefore, forest conservation and restoration are not only important for conserving biodiversity, but also for agriculture and ecosystem services.

Flower fly communities encompass a variety of larval functional groups (e.g., predator, endoparastoids, phytophagous, mycophagous,

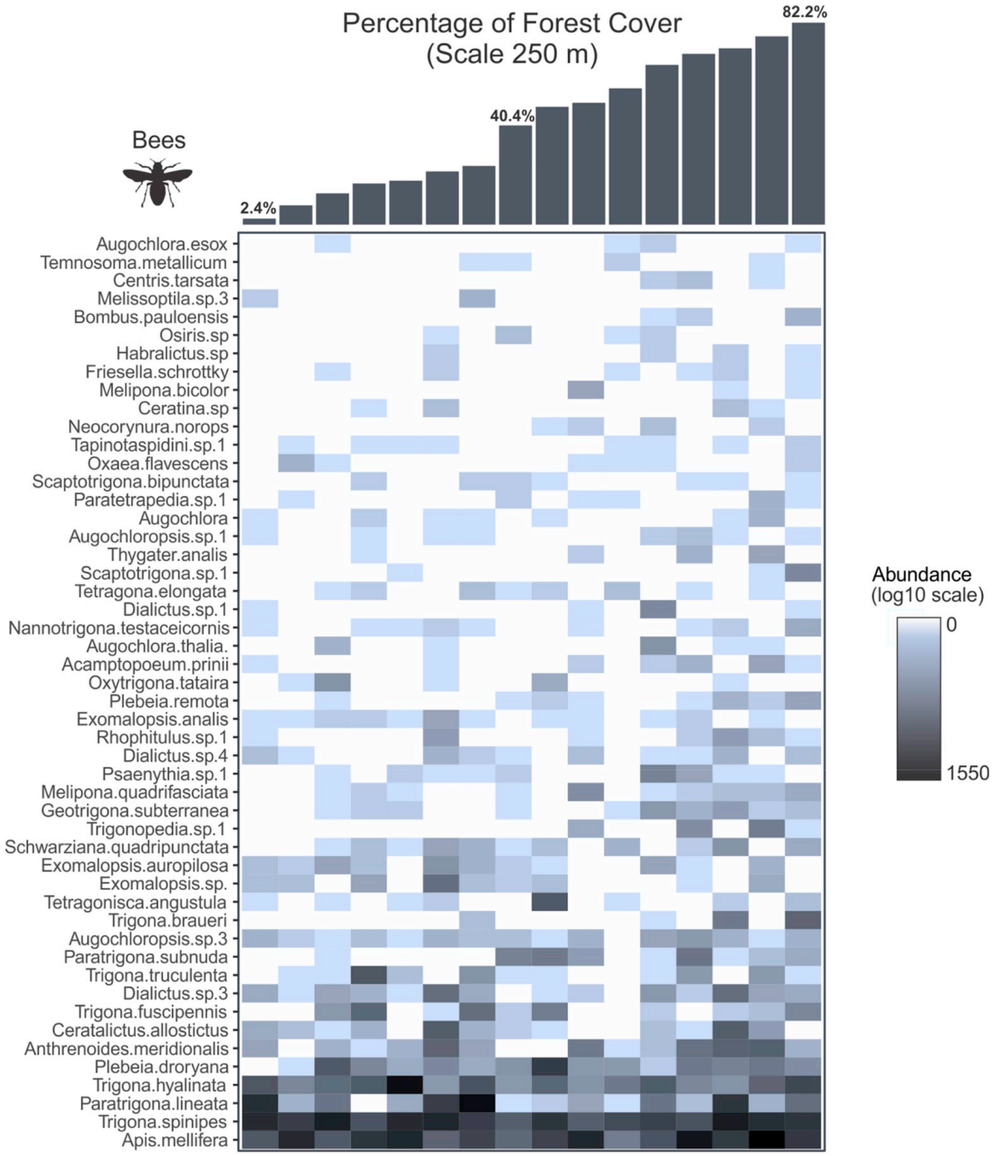

Fig. 3. Abundance of the 50 most abundant bee species in coffee producing landscapes across the gradient of forest cover at the 250 m scale. Species were sorted by abundance, which was log-transformed to improve visualization.

saprophagous) with specific habitat and food requirements that are not found in an agricultural matrix (Sommaggio, 1999; Sommaggio and Burgio, 2014; Jauker et al., 2009). Therefore, we expected that flower flies would also 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 and 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).

4.2. 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. These findings suggest that forest cover moderates dissimilarity of local communities of these beneficial insect groups, revealing species loss when forest cover is reduced within agricultural impoverished landscapes. The diversity of both bees and wasps is positively related to flower diversity (Tylianakis et al., 2006); therefore, coffee monocultural landscapes with low availability and diversity of floral resources 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. Thus, non-crop habitats like forest remnants act as key environments for the long-term maintenance of high pollinator and natural enemy diversity in farmland (Mandelik et al., 2012; González et al., 2015), providing complementary and constant supply of multiple resources that are available for short periods in crops (Tscharntke et al., 2012).

Although the alpha diversity of flower flies was not affected by any predictor, the turnover component of beta diversity was influenced by

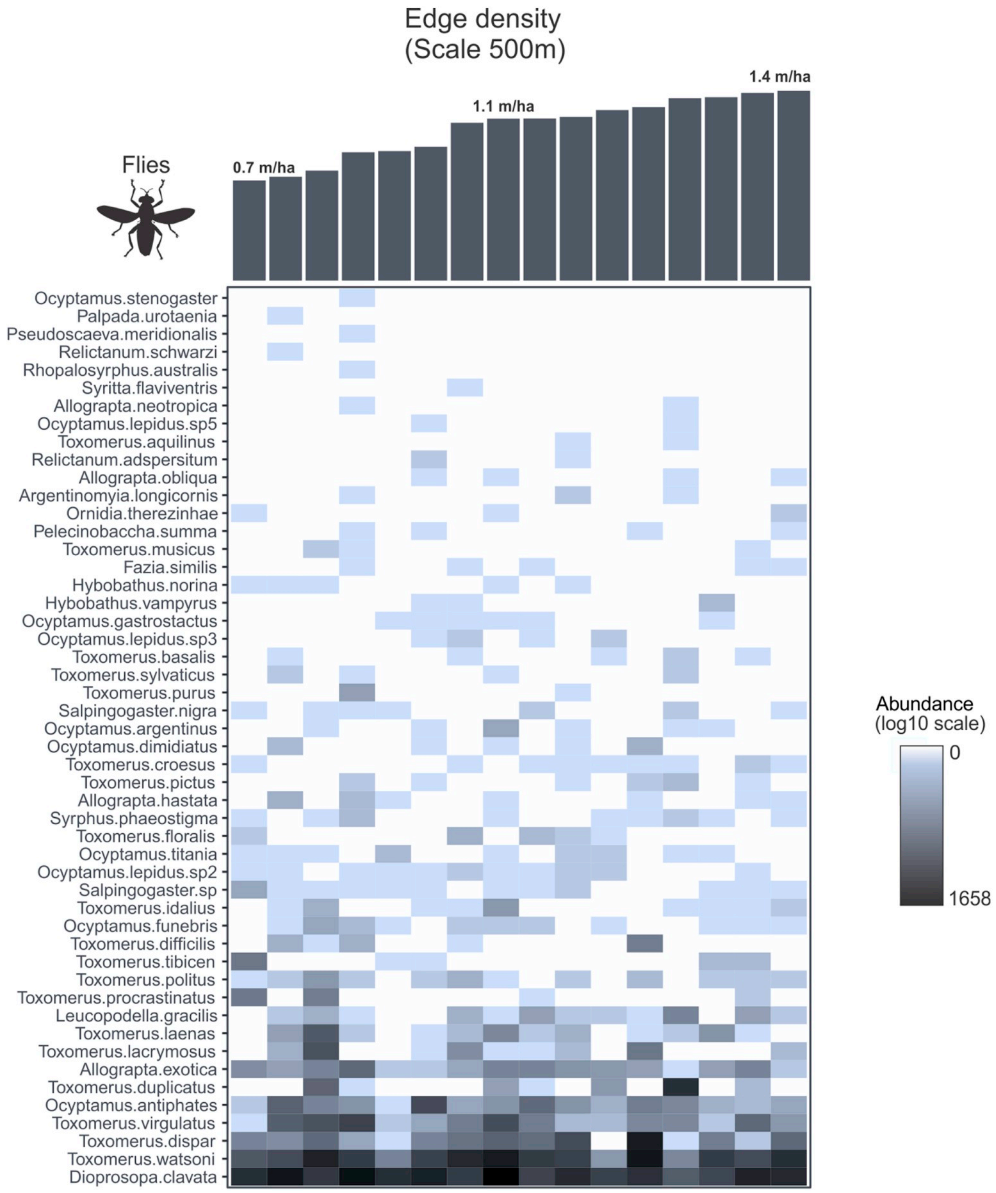

Fig. 4. Abundance of the 50 most abundant flower fly species in coffee producing landscapes across the gradient of edge density at the 500 m scale. Species were sorted by abundance, which was log-transformed to improve visualization.

Table 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 ΔAICc = 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
			wAICc	wAICc	wAICc	wAICc
Wasp	Richness	Forest cover (+)	0.937***	0.957***	0.970***	0.961***
	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	–	–	–	–

** $P < 0.01$.

*** $P < 0.001$.

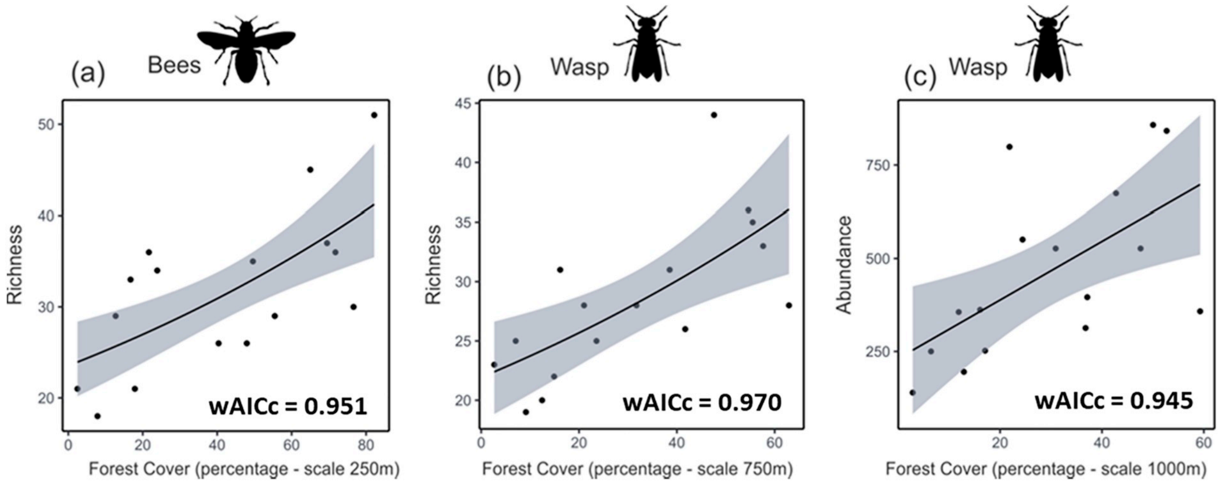

Fig. 5. The best-supported models and spatial scales (the highest wAICc value) of the relationship with forest cover for species richness of bees (a) and wasps (b), and abundance of wasps (c) in southeastern Brazil. Wasps and bees had similar responses at all spatial extents.

both compositional (landscape diversity) and configurational (edge density) landscape heterogeneity. Landscape heterogeneity is a key driver of flower flies communities (Andersson et al., 2013; Haenke et al., 2014; Larrieu et al., 2015; Villa et al., 2016), wherein species spillover between different crop and non-crop habitats to find a greater variety of resources. High variations in landscape diversity and edge density between landscapes resulted in species replacement suggesting that pairs of landscapes with high and low diversity of habitat types and edge density harbor different flower fly species. In the study region, low landscape diversity and edge density mean that the landscape is mainly composed of coffee monocultures and forest remnants, while high diverse landscapes can be composed of 10 different crop and non-crop habitat types. Our findings suggest that there are two distinct flowers fly community groups within the regional species pool which rely on different elements of landscape to access landscape complementation and supplementation. One community group relies on distinct habitat types and edge environments in high heterogeneous landscapes to gather all resources necessary to fulfill their needs. The other group seems to thrive in more homogeneous coffee-forest dominated landscapes, where species probably find a constant supply of floral resources and specific larval microhabitats within Atlantic Forest remnants (Souza et al., 2014; Medeiros et al., 2018).

4.3. *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 lead 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, the influence of landscape heterogeneity indicates that 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 flower flies (Speight and Castella, 2015) to undisturbed nesting sites for wasps and bees (Morato and 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) as well as forest and crop-associated species.

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

Table 3
Coefficients of determination (R^2) of the permutation test statistics of each explanatory variable and residuals of the redundancy analysis for explaining beta diversity components (Nested and Turnover) of wasps, bees and flower flies within coffee producing landscapes in southeastern Brazil.

Taxon	Component	Spatial extents	Forest cover	Edge density	Landscape diversity
Bees	Nested	250	12.44/0.45*	–	–
		500	10.29/0.42*	–	–
		750	11.50/0.45*	–	–
		1000	11/50/0.48*	–	–
Wasp	Nested	250	15.85/0.51***	–	–
		500	16.15/0.49**	–	–
		750	16.83/0.55***	–	–
		1000	14.76/0.53**	–	–
Flower flies	Turnover	250	–	2.38/0.11*	1.99/0.14**
		500	–	2.17/0.16**	–
		750	–	2.13/0.13*	–
		1000	–	2.13/0.13*	–

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

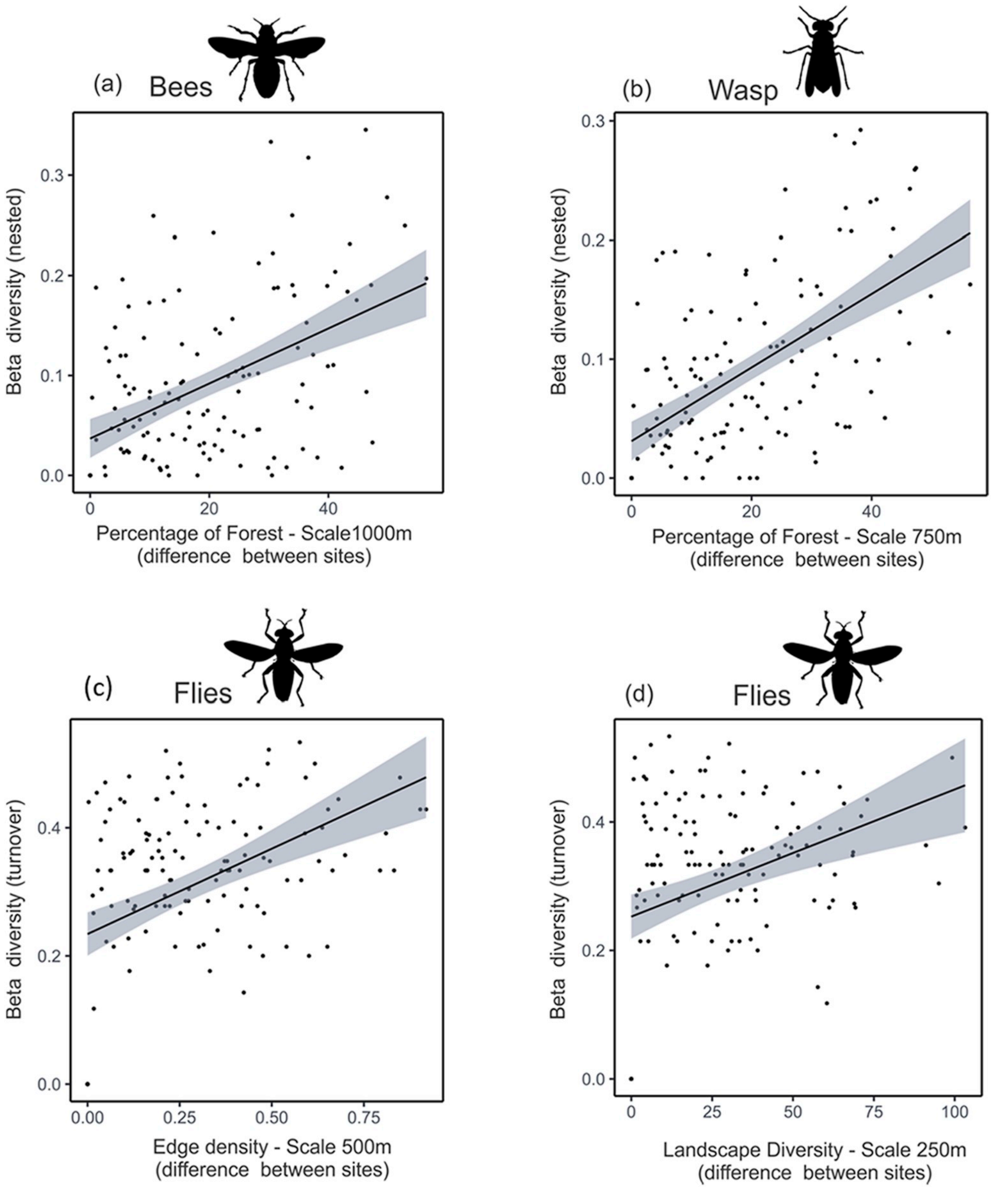

Fig. 6. The best-supported models and spatial scales for the nested component of beta diversity of bees (a) and wasps (b) versus the differences in forest cover (%) between paired landscapes and the turnover component of beta diversity of flower flies (c and d) versus the differences in edge density and landscape diversity between paired landscapes. Similar results were observed at all spatial extents.

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. Beta diversity detected important landscape effects on flower fly communities that were not captured by alpha diversity highlighting the importance of considering differences between communities and their drivers to better understand how landscape structure affects biodiversity. We also 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 synergistic implementation of sustainable agricultural practices and biodiversity conservation initiatives as well as the selection of appropriate spatial scales in landscape planning and management.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2019.07.038.

References

Albert, C., Aronson, J., Fürst, C., Opdam, P., 2014. Integrating ecosystem services in landscape planning: requirements, approaches, and impacts. Landsc. Ecol. 29, 1277–1285. https://doi.org/10.1007/s10980-014-0085-0.

Allen-Wardell, G., et al., 1998. The potential consequences of pollinator declines on the conservation of biodiversity and stability of crop yields. Conserv. Biol. 12, 8–17. https://doi.org/10.1046/j.1523-1739.1998.97154.x.

Altieri, M.A., 1999. The ecological role of biodiversity in agroe-cosystems. Agric. Ecosyst. Environ. 74, 19–31. https://doi.org/10.1016/S0167-8809(99)00028-6.

Anderson, M.J., 2017. Permutational Multivariate Analysis of Variance (PERMANOVA). Wiley StatsRef, pp. 1–15. https://doi.org/10.1002/9781118445112.stat07841. Statistics Reference Online.

Andersson, G.K., Birkhofer, K., Rundlöf, M., Smith, H.G., 2013. Landscape heterogeneity and farming practice alter the species composition and taxonomic breadth of pollinator communities. Basic Appl. Ecol. 14, 540–546. https://doi.org/10.1016/j.baae.2013.08.003.

Androcioli, H.G., Hoshino, T.H., Menezes Júnior, A.O., Morais, H., Bianco, R., Caramori, P.H., 2018. Coffee leaf miner incidence and its predation by wasps in coffee intercropped with rubber trees. Coffee Science 13, 389–400. https://doi.org/10.25186/cs.v13i3.1487.

Aristizabal, N., Metzger, J.P., 2019. Landscape structure regulates pest control provided by ants in sun coffee farms. J. Appl. Ecol. 56, 21–30. https://doi.org/10.1111/1365-2664.13283.

Barros, D.A., Guimarães, J.C.C., Pereira, J.A.A., Borges, L.A.C., Silva, R.A., Pereira, A.A.S., 2012. Characterization of the bauxite mining of the Poços de Caldas alkaline massif and its socio-environmental impacts. Rev. Esc. Minas. 65, 127–133. https://doi.org/10.1590/S0370-44672012000100018.

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Glob. Ecol. Biogeogr. 19, 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x.

Baselga, A., Orme, C.D.L., 2012. Betapart: an R package for the study of beta diversity. Methods Ecol. Evol. 3, 808–812. https://doi.org/10.1111/j.2041-210X.2012.00224.x.

Bianchi, F.J.J.A., Booij, C.J.H., Tscharntke, T., 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proc. R. Soc. Lond. B 273, 1715–1727. https://doi.org/10.1098/rspb.2006.3530.

Bolker, B.M., 2010. Bbmle: Tools for General Maximum Likelihood Estimation. The Comprehensive R Archive Network (CRAN), Vienna.

Bommarco, R., Kleijn, D., Potts, S.G., 2013. Ecological intensification: harnessing ecosystem services for food security. Trends Ecol. Evol. 28, 230–238. https://doi.org/10.1016/j.tree.2012.10.012.

Boscolo, D., Tokumoto, P.M., Ferreira, P.A., Ribeiro, J.W., Santos, J.S., 2017. Positive responses of flower visiting bees to landscape heterogeneity depend on functional connectivity levels. Perspect. Ecol. Conser. 15, 18–24. https://doi.org/10.1016/j.pecon.2017.03.002.

Burnham, K.P., Anderson, D.R., 1998. Model Selection and Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretical Approach, second ed. Springer-Verlag, New York.

Butchart, S.H.M., et al., 2010. Global biodiversity: indicators of recent declines. Science 328, 1164–1168. https://doi.org/10.1126/science.1187512.

Campbell, A.J., Wilby, A., Sutton, P., Wäckers, F.L., 2017. Do sown flower strips boost wild pollinator abundance and pollination services in a spring-flowering crop? A case study from UK cider apple orchards. Agric. Ecosyst. Environ. 239, 20–29. https://doi.org/10.1016/j.agee.2017.01.005.

Cipriani, H.N., Pereira, J.A.A., Silva, R.A., Freitas, S.G., Oliveira, L.T., 2011. Fire risk map for the Serra de São Domingos Municipal Park, Poços de Caldas, MG. Cerne 17, 77–83. https://doi.org/10.1590/S0104-77602011000100009.

Clough, Y., Holzschuh, A., Gabriel, D., Purtauf, T., Kleijn, D., Kruess, A., Steffan-Dewenter, I., Tscharntke, T., 2007. Alpha and beta diversity of arthropods and plants in organically and conventionally managed wheat fields. J. Appl. Ecol. 44, 804–812. https://doi.org/10.1111/j.1365-2664.2007.01294.x.

Costanza, R., et al., 1997. The value of the world's ecosystem services and natural capital. Nature 387, 253–260. https://www.nature.com/articles/387253a0.

da Cruz, J.D., Giannotti, E., Santos, G.M.M., Bichara, C.C., Rocha, A.A., 2006. Nest site selection and flying capacity of neotropical wasp *Angiopolybia pallens* (Hymenoptera: Vespidae) in the Atlantic Rain Forest, Bahia state, Brazil. Sociobiology 47, 739–749. https://repositorio.unesp.br/handle/11449/68916.

Danner, N., Molitor, A.M., Schiele, S., Haertel, S., Steffan-Dewenter, I., 2016. Season and landscape composition affect pollen foraging distances and habitat use of honey bees. Ecol. Appl. 26, 1920–1929. https://doi.org/10.1890/15-1840.1.

De Sousa, J.M.T., Marinoni, R.C., Marinoni, L., 2014. Open and disturbed habitats support higher diversity of Syrphidae (Diptera)? A case study during three year of sampling in a fragment of Araucaria forest in Southern Brazil. J. Insect Sci. 14, 1–8. https://doi.org/10.1093/jisesa/ieu098.

Desneux, N., Decourtye, A., Delpuech, J.M., 2007. The sublethal effects of pesticides on beneficial arthropods. Annu. Rev. Entomol. 52, 81–106. https://doi.org/10.1146/annurev.ento.52.110405.091440.

Eckberg, J.O., Peterson, J.A., Borsh, C.P., Kaser, J.M., Johnson, G.A., Luhman, J.C., Wyse, D.L., Heimpel, G.E., 2015. Field abundance and performance of hoverflies (Diptera: Syrphidae) on soybean aphid. Ann. Entomol. Soc. Am. 108, 26–34. https://doi.org/10.1093/aesa/sau009.

Fahrig, L., 2017. Ecological responses to habitat fragmentation Per Se. Annu. Rev. Ecol. Evol. Syst. 48, 1–23. https://doi.org/10.1146/annurev-ecolsys-110316-022612.

Fischer, J., et al., 2014. Land sparing versus land sharing: moving forward. Conserv. Lett. 7, 149–157. https://doi.org/10.1111/conl.12084.

Frei, B., Renard, D., Mitchell, M.E.G., Seufert, V., Chaplin-Kramer, R., Rhemtulla, J.M., Bennett, E.M., 2018. Bright spots in agricultural landscapes: identifying areas exceeding expectations for multifunctionality and biodiversity. J. Appl. Ecol. 55, 1–13. https://doi.org/10.1111/1365-2664.13191.

Gabriel, D., Roschewitz, I., Tscharntke, T., Thies, C., 2006. Beta diversity at different spatial scales: plant communities in organic and conventional agriculture. Ecol. Appl. 16, 2011–2021. https://doi.org/10.1890/1051-0761(2006)016[2011:BDADSS]2.0.CO;2.

Gámez-Virués, S., Perović, D.J., Gossner, M.M., Börschig, C., Blüthgen, N., de Jong, H., … Westphal, C., 2015. Landscape simplification filters species traits and drives biotic homogenization. Nat. Commun. 6 (1). https://doi.org/10.1038/ncomms9568.

Geiger, F., et al., 2010. Persistent negative effects of pesticides on biodiversityand biological control potential on European farmland. Basic Appl. Ecol. 11, 97–105. https://doi.org/10.1016/j.baae.2009.12.001.

González, E., Salvo, A., Valladares, G., 2015. Sharing enemies: evidence of forest contribution to natural enemy communities in crops, at different spatial scales. Insect Conserv. Divers. 8, 359–366. https://doi.org/10.1111/icad.12117.

González, E., Salvo, A., Defagó, M.T., Valladares, G., 2016. A moveable feast: insects moving at the forest-crop interface are affected by crop phenology and the amount of forest in the landscape. PLoS One 11, e0158836. https://doi.org/10.1371/journal.pone.0158836.

Grab, H., Poveda, K., Danforth, B., Loeb, G., 2018. Landscape context shifts the balance of costs and benefits from wildflower borders on multiple ecosystem services. Proc. R. Soc. Lond. B 285. https://doi.org/10.1098/rspb.2018.1102.

Haenke, S., Scheid, B., Schaefer, M., Tscharntke, T., Thies, C., 2009. Increasing syrphid fly diversity and density in sown flower strips within simple vs. complex landscapes. J. Appl. Ecol. 46, 1106–1114. https://doi.org/10.1111/j.1365-2664.2009.01685.x.

Haenke, S., Kovács-Hostyánszki, A., Fründ, J., Batáry, P., Jauker, B., Tscharntke, T., Holzschuh, A., 2014. Landscape configuration of crops and hedgerows drives local syrphid fly abundance. J. Appl. Ecol. 51, 505–513. https://doi.org/10.1111/1365-2664.12221.

Hipólito, J., Boscolo, D., Viana, B.F., 2018. Landscape and crop management strategies to conserve pollination services and increase yields in tropical coffee farms. Agric. Ecosyst. Environ. 256, 218–225. https://doi.org/10.1016/j.agee.2017.09.038.

Hurvich, C.M., Tsai, C.L., 1989. Regression and time series model selection in small samples. Biometrika. 76, 297–307. https://doi.org/10.1093/biomet/76.2.297.

Inouye, D., Larson, B.M.H., Ssymank, A., Kevan, P.G., 2015. Flies and flowers III: ecology of foraging and pollination. J. Pollinat. Ecol. 16, 115–133. https://doi.org/10.26786/1920-7603%282015%2915.

Jauker, F., Diekötter, T., Schwarzbach, F., Wolters, V., 2009. Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and flower flies to landscape structure and distance from main habitat. Landsc. Ecol. 24, 547–555. https://doi.org/10.1007/s10980-009-9331-2.

Johnson, C.N., Balmford, A., Brook, B.W., Buettel, J.C., Galetti, M., Guangchun, L., Wilmshurst, J.M., 2017. Biodiversity losses and conservation responses in the Anthropocene. Science 356, 270–275. https://doi.org/10.1126/science.aam9317.

Karp, D.S., Rominger, A.J., Ranganathan, J.Z.J., Ehrlich, P.R., Daily, G.D., 2012. Intensive agriculture erodes β-diversity at large scales. Ecol. Lett. 15, 963–970. https://doi.org/10.1111/j.1461-0248.2012.01815.x.

Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., … Kremen, C., 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. Ecol. Lett. 16, 584–599. https://doi.org/10.1111/ele.12082.

Kleijn, D., van Langevelde, F., 2006. Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. Basic Appl. Ecol. 7, 201–214. https://doi.org/10.1016/j.baae.2005.07.011.

Kleijn, D., et al., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, I., … Potts, S.G., 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. Nat. Commun. 6, 1–8. https://www.nature.com/articles/ncomms8414.

Klein, A.M., Steffan-Dewenter, I., Tscharntke, T., 2003. Fruit set of highland coffee increases with the diversity of pollinating bees. Proc. R. Soc. Lond. B 270, 955–961. https://doi.org/10.1098/rspb.2002.2306.

Klein, A.M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunnigham, S., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. Proc. R. Soc. Lond. B 274, 303–313. https://doi.org/10.1098/rspb.2006.3721.

Klein, A.M., Cunningham, S.A., Bos, M., Steffan-Dewenter, I., 2008. Advances in pollination ecology from tropical plantation crops. Ecology 89, 935–943. https://doi.org/10.1890/07-0088.1.

Kratschmer, S., Pachinger, B., Schwantzer, M., Paredes, D., Guernion, M., … Winter, S., 2018. Tillage intensity or landscape features: what matters most for wild bee diversity in vineyards? Agric. Ecosyst. Environ. 266, 142–152. https://doi.org/10.1016/j.agee.2018.07.018.

Kremen, C., 2015. Reframing the land-sparing/land-sharing debate for biodiversity conservation. Ann. N. Y. Acad. Sci. 1355, 52–76. https://doi.org/10.1111/nyas.12845.

Kremen, C., Williams, N.M., Thorp, R.W., 2002. Crop pollination from native bees at risk from agricultural intensification. PNAS 99, 16812–16816. https://doi.org/10.1073/

pnas.262413599.

Landis, D.A., Wratten, S.D., Gurr, G.M., 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. Annu. Rev. Entomol. 45, 175–201. https://doi.org/10.1146/annurev.ento.45.1.175.

Landis, D.A., Gardiner, M.M., van der Werf, W., Swinton, S.M., 2008. Increasing corn for biofuel production reduces biocontrol services in agricultural landscapes. PNAS 105, 552–557. https://doi.org/10.1073/pnas.0804951106.

LARG - Landscape and Resource Management Research Group, 2006. V-LATE—Vector-Based Landscape Analysis Tools Extension. LARG. http://www.geo.sbg.ac.at/larg/vlate.htm, Accessed date: 13 April 2016.

Larrieu, L., Cabanettes, A., Sarthou, J.P., 2015. Hoverfly (Diptera: Syrphidae) richness and abundance vary with forest stand heterogeneity: preliminary evidence from a montane beech fir forest. Eur. J. Entomol. 112, 755–769. https://doi.org/10.14411/eje.2015.083.

Lichstein, J.W., 2007. Multiple regression on distance matrices: a multivariate spatial analysis tool. Plant Ecol. 188, 117–131. https://doi.org/10.1007/s11258-006-9126-3.

Locher, A.G., Togni, O.C., Silveira, O.T., Giannotti, E., 2014. The social wasp fauna of a riparian forest in Southeastern Brazil (Hymenoptera, Vespidae). Sociobiology 61, 225–233. https://doi.org/10.13102/sociobiology.v61i2.225-233.

Losey, J.E., Vaughan, M., 2006. The economic value of ecological services provided by insects. BioScience 56, 311–323. https://doi.org/10.1641/0006-3568(2006)56[311:TEVOES]2.0.CO;2.

Lucas, A., Bull, J.C., de Vere, N., Neyland, P.J., Forman, D.W., 2017. Flower resource and land management drives hoverfly communities and bee abundance in seminatural and agricultural grasslands. Ecol. Evol. 7, 8073–8086. https://doi.org/10.1002/ece3.3303.

Lucas, A., Bodger, O., Brosi, B.J., Ford, C.R., Forman, D.W., Greig, C., de Vere, N., 2018. Floral resource partitioning by individuals within generalised hoverfly pollination networks revealed by DNA metabarcoding. Sci. Rep. 8, 5133. https://www.nature.com/articles/s41598-018-23103-0.

Mandelik, Y., Winfree, R., Neeson, T., Kremen, C., 2012. Complementary habitat use by wild bees in agro-natural landscapes. Ecol. Appl. 22, 1535–1546. https://doi.org/10.1890/11-1299.1.

McGarigal, K., 2015. Fragstats help. http://www.umass.edu/landeco/research/fragstats/documents/fragstats_documents.html, Accessed date: 24 July 2018.

Medeiros, H.R., Hoshino, A.T., Ribeiro, M.C., Morales, M.N., Martello, F., Neto, O.C.P., Carstensen, D.W., Menezes Jr., A.O., 2018. Non-crop habitats modulate alpha and beta diversity of flower flies (Diptera, Syrphidae) in Brazilian agricultural landscapes. Biodivers. Conserv. 27, 1309–1326. https://doi.org/10.1007/s10531-017-1495-5.

Meehan, T.D., Werling, B.P., Landis, D.A., Gratton, C., 2011. Agricultural landscape simplification and insecticide use in the Midwestern United States. PNAS 108, 11500–11505. https://doi.org/10.1073/pnas.1100751108.

Meyer, B., Jauker, F., Steffan-Dewenter, I., 2009. Contrasting resource-dependent responses of flowerfly richness and density to landscape structure. Basic Appl. Ecol. 10, 178–186. https://doi.org/10.1016/j.baae.2008.01.001.

Morato, E.F., Martins, R.P., 2006. An overview of proximate factors affecting the nesting behaviour of solitary wasps and bees (Hymenoptera: Aculeata) in preexisting cavities in wood. Neotrop. Entomol. 35, 285–298. https://doi.org/10.1590/S1519-566X2006000300001.

Moreira, E.F., Boscolo, D., Viana, B.F., 2015. Spatial heterogeneity regulates plant-pollinator networks across multiple landscape scales. PLoS One 10, e0123628. https://doi.org/10.1371/journal.pone.0123628.

Mori, A.S., Isbell, F., Seidl, R., 2018. β-Diversity, community assembly, and ecosystem functioning. Trends Ecol. Evol. 33, 549–564. https://doi.org/10.1016/j.tree.2018.04.012.

Murray-Smith, C., Brummitt, N.A., Oliveira-Filho, A.T., Bachman, S., Moat, J., Lughadha, E.M.N., Lucas, E.J., 2009. Plant diversity hotspots in the Atlantic coastal forests of Brazil. Conserv. Biol. 23, 151–163. https://doi.org/10.1111/j.1523-1739.2008.01075.x.

Muylaert, R.L., Vancine, M.H., Bernardo, R., Oshima, J.E.F., Sobral-Souza, T., Tonetti, V.R., Niebuhr, B.B.S., Ribeiro, M.C., 2018. Uma nota sobre os limites territoriais da mata atlântica. Oecologia Australis 22, 302–311. https://doi.org/10.4257/oeco.2018.2203.09.

Nelson, E.H., Hogg, B.N., Mills, N.J., Daane, K.M., 2012. Syrphid flies suppress lettuce aphids. BioControl 57, 819–826. https://doi.org/10.1007/s10526-012-9457-z.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M.H.H., 2007. The vegan package. Community ecology package. 10, 631–637. https://cran.r-project.org/web/packages/vegan/vegan.pdf.

Ollerton, J., 2017. Pollinator diversity: distribution, ecological function, and conservation. Annu. Rev. Ecol. Evol. Syst. 48, 353–376. https://doi.org/10.1146/annurev-ecolsys-110316-022919.

Ouin, A., Aviron, S., Dover, J., Burel, F., 2004. Complementation/supplementation of resources for butterflies in agricultural landscapes. Agric. Ecosyst. Environ. 103, 473–479. https://doi.org/10.1016/j.agee.2003.11.003.

Palacios-Agundez, I., Fernandez, B., Rodríguez-Loinaz, G., Pena, L., Amezaga, I., Alday, J.G., Casado-Arzuaga, I., Madariaga, I., Arana, X., Onaindia, O., 2014. Integrating stakeholders' demands and scientific knowledge for the inclusion of ecosystem services in landscape planning. Landsc. Ecol. 29, 1423–1433. https://doi.org/10.1007/s10980-014-0085-0.

Pereira, E.J.G., Picanço, M.C., Bacci, L., Crespo, A.L.B., Guedes, R.N.C., 2007. Seasonal mortality factors of the coffee leaf miner, *Leucoptera coffeella*. Bull. Entomol. Res. 97, 421–432. https://doi.org/10.1017/S0007485307005202.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. Trends Ecol. Evol. 25, 345–353. https://doi.org/10.1016/j.tree.2010.01.007.

Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D., Dicks, L.V., Garibaldi, L.A., Hill, R., Settele, J., Vanbergen, A.J., 2016. Safeguarding pollinators and their values to human well-being. Nature 540, 220–229. https://www.nature.com/articles/nature20588.

R Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Ramalho, M., 2004. Stingless bees and mass flowering trees in the canopy of Atlantic Forest: a tight relationship. Acta Bot. Bras. 18, 37–47. https://doi.org/10.1590/S0102-33062004000100005.

Rempel, R.S., Kaukinen, D., Carr, A.P., 2012. Patch Analyst and Patch Grid. Ontario Ministry of Natural Resources, Thunder Bay.

Rezende, C.L., Scarano, F.R., Assad, E.D., Joly, C.A., Metzger, J.P., Strassburg, B.N.B., Tabarelli, M., Fonseca, G.A., Mittermeier, R.A., 2018. From hotspot to hopespot: an opportunity for the Brazilian Atlantic Forest. Perspect. Ecol. Conser. 16, 208–214. https://doi.org/10.1016/j.pecon.2018.10.002.

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J., Hirota, M.M., 2009. The Brazilian Atlantic forest: how much is left, and how is the remaining forest distributed? Implications for conservation. Biol. Conserv. 142, 1141–1153. https://doi.org/10.1016/j.biocon.2009.02.021.

Ricarte, A., Marcos-García, M.A., Moreno, C.E., 2011. Assessing the effects of vegetation type on hoverfly (Diptera: Syrphidae) diversity in a Mediterranean landscape: implications for conservation. J. Insect Conserv. 15, 865–877. https://doi.org/10.1007/s10841-011-9384-9.

Richter, M.R., 2000. Social wasp (Hymenoptera: Vespidae) foraging behavior. Annu. Rev. Entomol. 45, 121–150. https://doi.org/10.1146/annurev.ento.45.1.121.

Ricketts, T.H., Daily, G.C., Ehrlich, P.R., Michener, C.D., 2004. Economic value of tropical forest to coffee production. PNAS 101, 12579–12582. https://doi.org/10.1073/pnas.0405147101.

Rodríguez-Loinaz, G., Alday, J.G., Onaindia, M., 2014. Multiple ecosystem services landscape index: a tool for multifunctional landscapes conservation. J. Environ. Manag. 147, 152–163. https://doi.org/10.1016/j.jenvman.2014.09.001.

Rojo, S., Gilbert, F., Marcos-García, M.A., Nieto, J.M., Mier, M.P., 2003. A World Review of Predatory Flower Flies (Diptera, Syrphidae: Syrphinae) and Their Prey. Cibio ediciones, Alicante.

Roubik, D.W., 2002. The value of bees to the coffee harvest. Nature 417, 708. https://www.nature.com/articles/417708a.

Samejima, H., Marzuki, M., Nagamitsu, T., Nakasizuka, T., 2004. The effects of human disturbance on a stingless bee community in a tropical rainforest. Biol. Conserv. 120, 577–587. https://doi.org/10.1016/j.biocon.2004.03.030.

Santos, G.M.M., Santana-Reis, V.P.G., Resende, J.J., De Marco, P., Bichara Filho, C.C., 2000. Flying capacity of swarm founding wasp *Polybia occidentalis* Oliver, 1791 (Hymenoptera, Vespidae). Rev. Bras. de Zoocienc 2, 33–39. http://ojs2.ufjf.emnuvens.com.br/zoociencias/article/view/24263/13532.

Saturni, F.T., Jaffé, R., Metzger, J.P., 2016. Landscape structure influences bee community and coffee pollination at different spatial scales. Agric. Ecosyst. Environ. 235, 1–12. https://doi.org/10.1016/j.agee.2016.10.008.

Schmidt, M.H., Thewes, U., Thies, C., Tscharntke, T., 2004. Aphid suppression by natural enemies in mulched cereals. Entomol. Exp. Appl. 113, 87–93. https://doi.org/10.1111/j.0013-8703.2004.00205.x.

Seppä, P., Queller, D.C., Strassmann, J.E., 2002. Reproduction in foundress associations of the social wasp, *Polistes carolina*: conventions, competition, and skew. Behav. Ecol. 13, 531–542. https://doi.org/10.1093/beheco/13.4.531.

Silva, P.G., Hernández, M.I.M., 2018. Spatial but not temporal dung beetle β-diversity components are scale dependent in mainland island scenario. Austral Ecol. 43, 915–925. https://doi.org/10.1111/aec.12641.

Silva, D.P., Nogueira, D.S., De Marco Jr., P., 2017. Contrasting patterns in solitary and eusocial bees while responding to landscape features in the Brazilian Cerrado: a multiscaled perspective. Neotrop. Entomol. 46, 264–274. https://doi.org/10.1007/s13744-016-0461-3.

Siqueira, E.N.L., Bartelli, B.F., Nascimento, A.R.T., Nogueira-Ferreira, F.H., 2012. Diversity and nesting substrates of stingless bees (Hymenoptera, Meliponina) in a forest remnant. Psyche 2012, 1–9. https://doi.org/10.1155/2012/370895.

Socolar, J.B., Gilroy, J.J., Kunin, W.E., Edwards, D.P., 2016. How should beta-diversity inform biodiversity conservation? Trends Ecol. Evol. 31, 67–80. https://doi.org/10.1016/j.tree.2015.11.005.

Sommaggio, D., 1999. Syrphidae: can they be used as environmental bioindicators? Agric. Ecosyst. Environ. 74, 343–356. https://doi.org/10.1016/S0167-8809(99)00042-0.

Sommaggio, D., Burgio, G., 2014. The use of Syrphidae as functional bioindicator to compare vineyards with different managements. B. Insectol. 67, 147–156. https://efsa.onlinelibrary.wiley.com/doi/pdf/10.2903/j.efsa.2015.3996.

Souza, M.M., Louzada, J., Serrão, J.E., Zanuncio, J.C., 2010. Social wasps (Hymenoptera: Vespidae) as indicators of conservation degree of riparian forests in Southeast Brazil. Sociobiology 56, 387–396. https://www.researchgate.net/publication/261833422.

Souza, M.M., Pires, E.P., Elpino-Campos, A., Louzada, J.N.C., 2014. Nesting of social wasps (Hymenoptera: Vespidae) in a riparian forest of rio das Mortes in southeastern Brazil. Acta Sci. Biol. Sci. 36, 189–196. https://doi.org/10.4025/actascibiolsci.v36i2.21460.

Souza, M.M., Pires, E.P., Silva-Filho, R., Ladeira, T.E., 2015. Community of social wasps (Hymenoptera: Vespidae) in areas of semideciduous seasonal montane forest. Sociobiology 62, 598–603. https://doi.org/10.13102/sociobiology.v62i4.445.

Speight, M.C.D., Castella, E., 2015. StN Database: Content and Glossary of Terms, 2015. Syrph the Net, the Database of European Syrphidae. Syrph the Net publications, Dublin.

Stapel, J.O., Cortesero, A.M., Lewis, W.J., 2000. Disruptive sublethal effects of insecticides on biological control: altered foraging ability and life span of a parasitoid after feeding on extrafloral nectar of cotton treated with systemic insecticides. Biol.

Control 17, 243–249. https://doi.org/10.1006/bcon.1999.0795.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. Ecol. Lett. 8, 857–874. https://doi.org/10.1111/j.1461-0248.2005.00782.x.

Tscharntke, T., et al., 2012. Landscape moderation of biodiversity patterns and processes—eight hypotheses. Biol. Rev. 87, 661–685. https://doi.org/10.1111/j.1469-185X.2011.00216.x.

Tylianakis, J.M., Klein, A.M., Lozada, T., Tscharntke, T., 2006. Spatial scale of observation affects α, β and γ diversity of cavity-nesting bees and wasps across a tropical land-use gradient. J. Biogeogr 33, 1295–1304. https://doi.org/10.1111/j.1365-2699.2006.01493.x.

Vergara, C.H., Badano, E.I., 2009. Pollinator diversity increases fruit production in Mexican coffee plantations: the importance of rustic management systems. Agric. Ecosyst. Environ. 129, 117–123. https://doi.org/10.1016/j.agee.2008.08.001.

Villa, M., Santos, S.A., Marrão, R., Pinheiro, L.A., López-Saez, J.A., Mexia, A., Pereira, J.A., 2016. Syrphids feed on multiple patches in heterogeneous agricultural landscapes during the autumn season, a period of food scarcity. Agric. Ecosyst. Environ. 233, 262–269. https://doi.org/10.1016/j.agee.2016.09.014.