



RESEARCH ARTICLE

# Forest proximity rather than local forest cover affects bee diversity and coffee pollination services

Adrian González-Chaves · Rodolfo Jaffé · Jean Paul Metzger ·  
Astrid de M. P. Kleinert

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## Abstract

**Context** As agricultural demands for land continues to expand, strategies are urgently needed to balance agricultural production with biodiversity conservation and ecosystem service provision in agricultural landscapes.

**Objectives** We used a factorial landscape design to assess the relative contributions of forest proximity and local forest cover to bee diversity and the provision of coffee pollination services.

**Methods** We quantified bee diversity and fruit set in 24 sun-grown coffee fields in Southeast Region of Brazil that were selected following a factorial sampling design to test the independent effects of local forest cover (in a radius of 400 m) and proximity to forest fragments. To assess the impact of landscape simplification, we also evaluated local coffee cover.

**Results** Bee richness and abundance were higher in the proximity of forest fragments, but only bee abundance decreased when the coffee cover dominated the surrounding landscapes. Coffee fruit set was 16% higher overall with bee visitations compared with bee exclusion and increased to 20% when coffee bushes were near forest fragments, and the coffee cover was low. Surprisingly, local forest cover did not affect the bee community or coffee fruit set.

**Conclusion** Our results provide clear evidence that the proximity of coffee crops to forest fragments can affect the abundance and richness of bees visiting the coffee flowers and thereby facilitate the provision of pollination services. The positive association between forest proximity and fruit set reinforces the importance of natural vegetation in enhancing bee diversity and, therefore, in the provision of pollination services. The negative effect of coffee cover on fruit set at the local scale suggests that the service demand can surpass the capacity of pollinators to provide it. These effects were independent of the local forest cover, although all studied landscapes had more than 20% remaining forest cover (within a 2 km radius), which is considered the extinction threshold for Atlantic Forest species. Interspersion of forest fragments and coffee plantations in regions with more than 20% of forest cover left could thus be a useful landscape management target for facilitating pollinator flows to coffee crops and thus for increasing coffee yields.

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A. González-Chaves (✉) · R. Jaffé ·  
J. P. Metzger · A. de M. P. Kleinert  
Departamento de Ecologia, Universidade de São Paulo,  
Rua do Matão 321, São Paulo 05508-090, Brazil  
e-mail: [adgonzalez86@ib.usp.br](mailto:adgonzalez86@ib.usp.br)

R. Jaffé  
Instituto Tecnológico Vale, Rua Boaventura da Silva 955,  
Belém, PA 66055-090, Brazil

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## Introduction

Improving crop yields through the enhancement of pollinator richness and abundance represents a sustainable pathway to meet the increasing demand of pollinator-dependent crops (Aizen et al. 2009; Foley et al. 2011; Garibaldi et al. 2016; Dainese et al. 2019). Wild bees have been shown to be successful pollinators of crop species (Garibaldi et al. 2013). As those bees naturally occur in agricultural landscapes, by relying on natural/seminatural vegetation for nest and food resources (Losey and Vaughn 2006; Brosi et al. 2008; Tscharntke et al. 2012), agricultural landscapes can be managed to sustain those species, and thereby increase crop production. Nonetheless, the conversion of native vegetation to agriculture is the leading cause of pollinator decline (Potts et al. 2010), which causes pollination deficits and simultaneously increasing the demand for pollination service (Vanbergen 2013).

Understanding pollinator flow between the areas that support them (supply areas) and those demanding their services (crop areas) is crucial to maximizing agricultural production (Ekroos et al. 2014; Mitchell et al. 2015). Native vegetation should function as supply areas (when they have the minimum habitat requirements for pollinator species), favoring cross-habitat spillover of pollinators to crops, but the expansion of crop cover might counteract such benefits (Holzschuh et al. 2011, 2016; Blitzer et al. 2012).

Landscape composition and configuration can affect pollination services in different ways. The amount of habitat is known to regulate biodiversity in general (Fahrig 2013) including bee diversity (Kennedy et al. 2013). Habitat configuration, on the other hand, has shown weak effects on bee richness and abundance (Kennedy et al. 2013); however, recent studies have shown that the landscape configuration (density of crop/crop edges and crop/noncrop edges) could be relevant, depending on the landscape composition (Martin et al. 2019; Sirami et al. 2019). Former studies have shown reductions of more than 50% of native bee visitation rates for crops located

more than 1 km from natural vegetation patches, which can result in decreased fruit set (Ricketts et al. 2008; Garibaldi et al. 2011). This body of literature reinforces that forest fragments within agricultural landscapes supply pollinators and favor service provision (Taki et al. 2007; Brosi et al. 2008). However, it is less clear how pollination services respond to the interplay between crop proximity to native vegetation habitats and the surrounding landscape of crops. Previous studies have not always disentangled the effects of proximity and landscape composition (Moreira et al. 2015; Saturni et al. 2016; Hipólito et al. 2018).

Assessing how landscape configuration affects bee diversity and the provision of pollination services is crucial for landscapes with intermediate amounts of remnant habitats. Simplified landscapes (< 20% of native vegetation) would have low diversity and a higher abundance of generalist species that do not respond to landscape changes. In comparison, in landscapes composed predominantly of native vegetation (> 60%), the loss of local species can be buffered by species coming from the surrounding vegetation (Tscharntke et al. 2012). Landscapes with intermediate habitat amounts (20–60%) are most sensitive to steep losses of biodiversity (Banks-Leite et al. 2014; Boesing et al. 2018), which is precisely the habitat amount range at which landscape configuration varies the most (Villard and Metzger 2014), and where a large part of the crops are globally grown (Gibbs et al. 2010; Foley et al. 2011).

Coffee cultivation in Brazil mainly occurs in a highly fragmented biodiversity hotspot, which makes it an ideal system for testing the effects of landscape configuration and composition on pollination service provision. Several studies have reported that bee visitations to coffee flowers lead to higher fruit set and yields (Klein et al. 2003a; Klein 2009; Munyuli 2011; Saturni et al. 2016). Although past studies have measured the independent effects of forest proximity, forest cover and farm management on coffee pollination (Klein et al. 2003a; De Marco and Coelho 2004; Ricketts 2004; Krishnan et al. 2012; Saturni et al. 2016; Hipólito et al. 2018), no study has combined crop proximity to forest fragments and local composition surrounding the focal crop to compare the independent effects of landscape configuration and composition on bee diversity and pollination service provision. This is nevertheless essential for separating

the relative contributions of the habitat amount and landscape configuration (Fahrig 2003).

In this study we evaluated the independent effects of landscape cover and forest proximity on the bee assemblages visiting coffee flowers and the production of coffee berries. We expected that the amount of forest cover within the agricultural landscapes would increase coffee yields through enhanced pollination services by supporting bee populations. In the proximity of forest fragments, coffee bushes should receive more pollinators, so we predicted an increase in service provision with forest proximity. Additionally, we expect that an increase in coffee cover (i.e., demand) would be negatively related to pollinator diversity and fruit set. Thus, we tested whether local landscape structure can predict both (1) the diversity of bees visiting coffee bushes, and (2) the provision of pollination services through changes in bee diversity.

## Materials and methods

### Study area

The study region was the southeastern part of Minas Gerais state, Brazil, one of the leading coffee producing regions in the country, which is responsible for more than 30% of world exports (International coffee organization—ICO 2015). In southeastern Brazil, coffee cultivation historically contributed to the deforestation of the Brazilian Atlantic forests. Currently, the main land uses in the region are pastures and sun coffee plantations, which are scattered between Atlantic Forest fragments along with sugar cane plantations and *Eucalyptus* forests.

Our study areas comprised 24 coffee sites (local landscapes) located within three circular sample areas of 2 km in radius (Fig. 1) with similar forest cover (20–27%) but contrasting spatial configurations, where habitat configuration should be the most variable (Villard and Metzger 2014). The circular 2 km radius areas presented similar abiotic conditions and management practices. The dominant soil types in the region were either ferric latosols or argisols and at altitudes varying from 800 to 1300 m. The centroids of the circular areas were separated by at least 6 km (Saturni et al. 2016; Librán-Embid et al. 2017, Aristizábal and Metzger 2019, Boesing et al. 2018). A minimum of 150 m separated the eight coffee sites

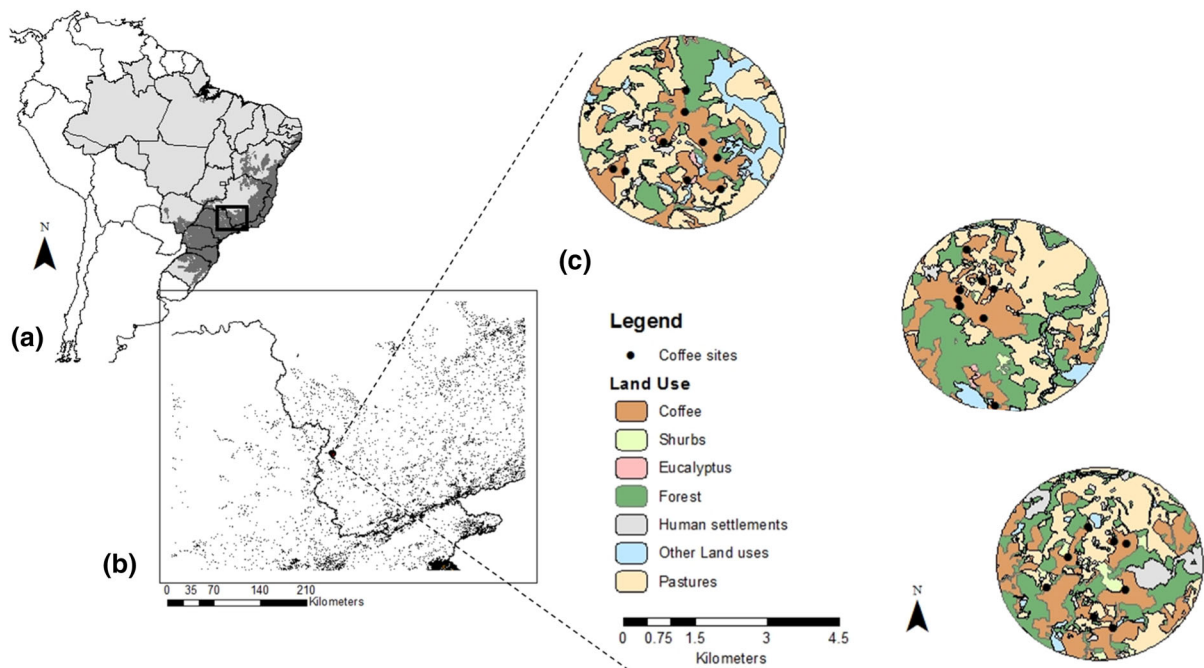
within each 2 km area (Fig. S1). There were no known beekeepers on the farms or in the vicinity of the farms where we worked between 2013 and 2017.

The landscape surrounding the coffee sites varied in local forest and coffee cover (within a 400 m radius) and in the proximity to a forest fragment. The local landscape radius of 400 m was selected with consideration of the minimum foraging range estimated for small bees (Araújo et al. 2004) and guaranteed the maximum forest cover variation with forest distance (Fig. S2). An economic assessment showed that the amount of intact forest within 400 m of coffee bushes influenced pollination services (Olschewski et al. 2006). We did not consider radii smaller than 400 m because in those cases, forest cover and proximity to forest fragment would be highly correlated.

We selected the study sites to test the independent effects of forest cover and proximity. To determine the locations of the local landscapes, we first calculated proximity (distance) to a forest fragment and local forest cover for each coffee pixel in the three subregions of a 2 km radius (Fig. S2). We used the relationship between forest proximity and local forest cover to choose four landscape conditions considering a factorial combination between far ( $> 175$  m) and near ( $< 50$  m) forest fragments, with high ( $> 20\%$ , and up to  $31\%$ ) and low ( $< 10\%$ ) local forest cover (Fig. S2, Table S1). The forest proximity threshold values were defined by considering that bees assemblages change within distances greater than 100 m from forest fragments (Ricketts et al. 2004). The high and low local forest cover classes were defined based on biological thresholds in fragmented landscapes (Banks-Leite et al. 2014; Boesing et al. 2018) also by considering that the local landscape structure, which comprised coffee bushes surrounded by high forest cover ( $> 40\%$ ) that were distant from a forest fragment ( $> 250$  m), was uncommon (Fig. S2c). We selected the final local landscapes in the field, with the farmers' help and took care in choosing coffee bushes of the two main coffee varieties (*Coffea arabica* L. var. Catuaí and Mundo Novo), which are physiologically similar and widely cultivated in the region.

### Local landscape metrics

We calculated for each coffee site the percentage of forest cover and coffee cover within a 400 m radius and the distance to the nearest forest fragment



**Fig. 1** **a** Former Atlantic Forest distribution (dark grey) in Brazil, and **b** a detail of the remaining forest areas around the study sites, at the division of Minas Gerais and São Paulo states. **c** The three regions of two-kilometre radius classified according to their main land use

(Table S1). Land-use maps were determined based on high-resolution images (ArcGIS 10.3 software by ESRI World Imagery data for 2009 to 2011; 0.5 m resolution) at a reference scale of 1:5000. Coffee cover varied independently of proximity and forest cover. Thus, we used it as a proxy for the proportion of pollination demand area in the landscape, given that there was considerable variation in coffee cover among the local landscapes (Table S1) and that the amount of mass-flowering crop cover has an impact on pollinators and pollination services (Veddeler et al. 2006; Holzschuh et al. 2011, 2016). We also calculated the cover of natural/seminatural habitat (SNH) by aggregating forest polygons with shrub (fallow) vegetation areas to test whether the coffee cover was inversely related to the amount of SNH in the landscape. The coffee cover was not associated with either forest cover ( $r = -0.1$ ) or SNH cover ( $r = -0.01$ ), nor was the relationship with distance to SNH different from distance to the forest. Instead, the metrics of forest cover and SNH cover were highly correlated ( $r > 0.90$ ), as were proximity to a forest fragment and proximity to an SNH patch ( $r > 0.67$ ).

#### *Bee diversity metrics*

We carried out bee surveys during the main coffee blooming period (end of September to October of 2014) using entomological nets. Net samplings took place along a 50 m transect between coffee lines. Each net sampling lasted two minutes, intensively sweeping the coffee visitors and was, carried out twice at each site. The sampling occurred at the beginning and end (third day) of the blooming period. We identified the bees according to the time and locations collected. They were brought to the Paulo Nogueira-Neto Entomological Collection at the Bee Lab of the University of São Paulo (<https://ecologia.ib.usp.br/beelab/home>) for identification to the species level and morphospecies when the species identification was not possible.

We calculated bee diversity metrics for each local landscape; specifically, we calculated the total number of bee individuals (abundance) and the total bee species (richness). Additionally, we ran a nonmetric dimensional scaling (NMDS) analysis based on a Bray–Curtis dissimilarity matrix of species abundances and extracted the first two axes as a proxy of the variation in the community composition (Table S2 &

Fig. S5). To interpret the resulting community variations, we correlated species abundances with the ordination axis scores to determine if certain species were associated with different axes (Table S3) (Quinn and Keough 2002). We used the intertegular distance of the sampled bees and their known nesting resources to better understand the functional traits associated with the bee diversity response to landscape variables and the effect of bee diversity on pollination services (see supplementary information on bee trait classification and Fig. S2 & S4).

#### *Coffee pollination service*

At each site, we measured bee pollination services on three coffee bushes using two indicators: coffee fruit set and dry bean weight. We compared 15 branches (5 per coffee bush), with flowers that were open and accessible for pollinators with the flowers of 15 branches (5 per coffee bush) where pollinators were excluded (Fig. S1). To exclude any insects from visiting the flowers, we used a thin mesh bag (3 mm), which allowed airflow. For each branch, we calculated the fruit set by counting the number of flowers that turned or do not turn into fruits. We counted the total number of flowers during the blooming period for the three nodes closest to each branch tip. The branches selected were 1 m above the ground. After a week of the flowering period, we marked the sampled branches and removed all bags to avoid any effects on fruit development from the mesh bag. During the harvesting period (May 2015), the coffee berries of the three nodes that were previously selected from each branch were harvested and brought to the lab. Using the number of coffee berries per branch, we calculated the coffee fruit set by considering the number of flowers during the blooming period. To determine the mean coffee berry weight per branch, we dried and weighed the coffee berries from each branch and divided it by the number of coffee fruits from the branch. We sampled a total of 360 branches for each exclusion treatment (24 sites  $\times$  3 bushes  $\times$  5 branches per bush).

#### Statistical analysis

##### *Local landscape effect on bee diversity*

To test the effects of the landscape structure (composition and configuration) on bee diversity, we fitted linear and generalized mixed models with *Poisson* and negative binomial distribution of errors for richness and abundance, respectively. Both utilize count data, but the negative binomial considers overdispersion. For both community composition axes (NMDS), we used a linear model, and we ran the analysis using the R package “lme4” (Bates et al. 2015). Given that our focus was to evaluate the differences among local landscape parameters, we included the three subregions of 2 km radius as random intercepts, to consider the nested property of our sampling region. We selected the best-fixed model structure from models that included local forest cover (percentage at 400 m radius), forest proximity, local percentage of coffee cover (400 m radius) separately and with additive effects with all possible combinations of noncorrelated ( $r < 0.5$ ) predictors, using pairs of landscape parameters to avoid overfitted models. We ran a model selection for each response variable in which each fixed effect contained one of the predictive metrics (Table S5). We selected the best models using a maximum likelihood approach with the corrected Akaike information criterion (AICc); in the model comparison, we included a null model (with the fixed effect equal to one) (Burnham and Anderson 2002). We considered all models with  $\Delta AIC \leq 2$  equally possible after comparison with the *MuMin* packages (Barton 2015). We used the residuals of the best models fitted to check for spatial autocorrelation, with Moran’s I test in the R package “DHARMa” (Hartig 2017). Previously, we tested whether SNH cover (which aggregated the forest and fallow land-use categories) was inversely correlated with coffee cover, and no correlation was found between coffee and forest. As the SNH and natural forest metrics were correlated with each other, we compared which forest metric (either forest or SNH) better predicted bee diversity and pollination services to define whether SNH or the forest metric should be incorporated into the model selection described above.



## Effect of bee diversity and landscape structure on pollination service

We considered two response variables to test whether pollination service was affected by variations in bee diversity or by landscape cover and forest fragment proximity: (1) the number of flowers that became fruits (coffee fruit set) and (2) the dry weight of coffee. For fruit set, the pollination services were represented as the difference between the exclusion experiments (open vs. bagged branches), and for each branch, the percentage of fruit set was calculated internally in the models with the “cbind” function, as the numbers of flowers per branch differed. Thus, we considered the number of flowers that became fruit along with the flowers that did not set instead of directly calculating the percentage of flowers that became fruit. Thus, we used pollinator exclusion treatment (open vs. bagged) as a fixed effect interacting with each of the predictive variables (bee diversity and landscape structure). We first performed model selection using bee metrics as predictors: bee richness, abundances (with and without *Apis mellifera*, and with *Meliponini* abundances only), and the community variation index (the first two NMDS axis).

*Apis mellifera* was the most abundant species, so we considered its abundance independently in model selection. Additionally, we also calculated overall bee abundances with and without *A. mellifera* since native bees are known to further enhance fruit set regardless of honey bee abundance (Garibaldi et al. 2013). Given that among the native bees, the stingless bees were the most abundant group, we considered *Meliponini* bee abundance as a predictive variable. Most of the bee metrics were strongly correlated. Thus, model comparisons were made using models that contained one bee diversity metric variable interacting with the exclusion treatment. The residual distribution of the generalized linear mixed models was with either binomial for coffee fruit set, or Gamma for dry fruit weight. We used the “glmer” function from the package “lme4” (Bates et al. 2015) in R version 3.5.0 (R Develop core team 2018). We incorporated the hierarchical structure associated with the three subregions of each branch from a specific coffee bush of a specific site as a random nested structure (*subregion:site:coffee\_bush*). We used the residuals of the best fitted models, with restricted maximum likelihood

to check for spatial autocorrelation with Moran’s I test in the R package “DHARMA” (Hartig 2017).

To test whether pollination services are directly affected by landscape structure, we compared models that included landscape metrics only. Apart from models with a single interaction between the treatment and a landscape parameter, we also included the additive effects between the landscape parameters interacting with the treatment. The fixed effect variable combination was the same for both of the pollination service metrics: coffee fruit set and coffee berry weight.

Because the proximity between sampling sites could violate spatial independence among our sampling sites, thus affecting our estimated model coefficients (and increasing Type 1 errors, Zuckerberg et al. 2012), we tested the robustness of our results by running all model selections after eliminating the overlapping landscapes. We compared the results of the model selection without overlapping landscapes (8 sites) with previous models containing all the 24 sites. We assessed the spatial autocorrelation of the selected models after removing the 8 overlapping landscapes from the 24 sites. The minimum distance between the two sites among the remaining 16 landscapes was 600 m.

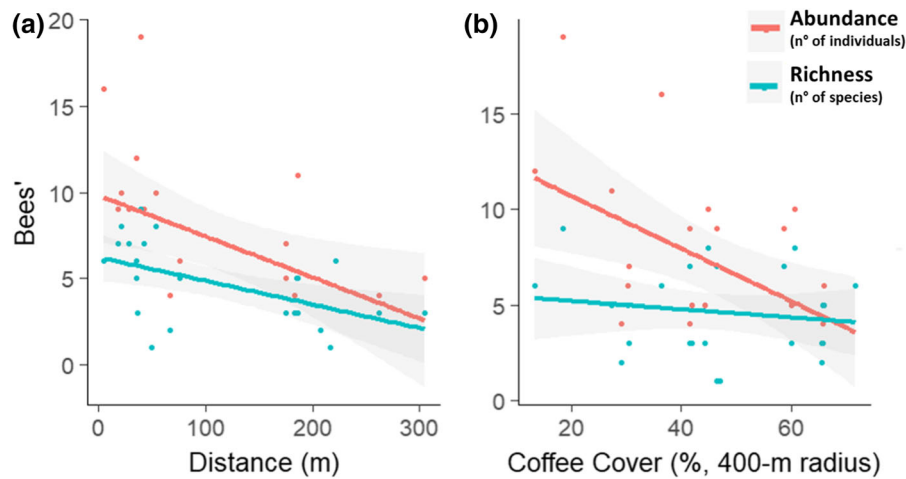
## Results

### Coffee flower bee visitors

During the main coffee blooming period at the end of October 2014, we sampled 169 bees using entomological nets (Fig. S3). Twenty bee species, which mainly belonged to the *Meliponini* tribe (16 species and 128 individuals), were collected, representing 77% of the total bees collected with nets. *A. mellifera* was the most abundant species, with 36 individuals netted (21%).

### Landscape effects on bee diversity

Overall, bees richness and abundance were positively associated with proximity to a forest fragment, as both richness and abundance decreased by half within 200 m of the forest (Fig. 2, S4). Forest cover did not affect bee diversity. Instead, bee abundance was negatively affected by the amount of coffee cover in



**Fig. 2** Relationship between bee richness (blue) and abundance (red) with **a** the Euclidean distance of the coffee sites to the nearest forest fragments and **b** with coffee cover in 400 m radius surrounding the coffee sites

the surroundings area (400 m radius), as bee abundance was two times higher in landscapes with 30% coffee cover (equivalent to 15 ha of coffee planted in the surroundings) in comparison to a landscape dominated by coffee (70%) (Fig. 2; Table 1, Fig S4). The bee diversity (Shannon index) and the community composition index (NMDS axes) were not related to any landscape variable. The local landscape variables also did not affect the abundance of *Apis mellifera*. However, the abundance of stingless bees visiting coffee (77% of the bee individuals) was higher close to a forest fragment and decreased local landscapes with

high coffee cover (Table 1c; Fig. S2, S4 & S5). Reductions in the abundance of stingless bees were associated with a sharp decrease in the presence of small and tree cavity nesting bees visiting coffee flowers far from a forest fragment (Fig S4b, Fig. S4c).

The proximity to a forest fragment explained the changes in bee richness and abundance better than the distance to any natural/SNH patch (see Table S5). Moreover, we did not find spatial autocorrelation in the bee response to landscape variables ( $p = 0.55$  for richness,  $p = 0.90$  for bee abundance,  $p = 0.95$  for *A. mellifera* abundance and  $p = 0.97$  for *Meliponini*

**Table 1** Summary of the top models for each of the bee diversity response variable: (a) bee richness, (b) bee abundance, (c) Meliponini bee abundance. The coefficients of the

predictive landscape variables are presented as columns, each line represents a model

Response	Forest cover	Proximity to forest	Coffee cover	AICc	$\Delta$ AICc	Weight
(a) Richness		− 0.29		106.0	0.00	0.45
		− 0.29	0.01	108.9	2.90	0.11
	0.00	− 0.29		109.0	2.91	0.11
(b) Abundance		− 0.25	− 0.23	135.5	0.00	0.41
		− 0.32		136.9	1.43	0.20
			− 0.30	137.0	1.51	0.19
	0.08		− 0.30	139.7	4.20	0.05
(c) Meliponini abundance			− 0.35	133.8	0.00	0.29
		− 0.27	− 0.28	133.8	0.03	0.29
		− 0.36		134.6	0.81	0.20
	0.13		− 0.35	136.2	2.42	0.09

abundance using Moran's I test), although the closest two pairs of sampling sites were separated by 150 m. The response of bee visits to coffee fields was robust to the exclusion of the overlapping sampling sites (8 sites; Supplementary Table S7). There was only a loss in the inference of the landscape effect on the overall bee richness and the *Meliponini* abundance when the overlapping landscape was removed, as the null model was among the selected models (Table S7, Fig. S8) along with the previously selected model that excluded overlapping landscapes.

#### Effect of bee diversity on pollination services

Fruit weight did not respond to bee metrics (Fig S5). However, the fruit set was higher for branches with open access to bee visitors (58%) than it was from branches without (50%) pollinators (Table 2), which represented an overall contribution of 16% of the coffee fruit set without pollinators. The selected best model contained the interaction between pollination exclusion treatments and the first axis of the community composition index (NMDS1) (Fig. 3a, Table 2). Therefore, the largest difference between treatments (up to 20% of the contribution associated with bee visitation) occurred for high community compositions with high index values. To further understand the variation in the community composition that affected the pollination services, we correlated the NMDS scores with the individual abundance of each species and to the proportionality between the most abundant species (Fig. 3b–e, Table S3). Considering the most abundant species, we found that the variation in the community composition (NMDS1) was highly correlated ( $r^2 = 0.87$ ) with the proportional abundances of *A. mellifera* in relationship to the abundance of the two *Trigona* species (*Trigona hyalinata* and *Trigona spinipes*). Together, the abundance of these three species represented 40% of the sampled bees (Fig. S3). Higher NMDS1 scores were associated with communities where *A. mellifera* were more abundant than both *Trigona* species (Table S3 & S4). This result suggested that at sites where *A. mellifera* was more abundant than the two species of the *Trigona* genus, the difference between flower exclusion treatments was higher. However, the abundances of *A. mellifera* alone did not explain the variation in the coffee fruit set (Table S4). Fruit set response to bee visitation did

not change after the data from the overlapping landscapes were excluded (Supplementary Table S8).

#### Landscape effect on pollination service

The variations in coffee fruit dry weight were not related to the exclusion treatment nor affected by any of the landscape variables (Fig. S7). However, the coffee fruit set responded differently between treatments depending on the local coffee cover and distance to forest fragments. The selected best model included the interaction between the exclusion treatment and proximity to a forest fragment and the interaction between the treatment and coffee cover (Table 2, Fig. 4). Therefore, the difference between exclusion treatments was higher (an increment of up to 20% was associated with pollination services) for coffee bushes near a forest fragment (Fig. 4a) and coffee bushes surrounded by a low amount of coffee cover for sites far from a forest fragment (Fig. 4b). The exclusion treatments showed no difference between branches for coffee bushes located more than 200 m from a forest fragment and with high coffee cover in the surroundings. Coffee cover in the local landscape negatively affected the differences between treatments, which varied caused variation of only 4% of the overall effect of pollination across the coffee cover gradient (Fig. 4). However, the effect of coffee cover was modulated by the distance to a forest fragment. Close to a forest fragment, there was little variation between treatments, although there was tendency to increase in coffee fruit set along the coffee cover gradient. At sites that were far from any forest fragment (further, than 200 m) the negative effect of coffee cover was steeper, despite having overall higher fructification when the coffee cover was low (Fig. 4). Moreover, forest proximity explained the changes in fruit set better than the proximity to natural/ SNH patches (Table S5). The tendencies were robust, even when the overlapping landscapes were excluded (Table S8).

#### Discussion

Our results corroborated others showing that *Coffea arabica* flowers visited by bees presented an increase of approximately 16% in coffee production (Klein et al. 2003b; Saturni et al. 2016; Hipólito et al. 2018).

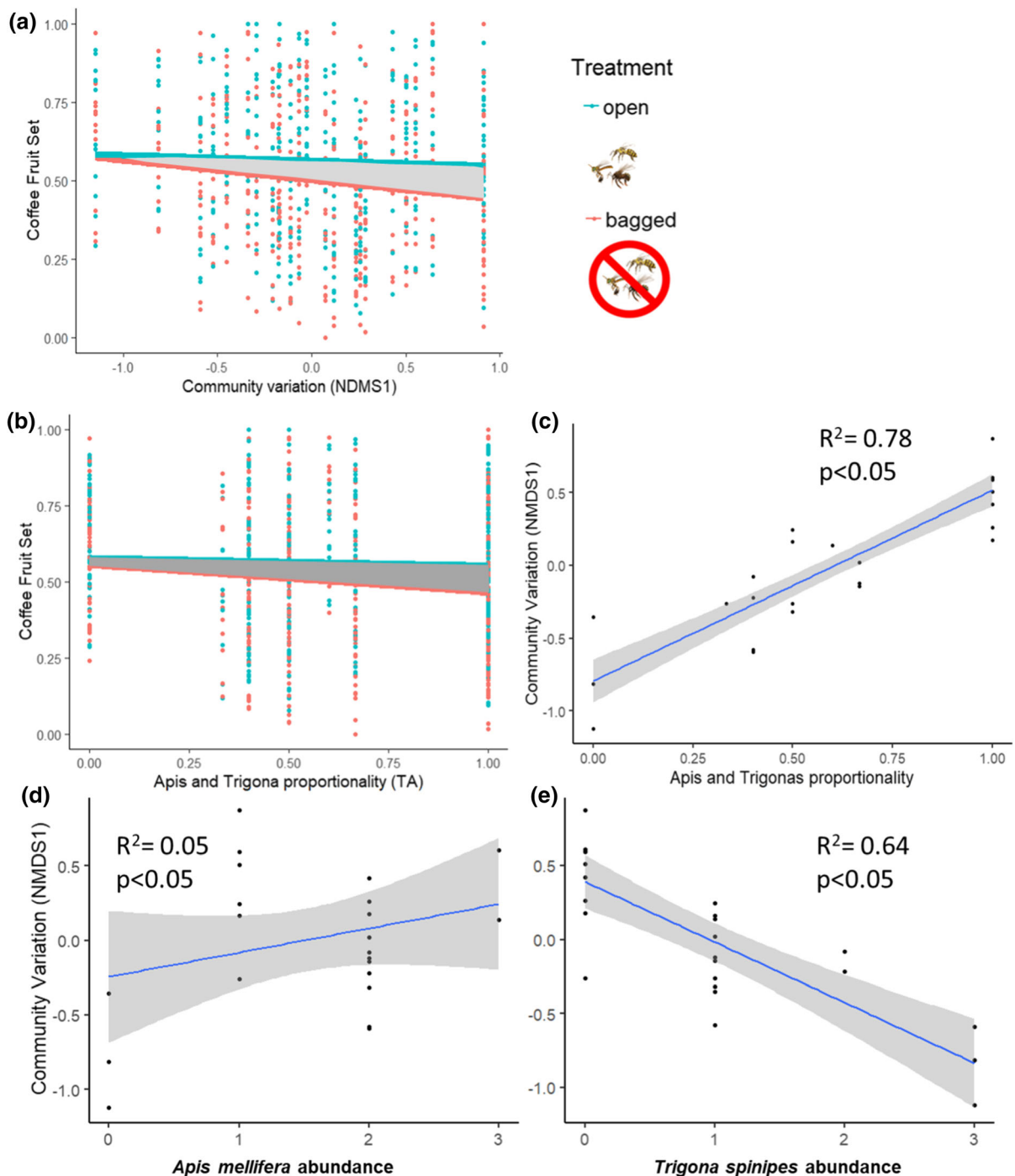


**Table 2** Summary of the top models for the Fruit set response variable: (a) using bee diversity metrics, (b) Fruit set using landscape metrics

Response	Predictive variables in the model	Estimate	Standard error	AIC	$\Delta$ AIC	Weight
(a) <i>Bee diversity effect on fruit set</i>						
Fruit set	Intercept	− 0.03	0.06	8239.6	0.00	0.746
	Exclusion treatment (open)	0.20	0.02			
	Community 1	− 0.12	0.06			
	Exclusion: Communit 1	0.07	0.02			
Fruit set	Intercept	− 0.02	0.06	8242.9	3.21	0.150
	Exclusion treatment (open)	0.20	0.02			
	Community 2	− 0.13	0.06			
	Exclusion: Communit 2	0.05	0.02			
Fruit set	Intercept	− 0.02	0.06	8245.9	6.30	0.032
	Exclusion treatment (open)	0.20	0.02			
(b) <i>Landscape effect on fruit set</i>						
Fruit set	Intercept	− 0.04	0.06	8205.3	0.00	0.995
	Exclusion treatment (open)	0.21	0.02			
	Proximity to forest	0.23	0.07			
	Coffee cover	− 0.19	0.07			
	Exclusion: Proximity	− 0.11	0.03			
	Exclusion: Coffee	− 0.05	0.03			
Fruit set	Intercept	− 0.06	0.06	8216.2	10.87	0.004
	Exclusion treatment (open)	0.20	0.02			
	Proximity to forest	0.16	0.07			
	Exclusion: Proximity	− 0.13	0.02			
	Intercept	− 0.02	0.06	8219.8	14.46	0.001
Fruit set	Exclusion treatment (open)	0.20	0.02			
	Proximity to forest	0.14	0.07			
	Forest cover	− 0.03	0.07			
	Exclusion: Proximity	− 0.13	0.03			
	Exclusion: Forest	− 0.01	0.03			

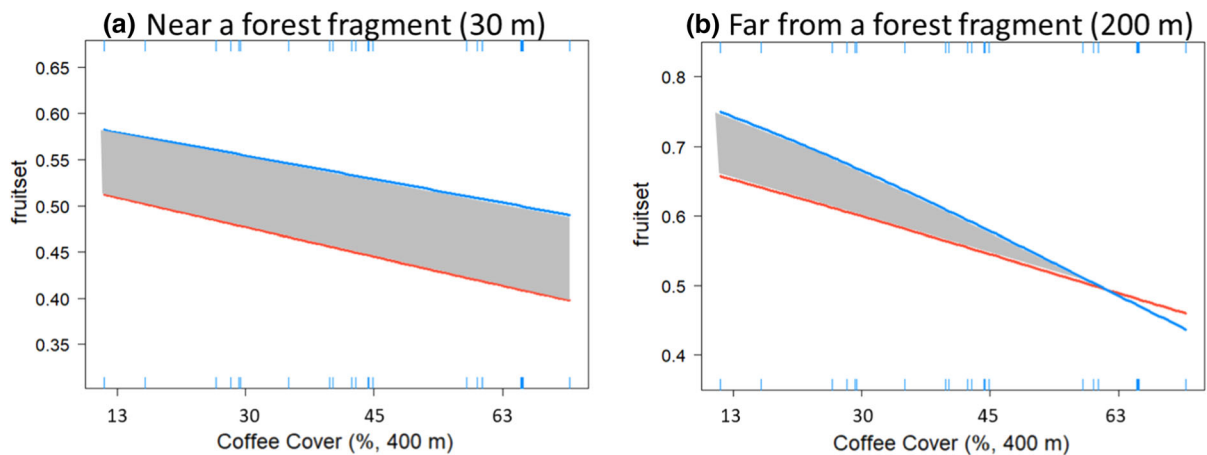
Furthermore, we presented evidence that the local landscape structure facilitated some of the pollination services by affecting bee diversity. Although local forest cover did not affect pollination services or bee diversity, as we expected, the crop proximity to a forest fragment and low coffee cover were positively related to bee diversity and pollination services. Our results suggested that service provision was not mainly influenced by the local supply of habitat amount but rather by access to supply areas through spillover of pollinators from forest fragments to crop areas as the pollination services and bee diversity were higher near the forest. Moreover, the effect of coffee cover

suggested that pollination services becomes diluted as the number of coffee flowers in the local landscape increased, since higher coffee cover reduces bee abundances, especially of stingless bees, but not bee richness. Nonetheless, pollination service were also associated with variation in the relative abundances of the most common bees visiting coffee (*A. mellifera* and *Trigona* species), which were not affected by changes in the local landscape. We found that the coffee sites where *T. spinipes* and *T. hyalinata* are dominant over *A. mellifera* would have the lowest pollination services, possibly due to nectar robbing behavior described for these *Trigona* species.



**Fig. 3** Coffee fruit set in relationship to: **a** community variation and **b** Proportional abundance (TA) between *A. mellifera* and two species of the *Trigona* genus (*T. spinipes* and *T. hyalinata*). Each point represents a branch ( $n = 720$ ) of the twenty three experimental sites, and each colour represents one of the exclusion experiments treatments, open to pollinators (blue) and bagged branches to exclude pollinators (red). The grey area

represents the pollination service (differences between open and bagged treatments). The three remaining plots show the relationship between the community variation index and: **c** to the proportionality between honey bees and the *Trigona* genus (TA); **d** to the *Apis mellifera* abundance and **e** to the *Trigona spinipes* abundance



**Fig. 4** Coffee fruit set predicted by the triple interaction between exclusion treatments, forest distance and local coffee cover. **a** the effect of coffee cover predicted when forest distance is in mean 30 m and **b** coffee cover effect for coffee bushes

located at 200 m distant from a forest fragment. The grey area represents the pollination service and each colour represents one of the exclusion experiments treatments, open to pollinators (blue) and bagged branches to exclude pollinators (red)

#### Local landscape structure and bee diversity

Stingless bees were more abundant near forest fragments, but contrary to our expectations, local forest cover was not related to bee richness or abundance. The main bee species visiting coffee flowers (*Apis mellifera*) was also not affected by the local landscape structure. The overall result suggested that proximity to forest fragments, independent of the amount of local forest, favors the spillover of a richer bee assemblage. This result indicates that within a regional context of landscapes with 20% to 30% of the remaining forest (within the three circular sample areas of 2 km in radius), the configuration effects on bee diversity are more important than the amount of forest at a more local (400 m) scale. Indeed, the richness and abundance of the bees visiting the coffee flowers were reduced by half when the coffee bushes were further than 175 m from a forest fragment. Nonetheless, the high richness of bee founds visiting coffee flowers, despite the small sampling effort (see Table S4), reinforces the importance of maintaining forest cover above an extinction threshold value at a regional scale to avoid steep biodiversity losses (> 20–30%; Banks-Leite et al. 2014; Boesing et al. 2018). Furthermore, such forest cover amounts are associated with high levels of configuration variability and potentially have greater importance for biodiversity (Martin et al. 2019), which we could manage to favor pollinator flow in croplands, by restricting coffee to areas adjacent to

forest fragments, where diversity tends to concentrate (Ricketts et al. 2004; Villard and Metzger 2014).

The lack of influence of forest cover on bee abundance and richness could be attributed to the scale considered (400 m) or to the proximity between the sampling sites, however our sampling design was careful to prevent landscapes with similar conditions from being close to each other. Moreover, no spatial autocorrelation was found in the models selected for bee abundance and richness, nor were the results significantly altered by eliminating the overlapping landscapes from the analysis. We found, as other studies have reported, that increasing landscape overlap does not necessarily result in increments in the autocorrelation of model residuals (Zuckerberg et al. 2012). Another alternative explanation was that species more tolerant to landscape modifications dominated the bee assemblages (Batista et al. 2003; Jaffé et al. 2015). Five of the seven most abundant stingless bees do not rely on tree cavities as a nesting resource: they either construct external nests out of mud (*T. spinipes* and *T. hyalinata*) or nests in the ground, traits associated with a higher tolerance to forest loss (Moure et al. 2012; Lichtenberg et al. 2017). Out of the seven most abundant stingless bees, the two species that nest in tree cavities, *Tetragonisca angustula* and *Nannotrigona testaceicornis*, have been reported to benefit from anthropogenic landscapes (Batista et al. 2003; Zanette et al. 2005; Vieira et al. 2016). Nonetheless, the higher bee richness near forest

fragments was related to a greater diversity of stingless bee nesting types (tree trunk cavity, exposed, and ground nesters), size (1–2.8 mm) and foraging behavior (Brosi et al. 2008) (Fig. S4), which reinforced that forest fragments provide resources for the many bee species that visit coffee flowers.

The effect of coffee cover on bee abundance was probably due to the dilution effect (Veddeler et al. 2006; Jha and Vandermeer 2009; Holzschuh et al. 2016), i.e., the number of bees was too low to visit the high numbers of localized coffee flowers. This interpretation was reinforced by the fact that only bee abundance was affected, and bee richness was unaffected. Moreover, our sampling design supported the idea that increasing the area of the mass-flowering coffee crop is independent of forest cover and forest proximity. Therefore, the expansion of conventional coffee monocultures (landscape simplification) either reduces the overall bee abundance in the landscape (Goulson et al. 2015) or bee recruitment is not further enhanced with the increment in coffee flower resources (Westphal et al. 2003; Veddeler et al. 2006). Either way, our results were consistent with other studies showing that landscape simplification and homogenization affect bee abundance and richness, which could result from the lack of or reduced food resources (Benton et al. 2003; Dainese et al. 2019). In a landscape with relatively low cover of native vegetation, management intensity is a strong predictor of bee diversity (Batáry et al. 2011; Kennedy et al. 2013) and thus can negatively impact bee diversity and pollination services (Connelly et al. 2015). Our results suggested that increasing the interspersed focal crops and forest fragments could facilitate the flow of pollinators and avoid crop areas with low pollinator abundance (Mitchell et al. 2015; Holzschuh et al. 2016).

#### Bee community composition and pollination service

The exclusion experiments showed an overall increase of 16% in fruit set between coffee flowers left open in comparison to the flowers where pollinators were excluded. The benefit found was within the reported values for the pollinator contributions to *Coffea arabica* (Ngo et al. 2011). However, it was lower than the benefit found the year before (28%) for the same region (Saturni et al. 2016). The slightly lower

pollination found could be attributed to the biennial characteristics of sun coffee production (DaMatta 2004), which suggests that years of low productivity benefit less from pollination services, or to the lower forest amount gradient considered here, which could have caused the observed benefits. The limited regional forest amount considered in our study (20–30%) seemed to be associated with a community dominated by bees with high tolerance of landscape changes. This remaining bee community could also explain the lower pollination service found and the lack of direct influence of bee richness and abundance on pollination service, although the overall bee richness was high compared with other studies in coffee landscapes (Table S6).

We found that coffee fruit set increased to 24% when *A. mellifera* dominated the community instead of *T. spinipes* (Ts) or *T. hyalinata* (Th). Both species of *Trigona* are known to damage the flower buds of other plants (Renner 1983; Saunders et al. 2015). Thus, the lack of direct association between bee richness and the abundances with pollination services could be attributed to the negative effect of communities dominated by bees from the *Trigona* species (Ts and Th) on fruit set. Although *A. mellifera*'s contribution to coffee yields is widely acknowledged (Roubik 2000; Ngo et al. 2011), its abundance alone did not explain coffee fruit set variations, which were also not explained by landscape variables. Therefore, our results suggest that relying on ecologically equivalent species such as *A. mellifera* and *T. spinipes* (Giannini et al. 2015), which are tolerant to landscape modifications (Brosi et al. 2008; Jaffé et al. 2015), does not guarantee safeguarding of service provision and thus attempts against agroecosystem resilience (Garibaldi et al. 2013).

Although neither bee richness nor abundances were directly related to pollination services, the local landscape characteristics that contributed to bee diversity were positively associated with pollination services. Therefore, our results strongly suggest that landscape management can contribute to the provision of pollination services (Benjamin et al. 2014; Saturni et al. 2016; Hipólito et al. 2018), as it was high near forest fragments where wild bee abundances and richness were also higher and low in local landscapes with high service demands, where the abundance of bees was low. This pattern was consistent with those of previous studies showing that increasing bee diversity can result in a higher increment in pollination services

(Garibaldi et al. 2016), as the negative effect of coffee cover on pollination services was absent when coffee flowers were near a forest fragment. Furthermore, our results emphasize the importance of landscape management as the interspersed forest fragments and coffee crops facilitated pollinator spillover and forest cover did not affect bee diversity or pollination services, at least within a regional context of 20–30% of forest cover.

### Implications and final remarks

Our results suggest that: (1) local forest cover does not affect the supply of bee diversity, within a regional context of intermediate forest cover; (2) increasing crop proximity to forest fragments would increase accessibility and facilitate the flow of pollinators to crops, and (3) a large extension of focal crops results in insufficient service provision due to pollinator dilution. Thus, we provided supporting evidence that maintaining croplands adjacent to forest fragments can have positive impacts on pollination service when regional forest cover is above an extinction threshold (Banks-Leite et al. 2014; Boesing et al. 2018). Interspersed forest can be achieved either by reducing the distance of crop to forest fragments and favoring pollinator spillover or by reducing local pollinator demand, by avoiding growing crops in areas with low bee diversity where pollination service would not be provided. Therefore, we suggest that expanding coffee plantations should maintain close distances to forest patches and avoid large continuous extensions of coffee. Managing the spatial configuration of cropland represents an alternative when it is not possible (Perfecto and Vandermeer 2010) or it is unacceptable for farmers (Burton et al. 2008) to increase forest cover.

Our research has clear conservation implications, as most of the remaining Atlantic Forest is distributed in small fragments within private lands (Ribeiro et al. 2009; Rezende et al. 2018), and the Brazilian Native Vegetation Protection Law has established a minimum requirement of 20% forest cover within each property (Metzger et al. 2019). The Atlantic Forest has been contributing to coffee production in Brazil for a long time, and increasing the interspersed forest within forest patches can further enhance this benefit.

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