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Efeito da estrutura da paisagem sobre a diversidade de  
polinizadores e a efetividade da polinização do café

Influence of landscape structure on pollinator diversity and  
coffee pollination effectiveness

São Paulo

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## General Introduction

The main research focus of landscape ecology is the relationship between spatial patterns and ecological processes at different spatial (and temporal) scales (Metzger, 2001). Landscape composition is defined by the type and amount of land use and land cover classes in a landscape and configuration is related to the spatial arrangement of those land use and land cover classes (Turner 2005). Those two components of the landscape structure are affected by human disturbances (Turner, 1989).

In a changing world, with strong agricultural expansion and increasing food demand (Godfray et al. 2010), biodiversity is suffering from natural habitat loss (Phalan *et al.* 2011, Banks-Leite *et al.* 2014) and fragmentation (Fahrig, 2002), which are impacting landscape composition and configuration. Currently, at least 43% of Earth's terrestrial ecosystems have been transformed (Barnosky *et al.* 2012), resulting in highly fragmented landscapes, with agricultural areas interspersed between natural habitat patches (Keitt 2009). In this context, the amount of remaining habitat is always an important feature to be considered for biodiversity conservation, as well as the habitat configuration, which can partially mitigate the effects of habitat loss (Villard & Metzger, 2014).

The landscape structure can also influence the provision of ecosystem services (Turner *et al.* 2012), defined as the products of ecological functions or processes that directly or indirectly contribute to human well-being, or have the potential to do so in the future (Farley & Daly 2004). The awareness of ecosystem benefits to humans is considered as an important factor to achieve global sustainable development (MEA 2005). Ecosystem services and landscape structure appears to be connected once previous studies indicate

that landscapes with greater biodiversity should increase the provision of ecosystem services (Garibaldi *et al.* 2011, Kremen & Miles 2012).

Pollination is an essential ecosystem function in natural habitats and also brings numerous benefits to society, through its role on food production and agriculture (Imperatriz-Fonseca 2004). Classified as a regulating service (MEA 2005), pollination service provided by animals can increase the size and quality of commercial harvests (Roubik 1995, Heard 1999, Klein *et al.* 2007, Aizen, Garibaldi *et al.* 2009). About 35% of global food production comes from crops that depend on pollination (Klein *et al.* 2007). A recent revision showed that 23 important world crops are on some level dependent on the pollination service (Kennedy *et al.* 2013) (Table 1).

Table 1. Crops dependence on pollinators. Data from Kennedy *et al.* 2013.

Crop	Pollinator dependence
Apple	Essential (>90%)
Cantaloupe	Essential (>90%)
Macadamia	Essential (>90%)
Passionfruit	Essential (>90%)
Red clover	Essential (>90%)
Squash	Essential (>90%)
Watermelon	Essential (>90%)
Almond	High (40–90%)
Blueberry	High (40–90%)
Buckwheat	High (40–90%)
Cherry	High (40–90%)
Cranberry	High (40–90%)
Mango	High (40–90%)
Canola	Medium (10–40%)
Coffee	Medium (10–40%)
Longan	Medium (10–40%)
Strawberry	Medium (10–40%)
Sunflower	Medium (10–40%)
Field bean	Little (< 10%)
Grapefruit	Little (< 10%)
Pepper	Little (< 10%)
Pigeonpea	Little (< 10%)
Tomato	Little (< 10%)

Most of these crops are more effectively pollinated by bees (Klein *et al.* 2007; Aizen *et al.* 2009). Giannini *et al.* (2014) identified 75 Brazilian agricultural crops effectively pollinated by bees. In this context, native bees can enhance fruit set of crops (Garibaldi *et al.* 2013). Because natural habitats supply the necessary resources for wild pollinators survival as food, nesting and others (Roubik 1992), the loss and fragmentation of this habitat affect pollination. Bee pollination services are increasingly threatened by the human-mediated modification of natural habitats (Biesmeijer *et al.* 2006, Kremen *et al.* 2007, Potts *et al.* 2010, Vanbergen and Initiative 2013). In particular, habitat loss and fragmentation have been identified among the major drivers of global bee declines (Brown & Paxton 2009, Potts *et al.* 2010, González-Varo *et al.* 2013). Accordingly, in agricultural landscapes, the stability of pollination services and

crop production decreases with increasing distance to natural habitats (revision in Garibaldi *et al.* 2011). It is thus important to evaluate how and how much changes in landscape pattern can reduce the productivity of pollinator-dependent crops (Viana *et al.* 2012).

Despite the importance of landscape structure for pollinators and crop pollination, few studies have actually quantified the effect of landscape structure on bee community and fruit set. Previous studies focused mainly on local factors, such as the type/intensity of farm management, while the analysis of landscape structure was limited to few landscape features (Table 2).

Table 2. Main focus of previous studies that evaluated the effects of landscape structure on bee community and fruit set.

Reference	Crop	Landscape Composition	Landscape Configuration	Farm Management
Saunders et al. 2004	Almond		x	
Benjamin et al. 2014	Blueberry	x		x
Klein et al. 2003b	Coffee ( <i>C. arabica</i> )		x	x
De Marco & Coelho 2004	Coffee ( <i>C. arabica</i> )		x	x
Rickets et al. 2004	Coffee ( <i>C. arabica</i> )		x	
Vergara & Badano 2009	Coffee ( <i>C. arabica</i> )		x	x
Jha & Vandermeer 2010	Coffee ( <i>C. arabica</i> )	x		x
Krishnan et al. 2012	Coffee ( <i>C. canephora</i> )		x	
Boreux et al. 2013	Coffee ( <i>C. canephora</i> )		x	x
Gemmill-Herren & Ochieng 2008	Eggplant	x	x	
Danner et al. 2014	Maize	x		
Carvalho et al. 2010	Mango		x	
Shuler et al. 2005	Pumpkin			x
Carvalho et al. 2011	Sunflower		x	x
Holzschuh et al. 2012	Sweet cherry	x		
Kremen et al. 2004	Watermelon	x		x
Brosi et al. 2008	Unspecific	x	x	
Holzschuh et al. 2010	Unspecific	x	x	x
Klein et al. 2002	Unspecific			x
Le Feón et al. 2010	Unspecific	x		x

Coffee is one of the most important crops in the world, involving 25 million farmers and 125 million people indirectly (Ngo *et al.* 2011). It arrived in Brazil in the 18<sup>th</sup> century (Conab 2015) and the country is now the world's largest coffee producer (Fig. 1, from FAOSTATS, 2014). Coffee exportation accounts for about 9% of Brazilian agribusiness exports (MAPA, 2013). The area for this crop in the country is declining (Jha *et al.* 2014), but production continues to grow due to the increase in productivity that grew from 491 to 1433 Kg/ha in the last 50 years (FAOSTATS, 2014). Coffee is mostly produced in Brazil in monoculture system under full sun (89% of all coffee grown in the country in 2012, Jha *et al.* 2014), very different from its natural habitat environment. *Coffea arabica* originates from tropical forests in Ethiopia, where it grows naturally in the understory of montane forests (Ngo *et al.* 2011). It belongs to the Rubiaceae family and the most cultivated species is *Coffea arabica*. Its flowers are white, aromatic, hermaphrodite, gathered in number from 2 to 6, forming clusters located in the armpit of the leaves. Coffee flowers usually open up early in the morning and remain open throughout the day, lasting 2-3 days (de Melo & Sousa 2011). Despite being self-compatible, presenting high rates of self-fertilization (Carvalho & Krug, 1949), coffee flowers can also be pollinated by insects (Kennedy *et al.* 2013 and revision in Ngo *et al.* 2011).

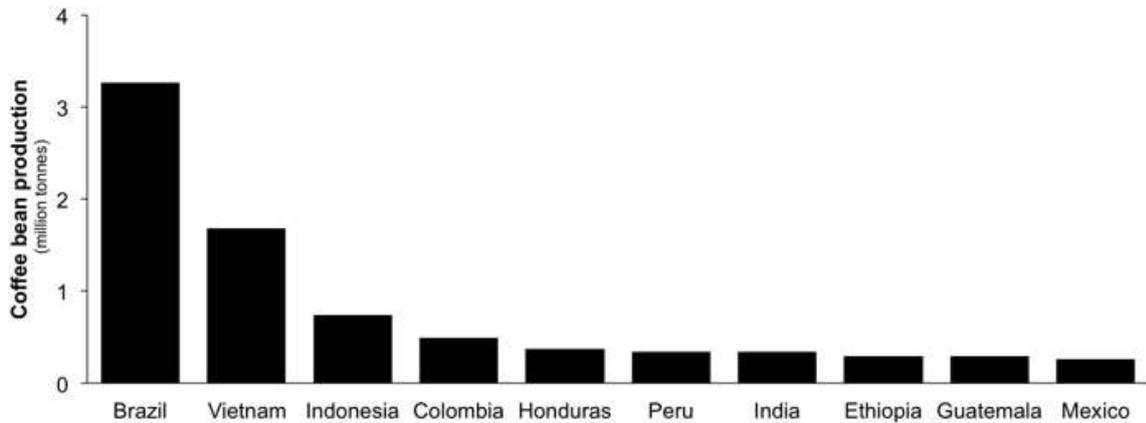


Figure 1. Top ten coffee-producing countries between 1993 and 2013 (FAOSTATS, 2014).

One of the most productive and traditional coffee production regions of Brazil is situated in areas previously covered by the Atlantic Forest, a highly diverse and endangered tropical forest (Joly *et al.* 2014). According to Ribeiro *et al.* (2009), less than 16% of this biome is left and the major part of the remnant fragments has less than 50 ha. Additionally, almost half of those fragments are less than 100 m of an edge (Ribeiro *et al.* 2009).

This region comprises areas in the south of Minas Gerais state (in Brazil known as “Sul de Minas”) and east of São Paulo state (“região Mogiana”) and is one of the most important region of *C. arabica* production in Brazil (Conab 2015). Due to its mountainous relief, preventing the mechanization of coffee harvest (which is done manually) and the existence of large monocultures, coffee plantations are typically distributed in relatively small patches. In this region, 71% of coffee farms have less than 10 hectares (Reis *et al.* 2001) and coffee trees are usually situated as < 300 from a forest fragment. However, the region is facing the third consecutive year with decreasing production, mainly because of climatic adversities (Conab 2015). Additionally, those farmers are suffering from the high cost of hand labor, especially labor-temporary work

(Lanna & Reis 2012). Despite this situation, there are few studies on the positive effects of landscape composition and configuration on coffee pollination. Moreover, there are no studies that looked to this relationship at different spatial scales.

In the present study, we explore this knowledge gap. We assessed a multi-scale relationship between landscape structure, bee community and the effectiveness of the pollination service, by analyzing nine landscapes from SE Brazil composed by coffee plantations and tropical forest fragments. We aimed to answer two questions: (1) How do landscape composition and configuration affects the bee community visiting coffee flowers? (2) How does the bee community, in turn, affect coffee pollination?

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# **Landscape structure influences bee community and coffee pollination at different spatial scales**

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## Introduction

Pollination is a key ecological function needed to maintain plant biodiversity (Roubik 1992; Nabhan & Buchmann 1997; Kearns, Inouye & Waser 1998) and enhance habitat quality (Wratten *et al.* 2012). In agricultural areas, pollination is considered a regulation ecosystem service (MEA, 2005), which mediates the increase in size and quality of harvests (Roubik 1995; Heard 1999; Klein *et al.* 2007; Aizen *et al.* 2009). A recent meta-analysis found a positive relationship between fruit production and visits by native pollinators across 41 crops distributed worldwide (Garibaldi *et al.* 2013). Actually, more than 70% of the world crops are dependent upon animal pollination and the majority of these crops are most effectively pollinated by bees (Klein *et al.* 2007; Aizen *et al.* 2009). The contribution of bees to agricultural production is therefore remarkable, as 35% of global food production comes from crops that depend on pollination (Klein *et al.* 2007).

Bee pollination services are increasingly threatened by the human-mediated modification of natural habitats (Biesmeijer *et al.* 2006; Kremen *et al.* 2007; Potts *et al.* 2010; Vanbergen & Initiative 2013). In particular, habitat loss and fragmentation have been identified among the major drivers of global bee declines (Brown & Paxton 2009; Potts *et al.* 2010; Gonzalez-Varo *et al.* 2013). Because natural habitats supply food and nesting resources for pollinators (Roubik 1992), the loss and fragmentation of these habitats can affect the density and behavior of pollinators (Hadley & Betts 2012). For instance, pollination services and crop production have been shown to decrease with increasing distance to natural habitats (revision in Garibaldi *et al.* 2011).

Despite the importance of landscape structure for pollinators and crop pollination, few studies have actually quantified the effect of landscape structure on bee community and fruit set. These include works in watermelon (Kremen *et al.* 2004), sweet cherry (Holzschuh *et al.* 2012), maize (Danner *et al.* 2014), blueberry (Benjamin *et al.* 2014), eggplant (Gemmill- Herren & Ochieng 2008) and coffee (Jha & Vandermeer 2010). However, in most cases, the analysis of landscape structure was limited to few landscape features, such as the distance to forest patches (Saunders *et al.* 2004, Ricketts *et al.* 2004, Carvalheiro *et al.* 2010, Krishnan *et al.* 2012) or the amount of native habitat (Brosi *et al.* 2008, Le Feón *et al.* 2010, Holzschuh *et al.* 2010). Most pollination studies are still focused on local factors, such as the type/intensity of farm management (Klein *et al.* 2002, Shuler *et al.* 2005), rarely associated with the landscape context (Klein, Steffan-Dewenter & Tscharrntke 2003b, De Marco & Coelho 2004, Vergara & Badano 2009, Carvalheiro *et al.* 2011, Boreux *et al.* 2013). There is thus a great need to better understand the pollination biology and pollinator requirements of many crops (Klein *et al.* 2007), and the influence of landscape structure on the provision of pollination services.

As the rates of pollinator loss seem to be faster in the tropics than in temperate regions (Ricketts *et al.* 2008, Viana *et al.* 2012), probably due to the fast conversion of natural habitats to agricultural landscapes (Hansen *et al.* 2013), there is a pressing need to understand land use impacts on the provision of pollination services. Coffee is one of the most widely cultivated and economically valuable crops in the tropics (Donald 2004, Jha *et al.* 2014), involving 25 million farmers and 125 million people indirectly (Ngo, Mojica & Packer 2011). It is also one of Brazil's main export commodities, representing

30% of the world production (ABIC 2012). Although its flowers are self-compatible and it presents high rates of self-pollination (Carvalho & Krug 1949), coffee exhibits increased per-bush fruit set and increased field-level crop yields when exposed to insect pollination (De Marco & Coelho 2004; Klein 2009; Klein *et al.* 2003; Ricketts 2004). Several studies have demonstrated that the presence of bees in coffee plantations results in an increase in grain production (Klein, Steffan-Dewenter & Tscharntke 2003a; De Marco & Coelho 2004; Ricketts *et al.* 2004; Vergara & Badano 2009; Ngo, Mojica & Packer 2011). Although some of these studies measured the effect of isolation to forest and farm management on coffee pollination (Klein, Steffan-Dewenter & Tscharntke 2003b; De Marco & Coelho 2004; Ricketts *et al.* 2004, Krishnan *et al.* 2012), no efforts have been directed to assess the effects of landscape composition and configuration at different spatial scales. Our study aimed to fill this knowledge gap, by assessing the multi-scale relationship between landscape structure, bee community and pollination effectiveness.

By analyzing nine landscapes from one of the main coffee-producing regions of Brazil, composed by mosaics of sun coffee plantations and Atlantic Forest fragments, we aimed to answer two main questions: (1) How do landscape composition and configuration affects the bee community visiting coffee flowers?; and (2) How does the bee community affect coffee pollination? We predicted that landscapes with higher forest cover and coffee trees closer to forest fragments would present higher bee abundance and a richer and more diversified bee community, which could in turn increase pollination service (Fig. 1).

## **Material and methods**

### STUDY AREA AND LANDSCAPE SELECTION

We selected nine landscapes located in northern São Paulo and southern Minas Gerais States, in one of the most productive and traditional coffee production regions of Brazil. The original vegetation in the area was the Atlantic Forest, a highly diverse and endangered tropical forest (Joly, Metzger & Tabarelli 2014). Nowadays, landscapes in the region are composed of a mosaic of Atlantic forest remnants with sun-grown coffee plantations, pasture, and in some cases sugar cane and Eucalyptus plantations.

Study landscapes were circular spatial samples with 2 km radius, chosen to encompass a wide range of forest cover (from around 10 to 50%), and to avoid extensive variation in abiotic conditions (soil types and altitude). We could not control for coffee variety and pesticide use, because all farms mix more than one variety and there is almost no organic coffee plantation in the region. The minimum distance between the centroids of any pair of our study landscapes was 6 km (Fig. 2). Within a 1 km radius from the centroid of each landscape, we randomly selected 15 coffee trees separated by at least 100 m (Fig. S1). Pollinator exclusion experiments were performed in 15 of them, while we collected floral visitors on 10 (Fig. S1).

### LANDSCAPE METRICS

Land use and land cover were mapped for each landscape, using high-resolution images (ArcGIS 10.3 basemap imagery from the DigitalGlobe satellites for 2009 to 2011, 0.5 m resolution) and a reference scale of 1:5,000. Landscape metrics were calculated from these maps, using three different spatial scales: The landscape level, considering landscape variables in 1 and 2

km radii; and the coffee tree level, considering landscape variables within 300 m around each tree. These radii were used in order to consider a wide range of bee flight distances (Araújo *et al.* 2004, Kremen *et al.* 2004, Benjamin, Reilly & Winfree 2014). Variables at the landscape and tree levels were uncorrelated with each other.

Landscape metrics comprised metrics of composition (which and how much land use and land cover classes are present) and configuration (how land use and land cover classes are spatially arranged) (Turner 2005). For landscape composition we calculated forest cover (within 300 m, 1 and 2 km) and matrix (i.e. non-forest) composition (within 1 and 2 km). For configuration, we calculated proximity index (within 1 and 2 km) and distance of each coffee tree to the nearest forest fragment.

Forest cover and proximity were calculated using ArcGIS 10.3 and Fragstats 4 (McGarigal, Cushman & Ene 2012). Proximity index is an isolation measure that considers the size and the distance of neighboring patches at the same time (McGarigal, Cushman & Ene 2012), and thus represents the availability of habitat in the surrounding landscape. In order to have an estimate of matrix composition we ran a Principal Component Analysis (PCA) using the percentage cover of each matrix land use type, with the *Vegan* R package (Oksanen *et al.* 2015). The two first axes of this analysis retained 73% and 22% of the variance, respectively. While the first axis was essentially related with pasture and sugarcane cover, the second axis was mostly related with coffee cover variation, clearly dividing landscapes with more coffee (negative values), from the ones with others predominant classes (i.e. sugarcane around 0.1 and pasture around 0.2 values) (Fig. S2). In order to give more importance to the

variation in coffee cover, we decided to consider the second axis of this PCA as a measure of matrix composition.

## FLORAL VISITORS

Using entomological nets we collected bees visiting coffee flowers in 10 of our selected trees from each landscape. All flower-visiting insects were collected for 10 continuous minutes between 8:00 and 15:00, when bees were active.

Data collection occurred during the 2013 bloom, from 16th of September to 18th of October. The identification of the collected bees was done using a specialized identification key (Silveira, Melo & Almeida 2002), a reference collection (Entomological Collection Paulo Nogueira Neto) and the assistance of a taxonomist (Dr. K. S. Ramos, Museum of Zoology of the University of São Paulo).

From the bee samples, we calculated native bee abundance, richness, diversity (Shannon index) and composition; and *Apis mellifera* abundance. For the landscape level analyses we considered the landscape-wide sum of the data collected in all trees, while for the tree level analyses we only considered the bees collected in each tree.

Native bee community composition was expressed as the first axis of a Principal Coordinate Analysis (PCoA) using the Bray-Curtis dissimilarity index on untransformed native species abundance. The Bray-Curtis coefficient has been recommended and used in ecological gradient studies with insects and other groups (see Banks & Cintra 2008 and references therein). The first axis of the PCoA retained 42% of the variance at the landscape level and 32% at the tree level (Fig. S3). We ran the PCoA analysis using the *Vegan* R package (Oksanen *et al.* 2015).

## POLLINATION SERVICE

To quantify pollination services we performed exclusion experiments. In the 15 selected coffee trees from each landscape we randomly chose branches at three different heights: high, medium and low. We assigned two treatments (at separated branches) for each height: “bagged flowers” and “open pollination”. In the “bagged flowers” treatment, branches were covered with tulle bags (mesh size 3 mm) for the whole duration of flowering. Bags prevented access of pollinating insects, but allowed the passage of pollen grains, water and wind. Bags were placed approximately 10 days before flowering, and then removed after the flowers had dried to minimize any potential effects of the bag on fruit development. In the “open pollination” treatment, branches were naturally exposed to floral visitors. We had a total of 405 branches per treatment (3 heights x 15 trees x 9 landscapes).

During flowering, we counted all flowers observed in bagged and open branches. We manually removed buds that were not open by the time the treatments were set. After 6 weeks, we counted the numbers of early fruits for each treatment. Coffee fruits were then collected, counted, weighed and measured 9 months later.

We used three fruit production indicators as measures of pollination service: *Fruit set* – Calculated as the proportion of flowers that yielded fruits; *Fresh Fruit Size* (mm) – The largest fruit length measured with a digital caliper; and *Dry Fruit Weight* (g) – The whole fruit weight measured with an analytical balance after drying it in an oven at  $65^{\circ}\text{C} \pm 5^{\circ}\text{C}$  until constant weight (about 24 hours) (Hastenreiter *et al.* 2007).

## STATISTICAL ANALYSES

We performed a two-step analysis using model selection: 1) We tested the effect of landscape composition and configuration on bee community. In this step, we used the bee metrics as response variables and the landscape metrics as predictor variables. 2) We tested the effect of the bee community composition on coffee pollination. For this step, we used the pollination metrics as response variables and bee metrics as predictor variables.

We fitted linear and generalized linear mixed models using the *lme4* R package (Bates *et al.* 2014). In both steps, we first tested the best random structure by comparing models with identical fixed structure fitted using Restricted Estimated Maximum Likelihood (REML). Because we were interested in assessing the relationship between landscape metrics and pollination service, we accounted for variation due to landscape, coffee tree, branch height and *C. Arabica* variety, including them as random intercepts on our models. Once the best random structure was found, we proceeded to select the best fixed structure, using maximum likelihood (ML), and including always a null model (with no fixed effects). Model selection was done using the corrected Akaike information criterion AICc (for models without random effects) or AIC (for models with random effects) (Burnham & Anderson 2002). All models with  $\Delta AIC < 2$  were considered as equally plausible. Model comparisons were performed using the *MuMIn* package (Barton 2014).

In order to robustly avoid spatial autocorrelation of bee community metrics at the landscape level, we performed Mantel tests using the *ade4* R package (Dray & Dufour 2007). One test was made for each bee community variable. For each test, two matrices were calculated: A 'distance matrix' consisting of the distances between all landscapes, and a 'correlation matrix'

consisting of the similarity between the bee community variable values in each landscape. The tests revealed no spatial autocorrelation (native bee abundance:  $p=0.06$ , native bee species richness:  $p=0.14$ ; native bee diversity:  $p=0.37$ ; native bee composition:  $p=0.07$ ; and honeybee abundance:  $p=0.76$ ; 9999 permutations in all cases).

## Results

Pollination service was studied in nine landscapes and for 135 coffee trees, covering a wide range of landscape conditions, both in composition and configuration aspects. Analyses at the three considered scales (Table 1), allowed us testing the effect of landscape structure on pollination.

A total of 22 flower-visiting bee species were collected, ranging from 2 to 10 at the landscape level and 0 to 5 at the tree level (Table 1). The richest tribe was Meliponini, with 12 species. The most abundant species was the honeybee *Apis mellifera* (Apini), followed by the stingless bees *Trigona spinipes*, *Trigona hyalinata*, *Paratrigona subnuda* and *Tetragonisca angustula* (Meliponini).

While native bee abundance, richness and diversity were not significantly affected by landscape variables (Table S1), landscape metrics were found to predict honeybee abundance and native bee community composition (Table 2). *Apis mellifera* abundance was positively associated with matrix composition at the landscape scale of 1 km radius (Table 2 and Fig. 3) and native bee community composition presented a negative relation with distance from forest at the tree level (Table 2 and Fig. 4).

Fruit set was the only pollination service indicator influenced by the pollination experiment ( $p<2e-16$ ,  $df=6$ ; Fig. 5). The mean proportion of flowers

turning into fruit (fruit set) was in average 28% higher in the open-pollination treatment ( $0.69\pm 0.27$ ) in relation to the obtained in bagged flowers ( $0.54\pm 0.30$ ). Considering these results, fruit set was the only fruit response analyzed in the subsequent models (see Table S2).

At the landscape level, fruit set was positively affected by *Apis mellifera* abundance and negatively affected by native bee abundance and diversity (Table 2 and Fig. 6). The difference between open pollination and bagged flower branches (gray shaded area in the figures) increased with increasing honeybee abundance, while decreased with increasing native bee abundance and diversity. However, at the tree level, fruit set was equally positively influenced by *Apis mellifera* abundance and native bee abundance and diversity (Table 2 and Fig.7). All models are presented in Table S3. In order to detect additional indirect effects of landscape variables on fruit set, we ran additional models using fruit set as the response variable and landscape metrics as predictors. In all cases, the null model was selected as the best model, indicating a lack of direct association between landscape structure and fruit set (Table S4).

## **Discussion**

In this study we assessed the influence of landscape structure on coffee pollination mediated by bees. By performing exclusion experiments in 135 coffee trees distributed across nine different landscapes, we were able to quantify the net bee pollination services, free of the confounding effects of coffee variety, micro-climatic conditions, and farm management. Furthermore,

by performing our analyses at different spatial scales, we were able to gain a broad perspective of the effect of landscape structure on coffee pollination.

Landscape structure influenced native bee community composition and honeybee abundance. However, the observed influence of landscape structure on bee community composition was weaker than expected. Specifically, no effect was found for native bee abundance, species richness or diversity. One possible explanation for this could be related to the range of landscape structure covered by our sampling. Previous studies that detected an effect of landscape structure on bees considered a wider range of distance to the forest. For example, Klein, Steffan-Dewenter & Tscharntke (2003b) found that the number of bee species visiting coffee flowers decreased with distance to the forest in a range 0 – 1415 meters. For other crops, Carvalheiro *et al.* (2010) and Carvalheiro *et al.* (2011) also found a decrease in abundance and species richness with distance to the forest, in ranges of 0 – 650 m and 28 – 925 m, respectively. We posit that our smaller range of distances to forest fragments (0 – 324 m) (Fig. S4) might be the reason explaining the lack of a stronger effect of landscape structure on bees. The absence of such an effect was also reported by Brosi *et al.* (2008) and Vergara & Badano (2009), who considered a smaller range of distance to forest. Nevertheless, our samples span the whole range of landscape composition found in our study region, and thus our results suggest that remnant forest patches are affecting native bee abundance, richness and diversity homogeneously in this coffee production region. In larger and mechanized farms, like those found in Brazilian Cerrado, coffee is produced in much larger patches, and thus isolation of coffee plantation to forest remnants

is higher. In these cases, we expect a steeper decrease in native bee abundance and richness as distance to forest increases.

In spite of our small range of distance to forest, we detected a shift on bee community composition with increasing distance to forest, similarly to the shifts observed in coffee plantations from Costa Rica (Brosi *et al.* 2008). These changes can be driven by differences in species foraging and nesting biology (Brosi *et al.* 2008). In our study, communities comprising species with a higher reported flight range, such as *Melipona quadrifasciata* and *Bombus morio*, were found further from forest fragments. *Dialictus* spp. were also found in more distant trees, probably because these bees nest in the ground in highly disturbed areas, and are thus less dependent on forest (Wcislo *et al.* 1993).

Honey bees, which also have a large flight capacity (Jaffé *et al.* 2010), did not respond to isolation or forest cover, but responded to matrix composition. Landscapes with a higher cover of pasture within 1 km radius presented a higher abundance of *Apis mellifera*. This pattern was already reported in the literature and is explained by the fact that *Apis* can potentially colonize isolated and small forest fragments, or isolated pasture trees, more easily than stingless bees (Brosi *et al.* 2008).

The presence of bees resulted in an increase in fruit set. The 28% higher fruit set production observed in our open pollination treatments compared to bagged flower branches is consistent with previous results found in Indonesia (27%; Klein, Steffan-Dewenter & Tschardtke 2003a) and in Brazil (11 – 14.6%; Amaral 1952, Nogueira-Neto 1959, De Marco & Coelho 2004), showing that the range of contribution of bees to *C. arabica* production is around 10% to 30%. These findings challenge physiological studies that argue that coffee fruit set is

not affected by the degree of pollination (DaMatta *et al.* 2007). However, unlike Classen *et al.* (2014), who found an increase in fruit weight by an average of 7.4%, we did not find a bee pollination effect on fruit size or weight.

As expected by previous results (revision in Ngo *et al.* 2011), changes in bee community affected *Coffea arabica* early fruit set, and this pattern was strong both at the landscape and the tree levels. Honeybee abundance had a clear positive influence in fruit set, both at the landscape and tree levels. Indeed, there is extensive evidence that honeybees are important coffee pollinators, and could be considered the most important pollinators in some areas (Ngo *et al.* 2011, Giannini *et al.* 2014 Roubik 2002). The success of *A. mellifera* pollination may come from its generally slower nectar intake rates, which might favor pollen transfer during floral visits (Roubik 1984). Additionally, individual foragers of honeybee visit more flowers during a foraging trip than individuals of other species (Roubik 1984). Although native bee pollination has been found to result in higher coffee fruit set in some regions (Garibaldi *et al.* 2013), the variation in fruit production was substantial, and in some cases honeybees produced a higher fruit set than native bees.

Native bee presence had opposing effects at the two considered spatial scales. Contrary to our expectation, at the landscape level native bee abundance and diversity had a negative effect on fruit set. Interestingly, at the tree level, native bee richness and diversity had a positive effect on the fruit set. While the tree level reflects the interaction between a specific bee community and fruit set in each coffee tree, the landscape level represents an average effect of bee community on fruit set. Our findings thus show that the effect of bee community in coffee pollination can change with the scale of the analyses.

Our results reinforce that wild pollinators enhance fruit set despite of honeybee abundance (Garibaldi *et al.* 2013) and that the presence of native bees could guarantee the stability of the pollination service at the tree level (Garibaldi *et al.* 2011).

Pollination efficiency probably varies between native bee species. For instance, solitary bees are the most efficient pollinators of *C. arabica* in Indonesia (Klein *et al.* 2003b), while social native bees are the most efficient pollinators of *C. canephora* in Uganda (Munyulli 2014). The opposing effects of honeybee and native bee abundance at the landscape level indicate that some native bee species can counter the positive effect of honeybees on coffee fruit set. Hence, the presence or higher abundance of some native bees species could be limiting the access of honeybees to flowers, hindering their pollination service. The more abundant native bee species, *Trigona spinipes*, has indeed been observed attacking and expelling honeybees from flowers (Minussi & Alves-dos-Santos 2007). This is a generalist and opportunistic pollinator, dominant in most pollinator networks, broadly distributed across South America, and considered the ecological equivalent of honeybees (Biesmeijer & Slaa 2006). However, *T. spinipes* is also an effective pollinator of coffee (Ngo *et al.* 2011). The detailed mechanisms mediating the influence of landscape structure on bee species, their interactions and, consequently, the provision of pollination services are still not clear. Future studies are thus needed to assess pollinator efficiency across different bee species, and quantify how it is affected by habitat loss. Likewise, there is a need to assess how different coffee varieties respond to pollinators.

Our results reinforce the importance of bees as efficient coffee pollinators, increasing fruit set. Furthermore, we show that native bee community composition and honeybee abundance are affected by landscape structure. Our findings also suggest that honeybees and native bees compete for floral resources, and that the relative importance of those groups for fruit set can change according to the spatial scale of the analyses. Our work thus highlights the importance of multi-scale analyses to understand the effect of the landscape structure on pollination services (Steffan-Dewenter *et al.* 2002).

The stronger influence of landscape structure on native bee community composition at the tree level than at the landscape level, suggests that land managers should consider small spatial scales, as suggested by Benjamin *et al.* (2014). The maintenance or creation of an heterogeneous landscape mosaics with abundant interfaces between forest and coffee plantations patches, limiting coffee tree distance to forest to < 300 m (which is below the mean foraging and dispersal distance of most pollinators; Keitt 2009), as observed in the study region (Fig. S4), should be an adequate strategy to maximize coffee pollination services. This is in agreement with a recent study which shows that landscape diversity may favor the maintenance of a greater diversity of floral visitors (Moreira *et al.* 2015). Despite the absence of a significant effect of forest cover on bee community and coffee pollination, the above conditions of isolation, with a reasonable habitat aggregation, will only be possible if forest cover is above 30% (Fig.S5), which can be considered as a minimum habitat amount in landscapes used for sun coffee plantations.

As an estimated 2101 km<sup>2</sup> of tropical forest are destroyed every year (Hansen *et al.* 2013), and the rate of land conversion to agriculture is expected

to further increase in response to a growing human population (Laurance *et al.* 2014), it is essential to understand the effects of landscape structure on crop pollination by tropical bees. Our study represents an important contribution in this direction, as it highlights that landscape structure can modulate pollinator communities and pollination services. From an applied perspective our work offers additional evidence that natural habitats are important to increase crop production, and reveals the minimum landscape conditions necessary to safeguard pollination services while aiding biodiversity conservation.

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# Figures

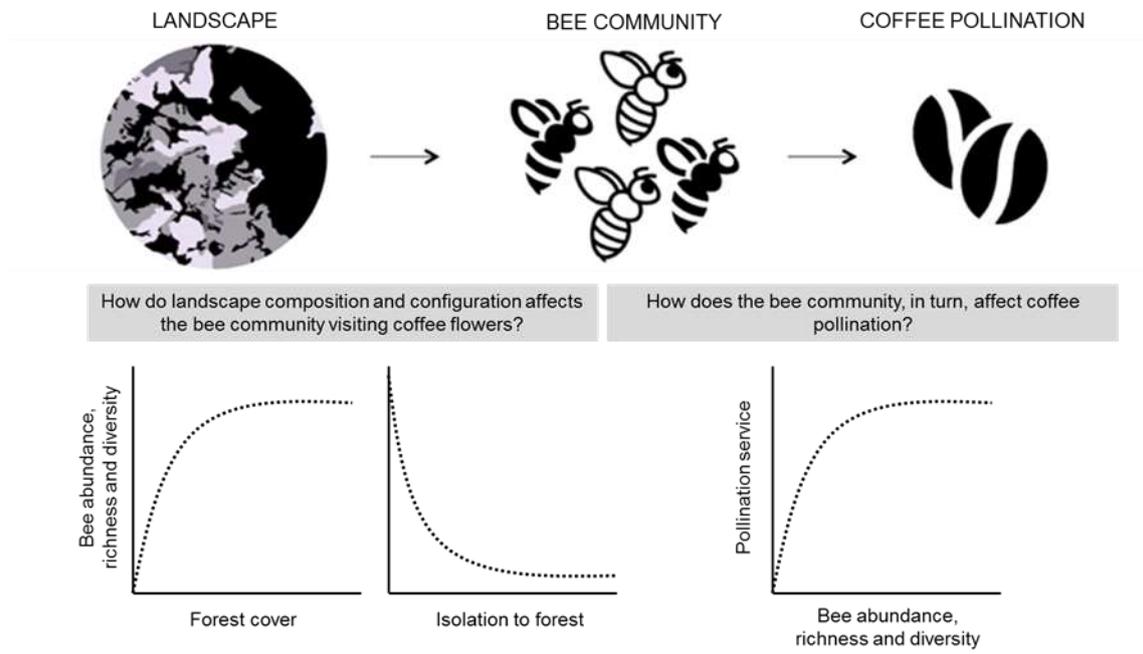


Figure 1. Study questions and expected results.

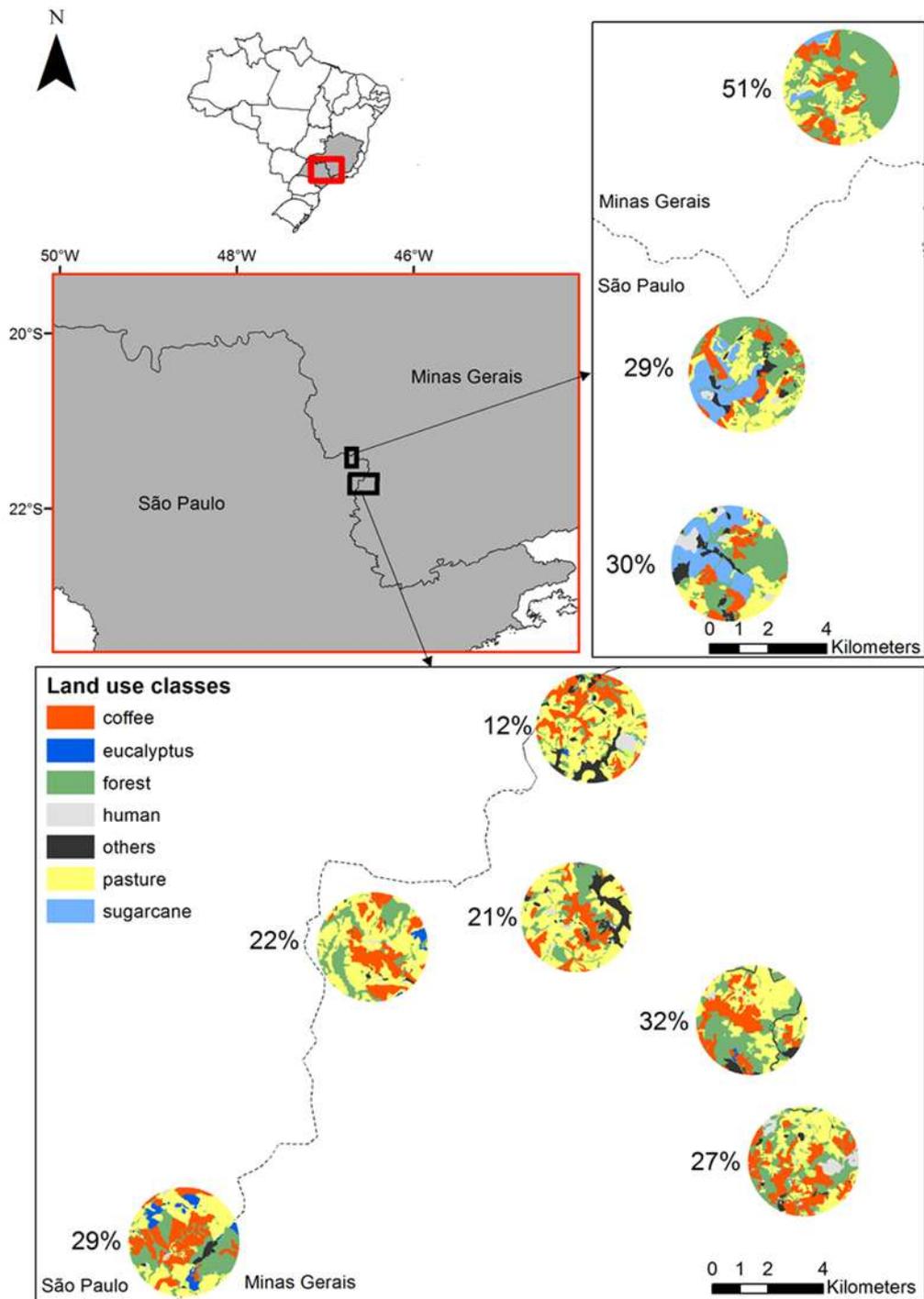


Figure 2. Location of the study landscapes in the States of São Paulo and Minas Gerais, Brazil. Land use and land cover maps are presented in a 2 km radius. The highlighted numbers next to the landscapes indicate forest cover.

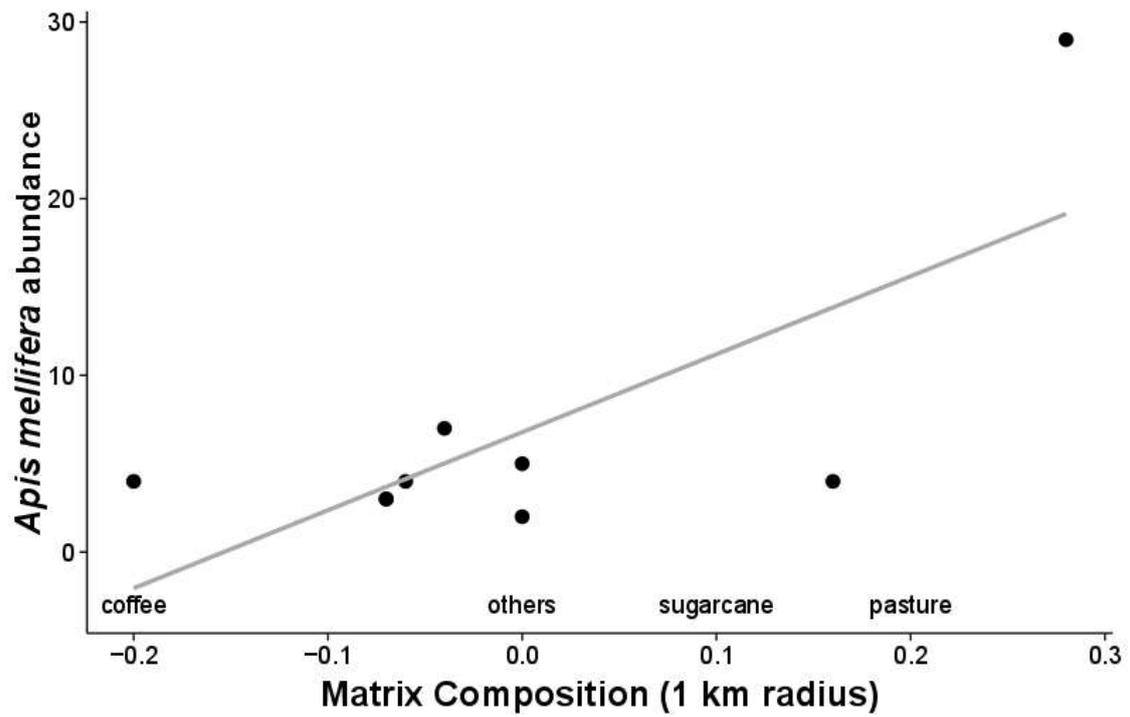


Figure 3. Relationship between *A. mellifera* abundance and matrix composition within 1 km radius for the nine study landscapes. The gray line shows the fitted model (Table 2).

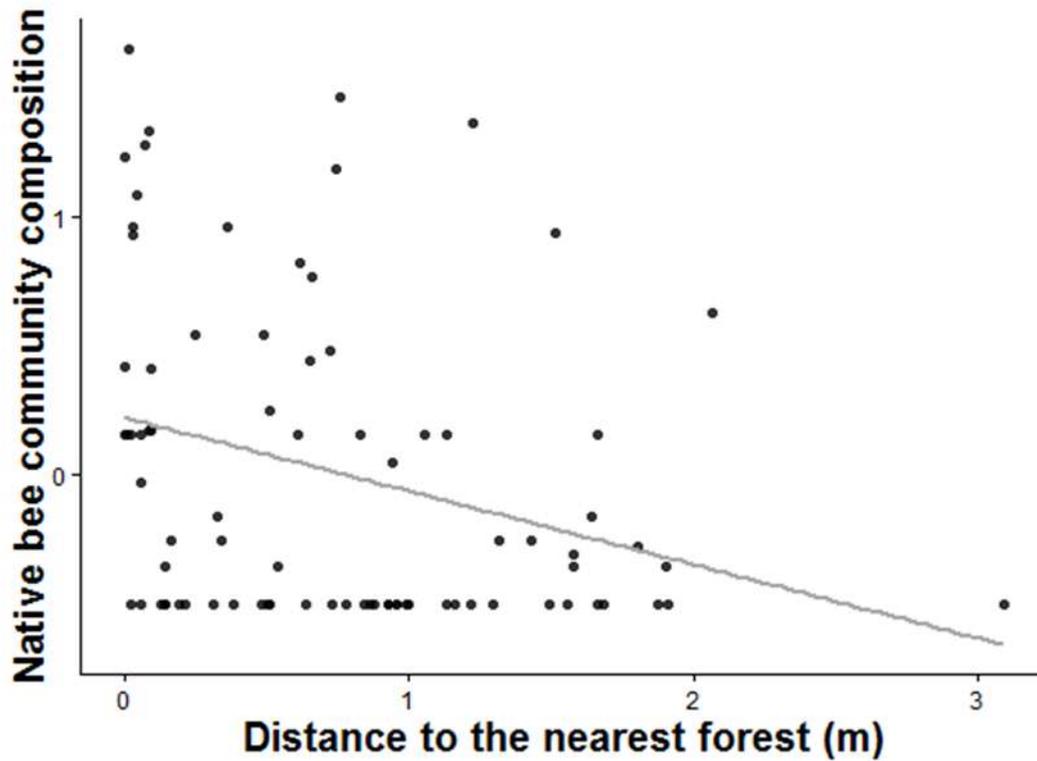


Figure 4. Relationship between native bee community composition (first PCoA axis) and distance to the nearest forest fragment (each point represent one tree; N= 119). Higher values of native bee composition indicate communities with *Melipona quadrifasciata*, *Bombus morio* or *Dialictus* spp. The gray line shows the fitted model (See Table 2).

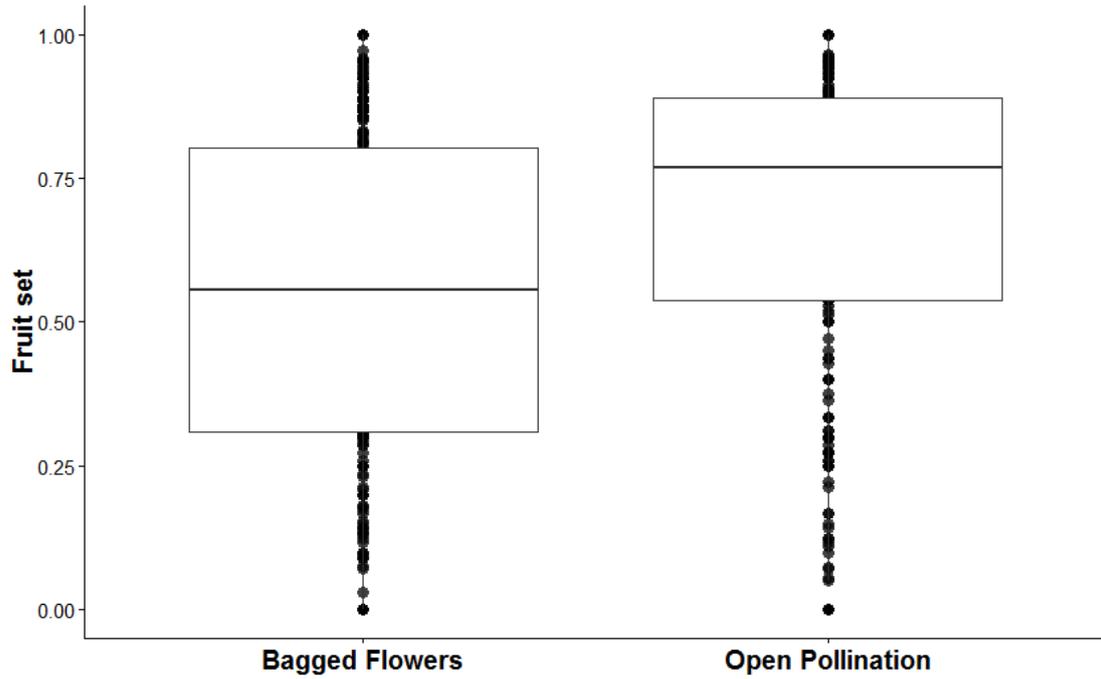


Figure 5. Variation in fruit set (number of fruits/ number of flowers) between the bagged flowers and the open pollination treatments. Mean increase value is 28%. Middle black bars represent median value, boxes are first and third quartiles, and whiskers are 95% confidence intervals.

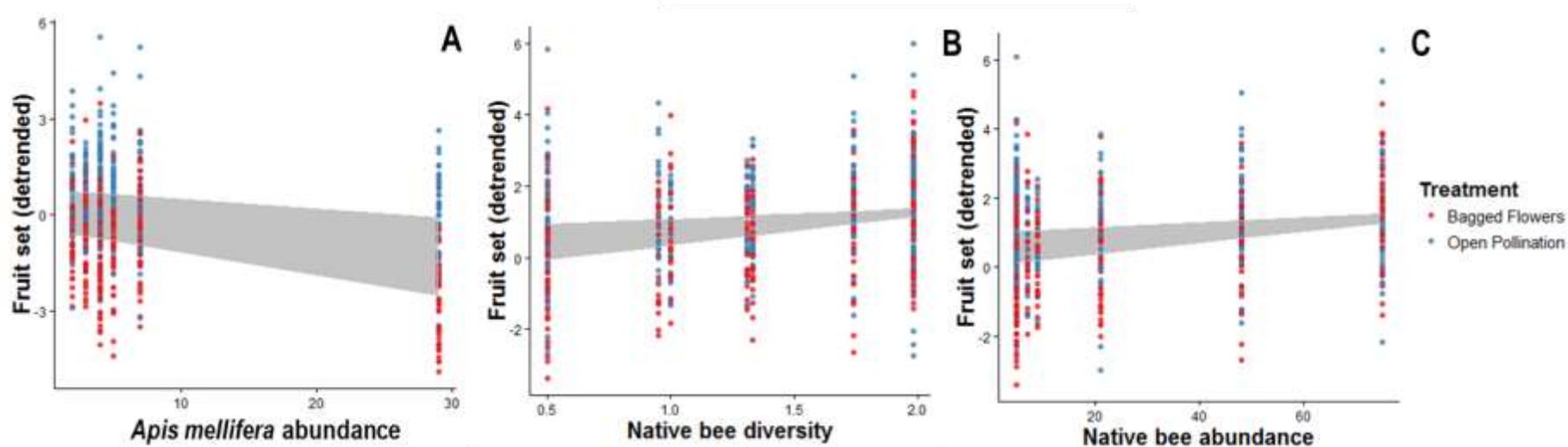


Figure 6. Relationship between fruit set and *Apis mellifera* abundance (A), native bee diversity (B) and native bee abundance (C) at the landscape level. The y-axis shows the detrended fruit set, to show the correct relationship between response and particular predictor variables (the effect of the other predictor variables has been subtracted out). Each point represents one fruit data in bagged flowers (red) and open pollination (blue) branches. The gray shaded areas represent the difference between treatments.

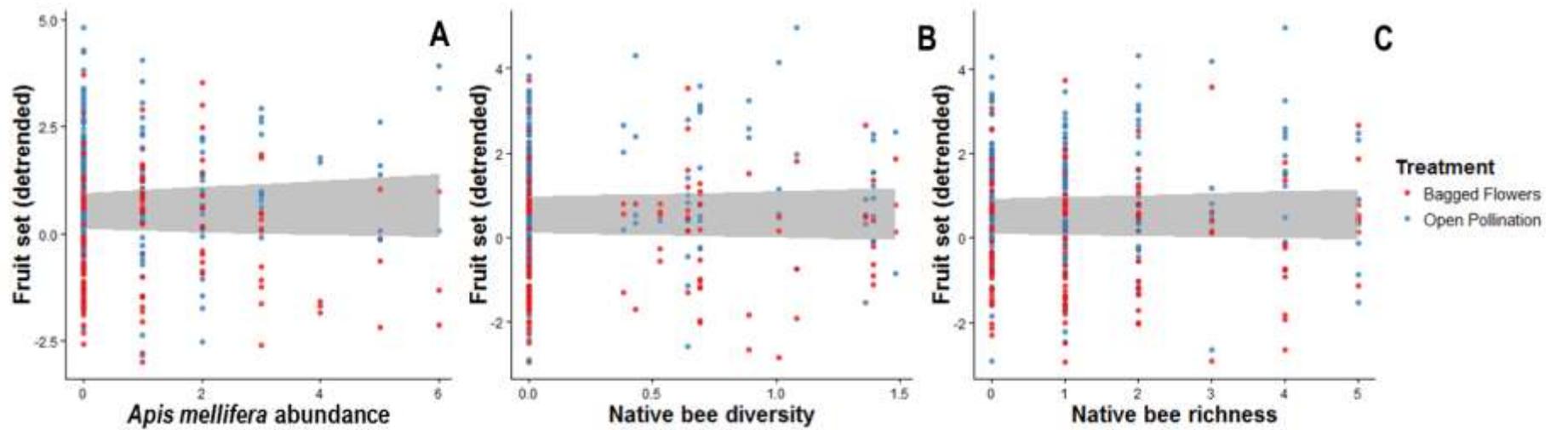


Figure 7. Relationship between fruit set and *Apis mellifera* abundance (A), native bee diversity (B) and native bee abundance (C) at the tree level. The y-axis shows the detrended fruit set, to show the correct relationship between response and particular predictor variables (the effect of the other predictor variables has been subtracted out). Each point represents one fruit data in bagged flowers (red) and open pollination (blue) branches. The gray shaded areas represent the difference between treatments.

## Tables

Table1. Landscape metrics, bee community variables and fruit production indicators at different levels. Note that for bee variables, there is just one value at the landscape level since the sampling trees were located just in the center of the landscapes (inner 1 km radius).

Variables	Level	Value range
<b>LANDSCAPE METRICS</b>		
<i>Composition</i>		
Forest cover (%)	Landscape (2 km)	12 – 51
	Landscape (1 km)	9 – 45
	Tree (300 m)	11 – 84
Matrix composition (2nd axis PCA value)	Landscape (2 km)	(-0.17) – 0.12
	Landscape (1 km)	(-0.20) – 0.28
<i>Configuration</i>		
Proximity index	Landscape (2 km)	22 – 5178
	Landscape (1 km)	8 – 284
Distance to the nearest forest fragment (m)	Tree	0 – 324
<b>BEE COMMUNITY</b>		
Native bee abundance	Landscape	5 – 75
	Tree	0 – 22
Native bee species richness	Landscape	2 – 10
	Tree	0 – 5
Native bee Shannon diversity index	Landscape	0.5 – 1.98
	Tree	0 – 1.48
Native bee community composition (1st axis PCoA value)	Landscape	(-1.17) – 0.66
	Tree	(-0.5) – 1.65
<i>Apis mellifera</i> abundance	Landscape	2 – 29
	Tree	0 – 6
<b>FRUIT PRODUCTION</b>		
Number of flower	Branch	1 – 74
Number of fruit	Branch	0 – 60
Fresh size (mm)	Branch	8.01 – 16.51
Dry weight (g)	Branch	0.06 – 2.08

Table 2. Summary statistics for the selected models ( $\Delta AIC < 2$ ) of landscape structure effect on bee community (a) and bee community effect on fruit production (b).

Response variable	Level	N	Predictors	Estimate	p-values
<b>(a) Landscape structure effect on bee community</b>					
<i>Apis mellifera</i> abundance	Landscape	9	Matrix composition 1 km		
			(Intercept)	6.78	0.01 *
Native bee composition	Tree	90	Distance		
			(Intercept)	0.21	0.17
			Distance	-0.26	8.81E-03 **
<b>(b) Bee community effect on pollination service</b>					
Fruit Set	Landscape	575	<i>Apis mellifera</i> abundance*Treatment + Native bee diversity*Treatment		
			(Intercept)	0.46	0.14
			<i>Apis mellifera</i> abundance	1.24	<2E-16 ***
			Native bee diversity	-0.07	8.55E-09 ***
			Treatment open pollination	0.81	6.63E-06 ***
			<i>Apis mellifera</i> abundance*Treatment open pollination	0.04	4.59E-08 ***
			Native bee diversity*Treatment open pollination	-0.52	1.81E-07 ***
Fruit Set	Landscape	575	<i>Apis mellifera</i> abundance*Treatment + Native bee abundance*Treatment		
			(Intercept)	0.06	0.76
			<i>Apis mellifera</i> abundance	0.92	<2E-16 ***
			Native bee abundance	0.56	1.87E-06 ***
			Treatment open pollination	-0.05	3.56E-06 ***
			<i>Apis mellifera</i> abundance*Treatment open pollination	-0.30	2.13E-06 ***
			Native bee abundance*Treatment open pollination	0.02	3.51E-04 ***
Fruit Set	Tree	375	<i>Apis mellifera</i> abundance*Treatment		
			(Intercept)	0.09	0.73
			<i>Apis mellifera</i> abundance	0.88	<2E-16 ***
			Treatment open pollination	-0.03	0.71
			<i>Apis mellifera</i> abundance*Treatment open pollination	0.11	0.02 *
Fruit Set	Tree	375	<i>Apis mellifera</i> abundance*Treatment + Native bee diversity*Treatment		
			(Intercept)	0.12	0.66
			<i>Apis mellifera</i> abundance	0.82	<2E-16 ***
			Native bee diversity	-0.03	0.76
			Treatment open pollination	-0.10	0.71
			<i>Apis mellifera</i> abundance*Treatment open pollination	0.10	0.04 *
			Native bee diversity*Treatment open pollination	0.24	0.09
Fruit Set	Tree	375	Native bee diversity*Treatment		
			(Intercept)	0.09	0.73
			Native bee diversity	0.90	<2E-16 ***
			Treatment open pollination	-0.10	0.71
			Native bee diversity*Treatment open pollination	0.29	0.04 *
Fruit Set	Tree	375	Treatment		
			(Intercept)	0.06	0.81
			Treatment open pollination	0.98	<2E-16 ***
Fruit Set	Tree	375	<i>Apis mellifera</i> abundance*Treatment + Native bee richness*Treatment		
			(Intercept)	0.13	0.65
			<i>Apis mellifera</i> abundance	0.80	<2E-16 ***
			Native bee richness	-0.03	0.74
			Treatment open pollination	-0.03	0.74
			<i>Apis mellifera</i> abundance*Treatment open pollination	0.10	0.04
			Native bee richness*Treatment open pollination	0.07	0.13

## Supporting Information

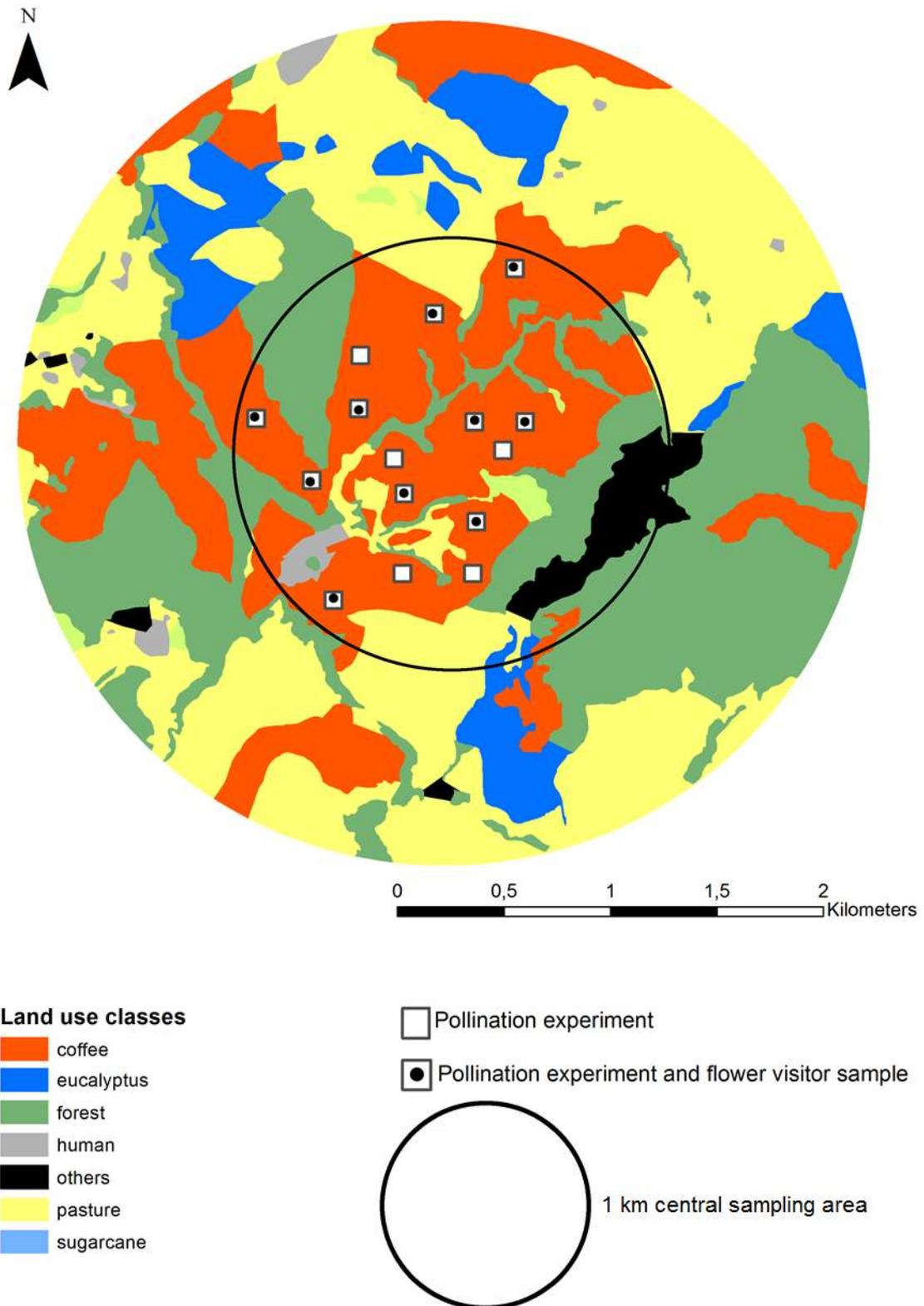


Figure S1. Location of the coffee trees used for pollination experiments and for visitors sampling in one studied landscape, with 29% forest cover.

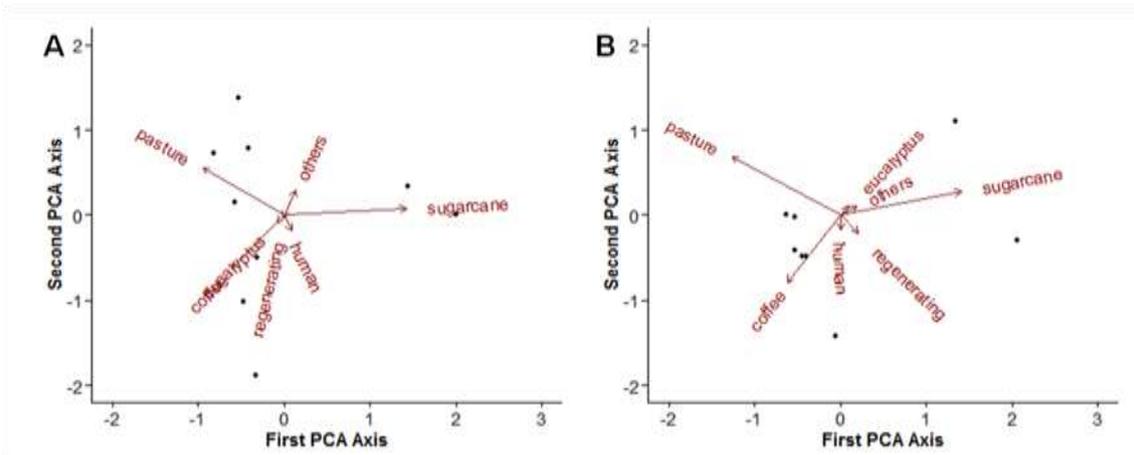


Figure S2. Principal component analysis (PCA) for the matrix composition variable in 2 km (A) and 1 km (B) radii. Each point represents one landscape and the names with arrows a land use or land cover class. The second axis was the axis used as variable in the models.

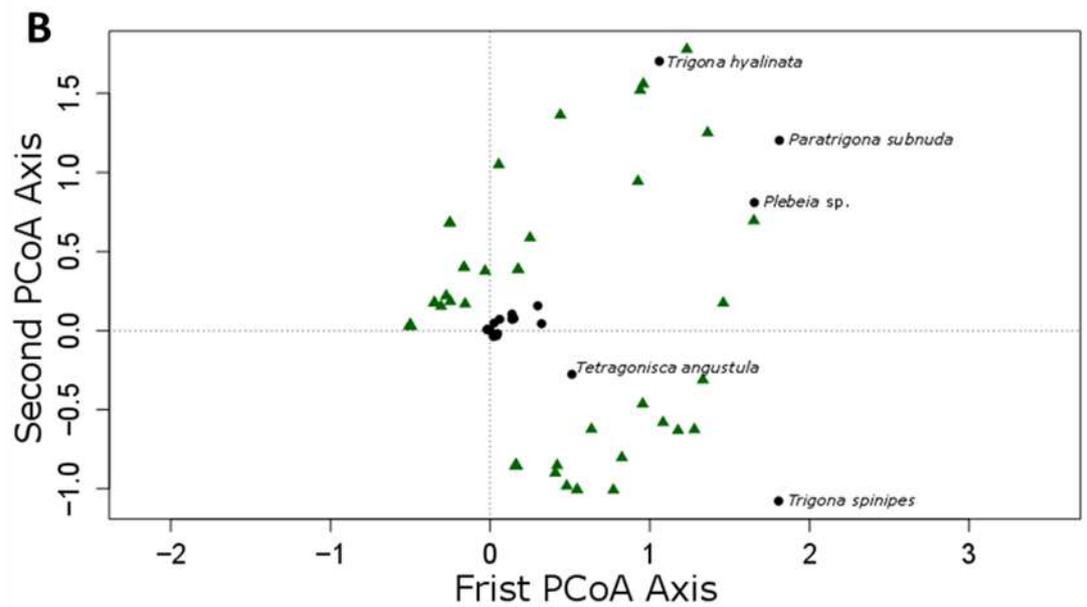
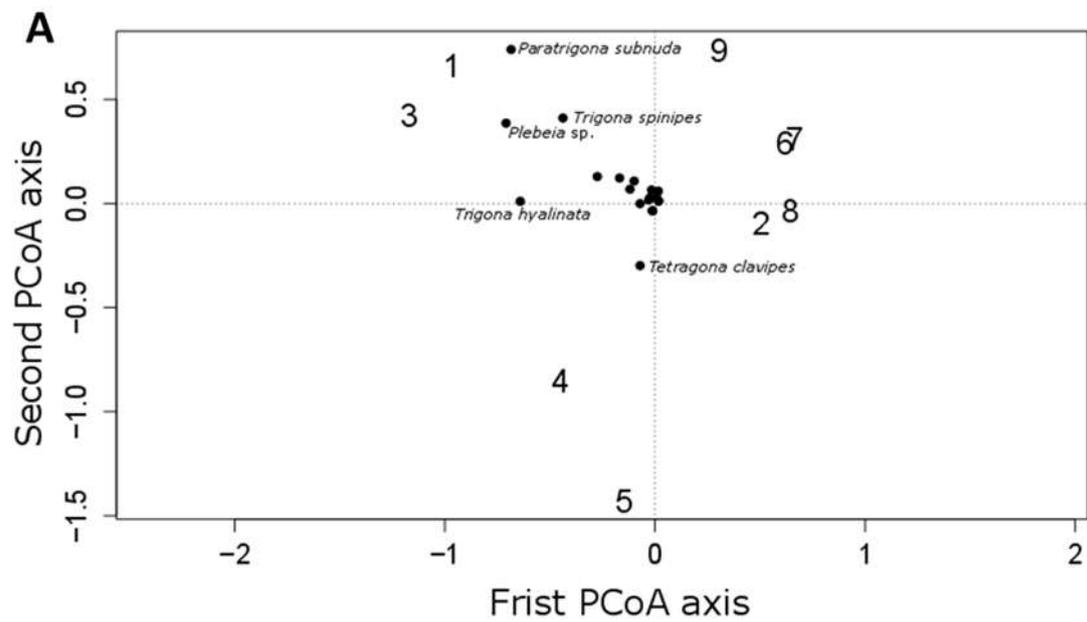


Figure S3. Principal coordinate analysis (PCoA) for the bee community composition variable at landscape (A) and tree (B) levels. In A, landscapes (numbers) and native bee species (points) are represented. In B, coffee tree (green triangles) and native bee species (points) are represented. The five most influential species are named. The first axis was the axis used as variable in the models.

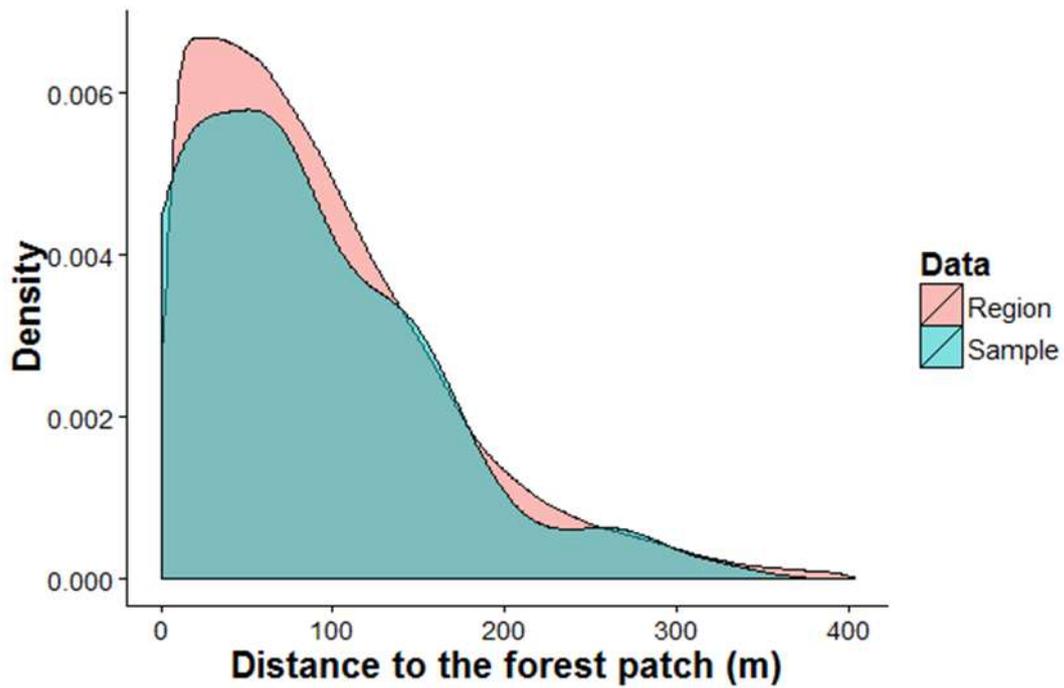


Figure S4. Density curves of distance to the nearest forest, for all coffee plantations in the studied landscapes (“Region” – in pink) and only for our sampled trees (“Sample” – in blue). The “Region” data was calculated considering all coffee pixels inside the 1 km central radius across the 9 landscapes.

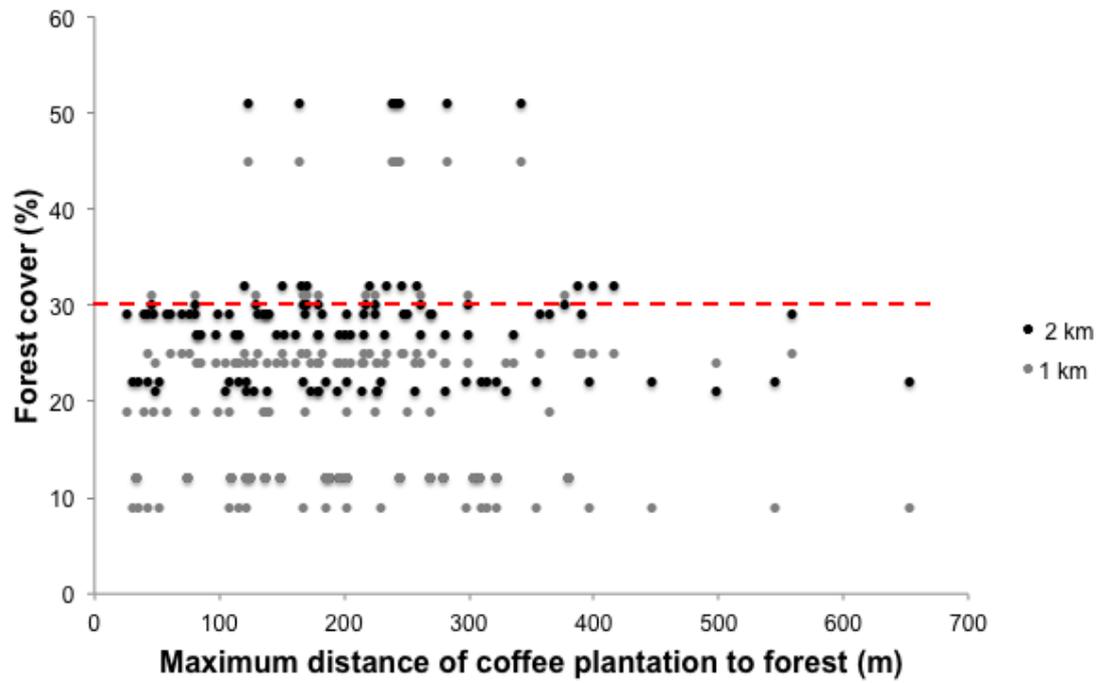


Figure S5. Relationship between landscapes forest cover in 1 and 2 km and the maximum distance of a coffee plantation to forest. Each point represents a coffee plantation (ArcGIS polygon), not limited to the 1 km central area.

Table S1. Model selection for the effect of landscape structure on bee community (step 1), at landscape and tree levels.

<i>LANDSCAPE LEVEL</i>				<i>TREE LEVEL</i>		
	AICc	ΔAICc	Weight	AIC	ΔAIC	Weight
(a) Native bee abundance				(a) Native bee abundance		
<b>NULL</b>	<b>88.4</b>	<b>0</b>	<b>0.315</b>	<b>Distance</b>	<b>452.9</b>	<b>0</b> <b>0.524</b>
<b>Proximity Index 1 km</b>	<b>88.7</b>	<b>0.24</b>	<b>0.279</b>	<b>NULL + random</b>	<b>453.2</b>	<b>0.31</b> <b>0.449</b>
<b>Forest Cover 1 km</b>	<b>89.4</b>	<b>1</b>	<b>0.191</b>	Forest Cover 300m + Distance	460.2	7.29 0.014
Proximity Index 2 km	90.8	2.41	0.094	Forest Cover 300m	460.5	7.64 0.011
Forest Cover 2 km	91.6	3.22	0.063	Forest Cover 300m * Distance	464.5	11.61 0.002
Matrix Composition 2 km	93.2	4.73	0.029	NULL	467.9	15.06 0
Matrix Composition 1 km	93.2	4.78	0.029			
(b) Native bee richness				(b) Native bee richness		
<b>NULL</b>	<b>51.7</b>	<b>0</b>	<b>0.531</b>	<b>Distance</b>	<b>268.5</b>	<b>0</b> <b>0.675</b>
Proximity Index 2 km	54.7	2.98	0.119	<b>NULL + random</b>	<b>270.1</b>	<b>1.58</b> <b>0.307</b>
Forest Cover 1 km	55.3	3.59	0.088	Forest Cover 300m + Distance	277.3	8.75 0.009
Proximity Index 1 km	55.6	3.87	0.077	NULL	278.2	9.63 0.005
Matrix Composition 1 km	55.7	3.94	0.074	Forest Cover 300m	279.2	10.62 0.003
Matrix Composition 2 km	56.2	4.48	0.056	Forest Cover 300m * Distance	284.1	15.61 0
Forest Cover 2 km	56.3	4.57	0.054			
(c) Native bee diversity				(c) Native bee diversity		
<b>NULL</b>	<b>20.3</b>	<b>0</b>	<b>0.618</b>	<b>NULL + random</b>	<b>82.1</b>	<b>0</b> <b>0.66</b>
Proximity Index 2 km	24.6	4.22	0.075	<b>Distance</b>	<b>83.6</b>	<b>1.54</b> <b>0.305</b>
Matrix Composition 1 km	24.8	4.46	0.066	NULL	88.4	6.29 0.028
Forest Cover 1 km	24.9	4.51	0.065	Forest Cover 300m	92.3	10.22 0.004
Matrix Composition 2 km	24.9	4.59	0.062	Forest Cover 300m + Distance	93.3	11.26 0.002
Proximity Index 1 km	25.1	4.75	0.058	Forest Cover 300m * Distance	104	21.92 0
Forest Cover 2 km	25.1	4.8	0.056			
(d) Native bee composition				(d) Native bee composition		
<b>NULL</b>	<b>24.5</b>	<b>0</b>	<b>0.397</b>	<b>Distance</b>	<b>146.5</b>	<b>0</b> <b>0.739</b>
Forest Cover 1 km	25.7	1.19	0.219	NULL + random	148.6	2.16 0.251
Proximity Index 2 km	26.6	2.11	0.138	NULL	156.6	10.1 0.005
Proximity Index 1 km	27.4	2.95	0.091	Forest Cover 300m + Distance	157.1	10.63 0.004
Matrix Composition 2 km	28.4	3.91	0.056	Forest Cover 300m	159.5	13.03 0.001
Forest Cover 2 km	28.5	3.99	0.054	Forest Cover 300m * Distance	167.2	20.7 0
Matrix Composition 1 km	28.8	4.36	0.045			
(e) <i>Apis mellifera</i> abundance				(e) <i>Apis mellifera</i> abundance		
<b>Matrix Composition 1 km</b>	<b>66.7</b>	<b>0</b>	<b>0.615</b>	<b>NULL + random</b>	<b>262.4</b>	<b>0</b> <b>0.722</b>
NULL	68.9	2.23	0.201	<b>Distance</b>	<b>264.4</b>	<b>1.97</b> <b>0.27</b>
Forest Cover 2 km	70.8	4.12	0.078	Forest Cover 300m	272	9.59 0.006
Forest Cover 1 km	72.5	5.79	0.034	Forest Cover 300m + Distance	274	11.62 0.002
Proximity Index 1 km	73	6.29	0.027	NULL	278	15.54 0
Matrix Composition 2 km	73.1	6.44	0.025	Forest Cover 300m * Distance	282	19.59 0
Proximity Index 2 km	73.5	6.83	0.02			

Table S2. Model selection for the effect of the exclusion experiment on fruit production indicators.

FRUIT VARIABLES	AIC	$\Delta$ AIC	Weight
(a) Fruit set			
<b>Treatment</b>	<b>3368</b>	<b>0</b>	<b>1</b>
NULL + Random	3668.1	300.14	0
NULL	5171.2	1803.23	0
(b) Fresh fruit size			
<b>NULL + Random</b>	<b>1002.2</b>	<b>0</b>	<b>0.782</b>
Treatment	1004.8	2.55	0.218
NULL	1104.4	102.13	0
(c) Fruit dry weight			
<b>NULL + Random</b>	<b>165.7</b>	<b>0</b>	<b>0.947</b>
Treatment	171.4	5.75	0.053
NULL	295	129.31	0

Table S3. Model selection for the effect of bee community on fruit set (step 2), at landscape and tree levels. The additive models in this step only considered bee variables that were not correlated with each other.

LANDSCAPE LEVEL			TREE LEVEL				
	AIC	ΔAIC	Weight		AIC	ΔAIC	Weight
Fruit set			Fruit set				
<b><i>Apis mellifera</i> abundance*Treatment + Native bee diversity*Treatment</b>	<b>3332.3</b>	<b>0.00</b>	<b>0.535</b>	<b><i>Apis mellifera</i> abundance*Treatment</b>	<b>2036.4</b>	<b>0.00</b>	<b>0.244</b>
<b><i>Apis mellifera</i> abundance*Treatment + Native bee abundance*Treatment</b>	<b>3334.1</b>	<b>1.85</b>	<b>0.212</b>	<b><i>Apis mellifera</i> abundance*Treatment + Native bee diversity*Treatment</b>	<b>2037.5</b>	<b>1.12</b>	<b>0.139</b>
<i>Apis mellifera</i> abundance*Treatment + Native bee composition*Treatment	3334.9	2.61	0.145	<b>Native bee diversity*Treatment</b>	<b>2037.8</b>	<b>1.45</b>	<b>0.118</b>
<i>Apis mellifera</i> abundance*Treatment + Native bee richness*Treatment	3335.4	3.20	0.108	<b>Treatment</b>	<b>2037.9</b>	<b>1.54</b>	<b>0.113</b>
Native bee abundance*Treatment	3349.8	17.59	0.000	<b><i>Apis mellifera</i> abundance*Treatment + Native bee richness*Treatment</b>	<b>2038.1</b>	<b>1.68</b>	<b>0.105</b>
Native bee composition*Treatment	3355.9	23.69	0.000	Native bee richness*Treatment	2038.5	2.10	0.085
<i>Apis mellifera</i> abundance*Treatment	3359.6	27.33	0.000	<i>Apis mellifera</i> abundance*Treatment + Native bee composition*Treatment	2038.5	2.12	0.085
Native bee diversity*Treatment	3364.9	32.62	0.000	Native bee composition*Treatment	2039.7	3.30	0.047
Native bee richness*Treatment	3365.1	32.83	0.000	<i>Apis mellifera</i> abundance*Treatment + Native bee abundance*Treatment	2039.8	3.38	0.045
Treatment	3368.0	35.72	0.000	Native bee abundance*Treatment	2041.6	5.19	0.018
NULL	3668.1	335.86	0.000	NULL	2281.0	244.59	0.000

Table S4. Model selection for landscape effects on fruit set in landscape and tree levels.

<b>LANDSCAPE LEVEL</b>	AICc	$\Delta$ AICc	Weight	<b>TREE LEVEL</b>	AIC	$\Delta$ AIC	Weight
Fruit set				Fruit set			
Forest Cover 2 km	3667	0	0.245	NULL + random	3173	0	0.544
Proximity Index 2 km	3667.7	0.76	0.168	Distance	3174	1.57	0.248
Proximity Index 1 km	3667.9	0.91	0.155	Forest Cover 300m	3175	1.92	0.208
NULL + random	3668.1	1.12	0.14				
Forest Cover 1 km	3668.2	1.24	0.132				
Matrix Composition 1 km	3668.6	1.63	0.108				
Matrix Composition 2 km	3670.1	3.12	0.051				

# Overall Discussion and Conclusions

Landscape structure in the study region influenced native bee community composition and honeybee abundance. Moreover, the presence of bees resulted in a 28% increase in coffee fruit set. *Apis mellifera* abundance positively affected fruit set, while the composition of the native bee community affected fruit set differently at different scales (Fig. 1).

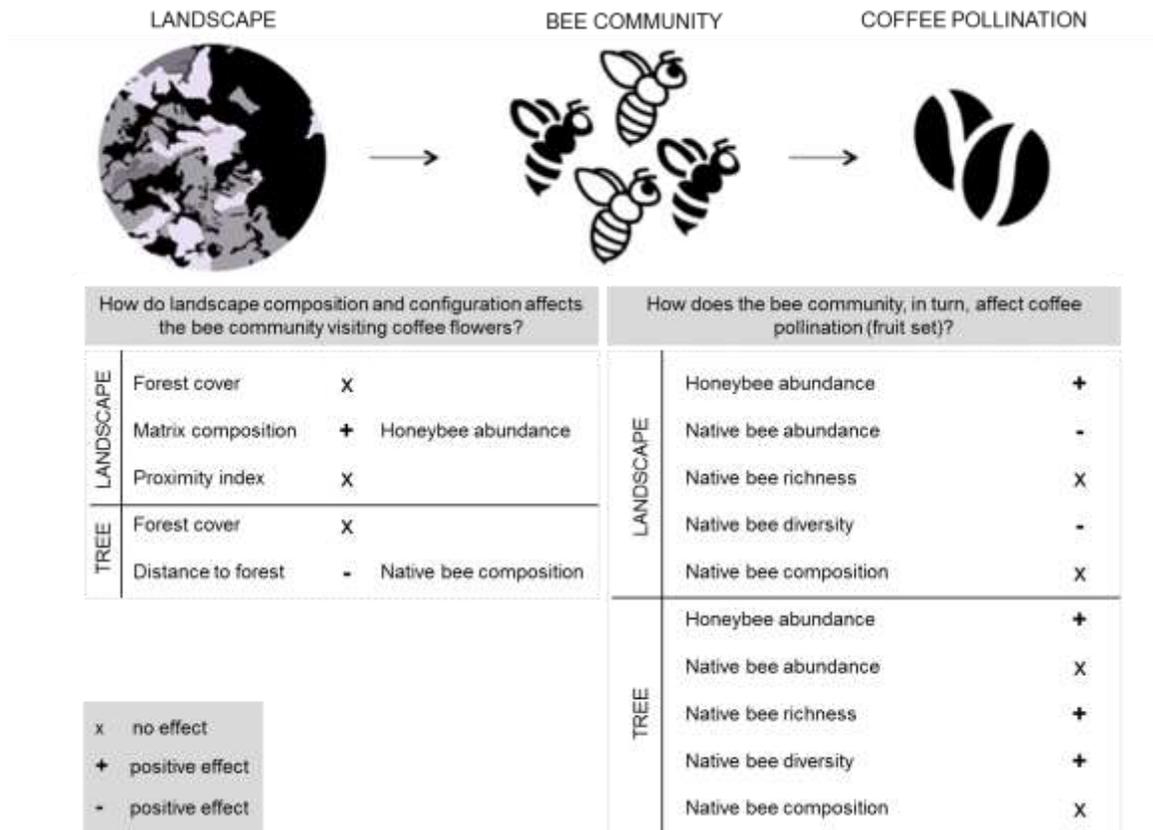


Figure 1. Main effects of landscape structure on bee community and coffee pollination in nine agricultural landscapes located in northern São Paulo and southern Minas Gerais States.

The results of this study help to understand the effects of landscape composition and configuration on coffee pollination by tropical bees. The results further reinforce the importance of bees as efficient coffee pollinators, increasing fruit set. They also illustrate that the response of fruit set to the presence/diversity of native bees varies at different analyzed spatial scales.

Our findings can be used to promote a more sustainable coffee production, which integrate economic gains with biodiversity conservation. The studied landscapes seem already good enough to maintain a rich bee community. Sun-coffee plantations can thus favor pollination services if situated in landscapes with appropriated composition and configuration (e.g., landscape mosaics with abundant interfaces between forest and coffee plantations, < 300 m of coffee tree distance to forest, > 30% of forest cover), making those landscapes more similar to tropical agroforestry systems and shaded coffee cultures in terms of bee species richness (Table 1).

Table 1. Comparison between studies in agroforestry coffee plantations and our study, regarding the bee species richness. It is important to notice that Ricketts et al. 2004 sampled bees in two different years.

Reference	Study region	Bee species	Coffee management	Maximum distance to forest	Minimum distance to forest
Our study	SouthEast, Brazil	22	Sun coffee	324	0
Klein, Steffan-Dewenter & Tschamtk 2003a	Central Sulawesi, Indonesia	29	Agroforestry	no information	no information
Ricketts <i>et al.</i> 2004	Valle General, Costa Rica	40	Shaded coffee	1600	50
Veddeler <i>et al.</i> 2008	Manabi, Ecuador	29	Agroforestry	no information	no information

This study also shows that maintaining bees close to plantations can be positive to coffee production. This could be achieved by introducing domesticated bees or by managing the landscape in order to optimize the pollination service

from native bees. The first option was adopted in some areas from India, where farmers controlled the timing of flowering through irrigation and managed domesticated honeybees hives. By this way, farmers effectively reduced the dependency on nearby forest cover for pollinator services, but these management practices incur costs that not every farmer could cover (Boreux *et al.* 2013). If the landscape is not too degraded, the second option can be better in terms of cost/benefit, once remnants of native habitat can provide pollinators species for free, and depending on the landscape structure, this service can be very effective. Particularly, our results suggest that landscapes where coffee plantations are at less than 300 meters from forest fragments seem to favor pollination services.

Additionally, we found a similar bee species composition in our landscapes with those obtained in the same region 66 to 10 years ago (Carvalho & Krug 1949, Nogueira-Neto *et al.* 1959, Amaral 1952, Malerbo-Souza *et al.* 2003, De Marco & Coelho 2004). Apparently there was few changes in the composition of bee species in coffee plantations in the last 66 years, at least for the most abundant ones. One can suppose then that the impacts of this highland coffee production might be stagnated. However, this situation may change rapidly with the recent modifications of the landscape structure. Indeed, due to financial problems, many farmers are substituting coffee plantations with pasture, sugarcane or Eucalyptus plantations, crops that might have negative impacts on native bee composition (personal observation), while favoring an increase in the abundance of honeybees.

Concluding, the study generated data on the relationship between landscape structure, bee community composition and ecosystem services that can provide reference to legal instruments and management plans, especially regarding the gain on fruit production in the presence of bees. Farmers and decision makers can use our results to design agricultural landscapes that facilitate bee movements between forest patches, allowing them to cross the coffee matrix, providing pollination service. Those results are particularly relevant given the historical competition for land between those who focus on the economic development and those who seek for biodiversity conservation, evidenced by discussions on the recent changes in the Brazilian Forest Code (Metzger, 2010). Our results can be a first step in the definition of adequate landscape structures for sun-coffee production, which optimize the positive effects of forest set-asides on coffee pollination, improving coffee production and at the same time allowing the maintenance of a rich and diversified bee community.

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## Resumo

Apesar de vários estudos terem demonstrado que a presença de abelhas resulta em aumento da produtividade de culturas agrícolas, os mecanismos que determinam a eficácia da polinização em escalas espaciais mais amplas ainda são desconhecidos. Avaliamos a influência da composição e configuração da paisagem sobre a composição da comunidade de abelhas e a polinização do café (*Coffea arabica*). Nosso estudo foi realizado em uma das regiões cafeeiras mais importantes do Brasil, em nove paisagens compostas de cafezais e diferentes quantidades de remanescentes de Mata Atlântica. Utilizando experimentos de exclusão floral, avaliamos a polinização em 15 pés de café por paisagem. A eficiência da polinização foi medida através da contagem e pesagem dos frutos formados. Também coletamos e identificamos os visitantes florais. Nossas análises foram feitas no nível de paisagem, com 1 e 2 km de raio, e no nível do pé de café, com 300 m de raio em torno de cada árvore. Foram coletados 241 indivíduos de abelhas e identificadas um total de 22 espécies. A abelha *Apis mellifera* (Apini) foi a espécie mais abundante, seguida de *Trigona spinipes* (Meliponini). A abundância *A. mellifera* foi afetada pela composição da matriz na paisagem e a composição da comunidade de abelhas nativas mudou com a distância ao fragmento florestal mais próximo. A presença das abelhas, por sua vez, resultou em um aumento 28% na produção de frutos. A abundância de *A. mellifera* afetou positivamente a frutificação, enquanto a composição da comunidade de abelhas nativas afetou a frutificação de modo diferente no nível da paisagem e do pé de café. Nossos resultados indicam que a estrutura da paisagem afeta a composição da comunidade de visitantes florais e que as flores expostas às abelhas apresentam um aumento na frutificação. Embora nossos resultados não permitam separar claramente os mecanismos responsáveis pelo aumento observado na frutificação, nosso trabalho mostra que o serviço de polinização das abelhas pode ser afetado pela estrutura da paisagem. Estes resultados podem ser utilizados na conservação e planejamento agrícola a fim de maximizar a produção de culturas e, ao mesmo tempo, conservar a biodiversidade e o serviço de polinização.

## Abstract

Although several studies have shown that the presence of bees results in increased crop yields, the mechanisms that determine pollination effectiveness on broader spatial scales are still largely unknown. We evaluated the influence of landscape composition and configuration over bee community composition and coffee (*Coffea arabica*) pollination. Our study was undertaken in one of the most important coffee-producing regions of Brazil, and comprised nine landscapes of sun coffee plantations surrounded by different amounts of Atlantic Forest remnants. Using floral exclusion experiments we evaluated pollination effectiveness in 15 coffee trees per landscape. Pollination effectiveness was measured by counting and weighing the fruit set. We also sampled the bees visiting coffee flowers. Our analyses were made at the landscape level, with 1 and 2 km radii, and at the coffee tree level, with 300 m radius around each tree. We collected 241 bee individuals and identified a total of 22 species. The honeybee *Apis mellifera* (Apini) was the most abundant species followed by *Trigona spinipes* (Meliponini). Honeybee abundance was affected by landscape matrix composition while native bee community composition changed with distance to the nearest forest fragment. The presence of bees resulted in an increase in coffee fruit set of 28%. *A. mellifera* abundance positively affected fruit set at both levels, while the composition of the native bee community affected fruit set differently at the landscape level than at the tree level. Landscape structure was found to affect the community composition of floral visitors, and coffee flowers exposed to bees showed an increase in fruit set compared to flowers excluded from pollinators. Although our results do not allow disentangling the mechanisms responsible for the observed increase in fruit set, our work shows that bee pollination services can be affected by landscape structure. These findings can be used in conservation and agricultural planning to maximize crop production while safeguarding biodiversity and the provision of pollination services.