

Universidade de São Paulo

Instituto de Biociências

Adrian David González Chaves

**COBERTURA FLORESTAL VS. ISOLAMENTO: EFEITO DA PAISAGEM SOBRE A
PROVISÃO DEMANDA E FLUXO DO SERVIÇO DE POLINIZAÇÃO**

**FOREST COVER vs. FOREST ISOLATION: THE LANDSCAPE EFFECT ON
POLLINATION SERVICE SUPPLY, DEMAND AND FLOW TO COFFEE CROP**

São Paulo

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Dissertação apresentada ao Instituto de Biociências da Universidade de São Paulo, para a obtenção de Título de Mestre em Ciências, na Área de Ecologia de Ecossistemas Terrestres e Aquáticos.

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Epígrafe

*...It is when we act freely,
for the sake of the action itself
rather than for ulterior motives,
that we learn to become more
than what we were.*

Mihaly Csikszentmihalyi

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COBERTURA FLORESTAL VS. ISOLAMENTO: EFEITO DA PAISAGEM SOBRE A PROVISÃO DO SERVIÇO DE POLINIZAÇÃO

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RESUMO

Na medida em que as demandas agrícolas continuam se expandindo, aumenta a necessidade de que a produção agrícola garanta a conservação da diversidade e a provisão de serviços ecossistêmicos. O intuito do trabalho é avaliar independentemente o efeito da distância aos fragmentos florestais e a cobertura florestal numa escala local. Quantificamos a diversidade de abelhas e a formação de frutos em 24 cultivos de café dentro de paisagens complexas de 2km de radio, compostas por mosaico de usos da terra, café, Mata Atlântica (20 – 27%) e outros usos. Adicionalmente estimamos a contribuição das espécies na formação de frutos depois de uma visita única, em cinco dos 24 pontos amostrais. No total foram identificadas 31 espécies de abelhas visitando o café, a maioria abelhas sem ferrão (Meliponini) e abelhas da família Halictidae. Não houve diferença na formação de frutos depois das visitas únicas pelas diversas espécies de abelhas, o que sugere que há uma complementaridade na provisão do serviço. No entanto, a maior produtividade esteve associada à abundância de abelhas nativas. Em geral, houve um incremento de 8% com a presença das abelhas, que diminuiu com o aumento da distância aos fragmentos de mata e com o aumento da quantidade de café em escala local (400 m de raio no entorno do ponto amostral). O efeito negativo da distância aos fragmentos reforça a importância da vegetação natural em prover diversidade de abelhas e portanto o serviço de polinização. O efeito negativo da cobertura de café sobre a frutificação sugere que há um excesso de demanda que excede a capacidade dos polinizadores de prover o serviço dentro de paisagens complexas. Nossos resultados mostram que a estrutura da paisagem afeta a densidade, a riqueza e a composição de espécies de polinizadores. Por tanto, recomendamos, como estratégia para incrementar a produção de café, sem necessidade de aumentar a cobertura florestal, o manejo das áreas agrícolas para aumentar a dispersão entre fragmentos florestais e plantios de café, com o intuito de criar paisagens mais fragmentadas que facilitem o fluxo de polinizadores ao café.

Palavras chaves: Agro ecossistema, mudanças nos usos da terra, e *Coffea arabica* L.

FOREST COVER vs. FOREST ISOLATION: THE LANDSCAPE EFFECT ON POLLINATION SERVICE SUPPLY TO COFFEE CROP

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ABSTRACT

As the demands on agricultural lands continue to expand, effective strategies are urgently needed to manage agricultural production to guarantee biodiversity conservation and ecosystem service provision. Here we assessed independently the effect of forest isolation and local forest cover over bee diversity and on the provision of pollination service to coffee. We quantified bee diversity of flower visitors and fruit set in 24 coffee fields within three complex landscape of 2km radius surrounded by mosaic of coffee plantations, Atlantic forest fragments (20 – 27%), pastures and other lands uses. Additionally, we estimated species contribution to fruit set after single visit in five of the 24 coffee sites. In total we identified 31 bee species visiting coffee flowers, most being stingless bees (Meliponini tribe) and sweat bees (Halictidae). The absence of difference in fruit set after single visit by *Apis* and natives bee suggest that service complementation. Although, higher abundances of sweat bees and stingless bees were positively related to fruit set. Coffee fruit set was overall 8% higher in the presence of bees, and responded negatively to isolation from forest fragments and to high coffee cover at a local landscape scale (400 m radius landscape surrounding each sampled coffee bush). The negative association between isolation and fruit set reinforces the importance of natural vegetation to enhance bee diversity and therefore the provision of pollination service. The negative effect of coffee cover on fruit set suggests that the service demand can surpass pollinators' capacity to provide service within complex landscape. Our results provide clear evidences that landscape structure can affect the abundance, richness and composition of pollinators' species, and thus can indirectly regulate the provision of pollination service. Therefore we recommend, as a strategy to increase coffee yields without necessarily expanding forest cover, to manage agricultural landscapes in order to increase interspersation between forest fragments and coffee plantation thus a more patchy landscape mosaic that may facilitate pollinators flows to coffee crop.

KEY WORDS: Agro-ecosystems, land-use change and *Coffea arabica* L.

INTRODUCTION

Animal pollination is extremely important to ensure the reproduction of more than 90% of all flowering plant species (Ollerton, Winfree & Tarrant 2011), contributing hence to the maintenance of plant diversity in natural ecosystems (Buchmann & Nabhan 1996; Kearns, Inouye & Waser 1998). Pollination services also contribute to food production, as 70% of the commercial crops have an increase in harvest size and/or quality in the presence of pollinators (Heard 1999; Klein *et al.* 2007; Aizen *et al.* 2009). As demands on agricultural landscapes increase, improving crop yields through the enhancement of pollinators density and richness (ecological intensification) represents an alternative to meet such demands (Foley *et al.* 2011). It was recently reported that the enhancement of pollinators could help achieve higher yields for pollinated dependent crops worldwide (Garibaldi *et al.* 2016).

Most flowering plants are pollinated by multiple insect species, thus plants reproduction relies on the pollinators abundance (Waser *et al.* 1996; Vázquez, Morris & Jordano 2005; Garibaldi *et al.* 2014). Managed bee species like *Apis mellifera* have been used to increase pollination service but they may not be able to account for all pollination demands as pollinator-dependent crops are increasing faster than honeybee populations (Aizen & Harder 2009). Moreover, higher pollinator diversity may increase temporal and spatial stability in visitation rate (Klein 2009; Garibaldi *et al.* 2011a). Hence, attention on wild pollinators has increased as they naturally occur in agricultural landscapes, by relying on adjacent natural/semi-natural vegetation for nest and food resources (Losey & Vaughn 2006; Brosi *et al.* 2008; Tscharrntke *et al.* 2012). Wild bees have proven to be successful pollinators of exotic plants (Garibaldi *et al.* 2013) either directly or indirectly by enhancing managed pollinator efficiency (Garibaldi *et al.* 2014). Diverse bee assemblages are known to promote changes in foraging behaviour or spatially complement service provision over the crop plants (Brittain *et al.* 2013; Brittain, Kremen & Klein 2013). Despite their importance both wild and managed pollinators are threatened by agricultural intensification (Bommarco *et al.* 2010).

Changes in the land use and land cover composition, mainly due to urbanization and agricultural intensification, have transformed natural habitats causing pollinator declines (Brown & Paxton 2009; Potts *et al.* 2010), threatening the provision of pollination services (Biesmeijer *et al.* 2006; Bommarco *et al.* 2010; Vanbergen 2013). Today croplands and pastures occupy ~40% of the Earth ice-free land surface (Ramankutty *et al.* 2008; Foley *et al.* 2011). Given that forest fragments adjacent to the focal crop work as pollinators' reservoirs (Taki, Kevan & Ascher 2007; Brosi *et al.* 2008; Taki *et al.* 2011), the habitat amount in the landscape is an important indicator in predicting biodiversity (Fahrig 2013),

and consequently pollination service (Garibaldi *et al.* 2013). This has been supported by recent meta-analysis which found that the main factor enhancing bee diversity was the amount of high-quality habitat, whereas the spatial arrangements of the type of land use or configuration of the land cover habitats on bee diversity was not important (Kennedy *et al.* 2013). However, in the aforementioned study the configuration was assessed through natural patches only, disregarding the spatial arrangement of the focal crop. Moreover, it was reported that bee diversity reliance on the amount of natural vegetation surrounding crop fields increases as fields become more homogeneous (large monocultures) (Batáry *et al.* 2011; Kennedy *et al.* 2013). For this reason, management practices to enhance bee diversity, like flower strips and/or hedgerows, are recommended for landscapes that have been severely altered (less than 20% of natural vegetation) (Batáry *et al.* 2011; Carvalheiro *et al.* 2011).

In contrast to studies that evaluate the effects of landscape on bee diversity, studies that have quantified the loss of pollination service, have measure it in relationship to isolation from natural patches (Ricketts *et al.* 2008; Garibaldi *et al.* 2011b), but have not differentiated between landscape configuration (e.g. isolation) and the surrounding landscape composition. However it is important to consider configuration and composition separately because under intermediate values of natural habitat there is the greatest variation of landscape configuration (Villard & Metzger 2014) and there is also a steep loss of biodiversity (Banks-Leite *et al.* 2014). Thus the needs to disentangle which landscape attributes are causing biodiversity and pollination service loss. Even more importantly is to understand how already transformed landscapes can be managed to enhance pollination service provision (Vandermeer & Perfecto 2007). Each landscape attributes can be associated to the elements on which service provision depends: supply, flow and demand (Mitchell *et al.* 2015), which in the case of pollination service associated as follows. Service supply would be the pool of pollinators in the landscapes, which could be represented by the habitat amount; Service flow which could be attributed to pollinators foraging behaviour over the crop land, thus restriction in the flow due to forest isolation could be interpreted as restriction in pollinators flow to crop. Whereas, the amount of crop cover in the landscape would represent the amount of crop that needs to be pollinated (service demand) (Mitchell *et al.* 2015). Thus understanding the relative effect of landscape attribute on ecosystem service provision could be better target management strategies.

Coffee is the second most important commodity in legal international trade (O'Brien & Kinnaird 2003) and Brazil is the main coffee producer, responsible for more than 30% of the world exportation (International coffee organization – ICO 2015). Coffee production in Brazil replaced the Atlantic forest of which less than 16% remains today, most in small fragments found on private properties

(Ribeiro *et al.* 2009). Although *Coffea arabica* L. has self-fertile flowers (auto-pollinated) (Ngo, Mojica & Packer 2011), it exhibits increased levels of fruit set and yields in the presence of insect pollinators (Klein, Steffan-Dewenter & Tschardt 2003a; De Marco & Coelho 2004; Ricketts 2004a; Klein 2009). Bees have been proposed as the main pollinators of coffee (Klein, Steffan-Dewenter & Tschardt 2003a; Munyuli 2011). Although past studies have measured the effect of forest isolation and farm management on coffee pollination (Klein, Steffan-Dewenter & Tschardt 2003a; De Marco & Coelho 2004; Ricketts 2004a; Krishnan *et al.* 2012), no study has ever combined crop isolation and local (surrounding) composition to test how the landscape enhance bee diversity and pollination service provision.

The main objective of this study is thus to understand how landscape structure, particularly forest cover, isolation and matrix composition, affect bee diversity and coffee production. We suppose that the presence of forest patches within agricultural landscapes, by supporting bee populations, will increase coffee yields through enhancement of pollination service. Within complex landscape, composed by a mosaic of different land use and land cover classes, with 20% to 50% of natural areas, overall isolation from natural habitat might be reduced (Saturni *et al.*, *in prep*). Thus we expect (1) that bee diversity will only be affected by isolation when there is low local forest cover surrounding crop sites. Coffee is expected to be pollinated by a variety of bee species; therefore we expect (2) that different species complement themselves in the service provision. Furthermore, bee movement between crop plants maximizes cross pollination, thus we expect higher chances of fructification after a single visit made by bees coming from a different bush than coming from the same bush (geitonogamy). If the former hypotheses are corroborated, we expect (3) coffee pollination to decay as bee diversity decreases. Furthermore, considering coffee cover in the local landscapes as a proxy of pollination demand, we expect shortages of pollinators supply and flow at sites with high coffee covers when isolated from forest fragments and/or with low local habitat amount.

By identifying key coffee pollinators, quantifying their relative contribution to pollination, and assessing how they are affected by landscape transformation, we hope to better understand how landscape contributes to stabilize and improve coffee production. By quantifying the independent effect of forest isolation and forest cover on mediating shifts in bee community composition and pollination service, we intend to fill knowledge gaps associated to relative effects of forest cover and configuration on pollination services (Fig. 1).

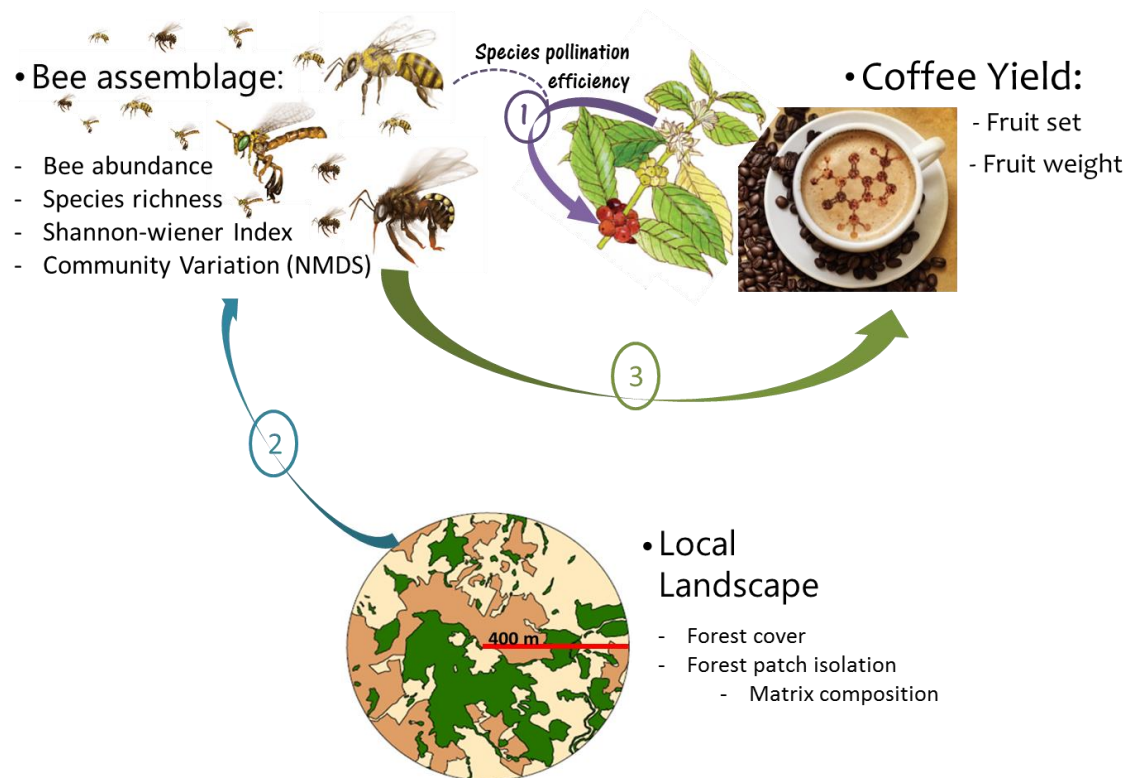


Fig. 1. Conceptual diagram presenting the main relationship (bullet points) explored in this study, the levels of analysis of the research (bullet points), each with the list of variables measured. We intended to evaluate the role of different species on coffee production using single visit experiments (1). In order to do so, landscape data of the focal crop was used to compare the relative effects of forest isolation and local forest cover on affects bee diversity (2). With the intention of testing how changes in bee assemblages affect coffee production (3).

MATERIALS AND METHODS

Study Area

The study region comprised the south east of Minas Gerais State, Brazil, one of the main coffee producing regions in the country. Sun coffee plantations are scattered between Atlantic Forest fragments along with pastures, sugar cane plantations and *Eucalyptus* forests. Our study areas comprised three circular landscapes of two-kilometre radius with coffee crops and similar forest cover, ranging from 20 to 27 % (Fig. 2), a cover range where typically spatial configuration should be more variable (Villard & Metzger 2014) . The amount of forest cover was determined based on high-resolution images (ArcGis 10.3 basemap imagery from DigitalGlobe satellites for 2009 to 2011, 0.5 m resolution) and a reference scale 1:5,000 (Fig. 3). In each landscape, we selected eight “local landscapes” (samples of landscape with 400 m radius) to evaluate the independent effects of local

forest cover and forest isolation on bee species assemblages and on pollination service. The local landscape radius was defined considering the maximum foraging range estimated for small bees (Araújo *et al.* 2004) and to guarantee the maximum forest cover variation in relation to isolation (Fig. 3). Given that after testing the relationship of forest cover with isolation for local landscape with different radii (200, 300 and 400 m) the proportion of isolated coffee pixels with high local forest cover decreased with decreasing the radius.

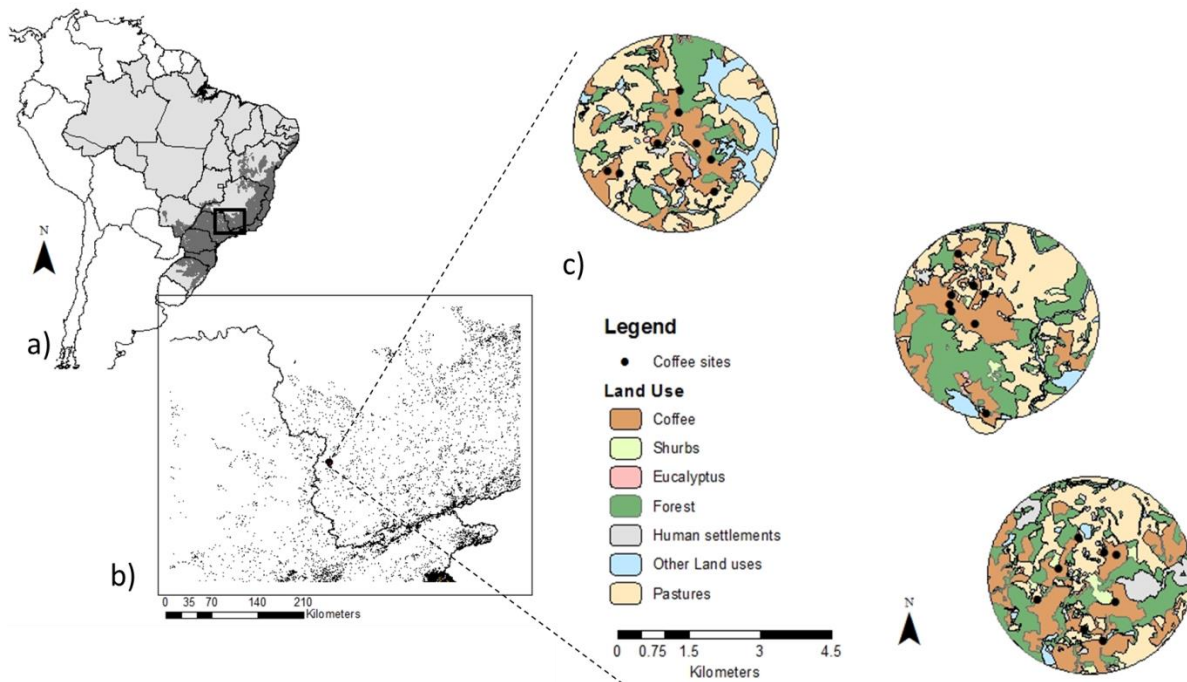


Fig. 2. Former Atlantic Forest distribution (grey) in Brazil (a), a close up to the division of Minas Gerais and Sao Paulo state, with the remaining forest fragments (b). The three (2 km) study landscapes classified according to their main land use (c).

To determine the location of the local landscapes we first calculated isolation and local forest cover for each coffee pixel in the three studied landscapes. From the relationship between forest isolation and local forest cover (Fig. 3), we studied four situations considering the combinations of high (> 175 m) and low (< 50 m) forest isolation with high ($> 20\%$) and low ($< 10\%$) local forest cover (Fig. 3B, Fig. S1). Forest isolation threshold values were defined considering that bees' assemblages changes have been reported after 100 m from forest fragments areas (Ricketts *et al.* 2004). The high and low local forest cover were defined based on biological thresholds in fragmented landscapes (Banks-Leite *et al.* 2014), but considering the existence of few areas with more than 20% of forest cover in the high isolation (> 100 m) situation (Fig. 3 – Step 3). After defining potential sites (Fig. 3) we selected the final local landscapes with farmers help, caring to choose coffee bushes of the two main coffee

varieties cultivated in the region (*Coffea arabica* L. var. Catuaí and Mundo novo). A minimum distance of 150 m was left between the centres of the local landscapes (Fig. 4, Table 1).

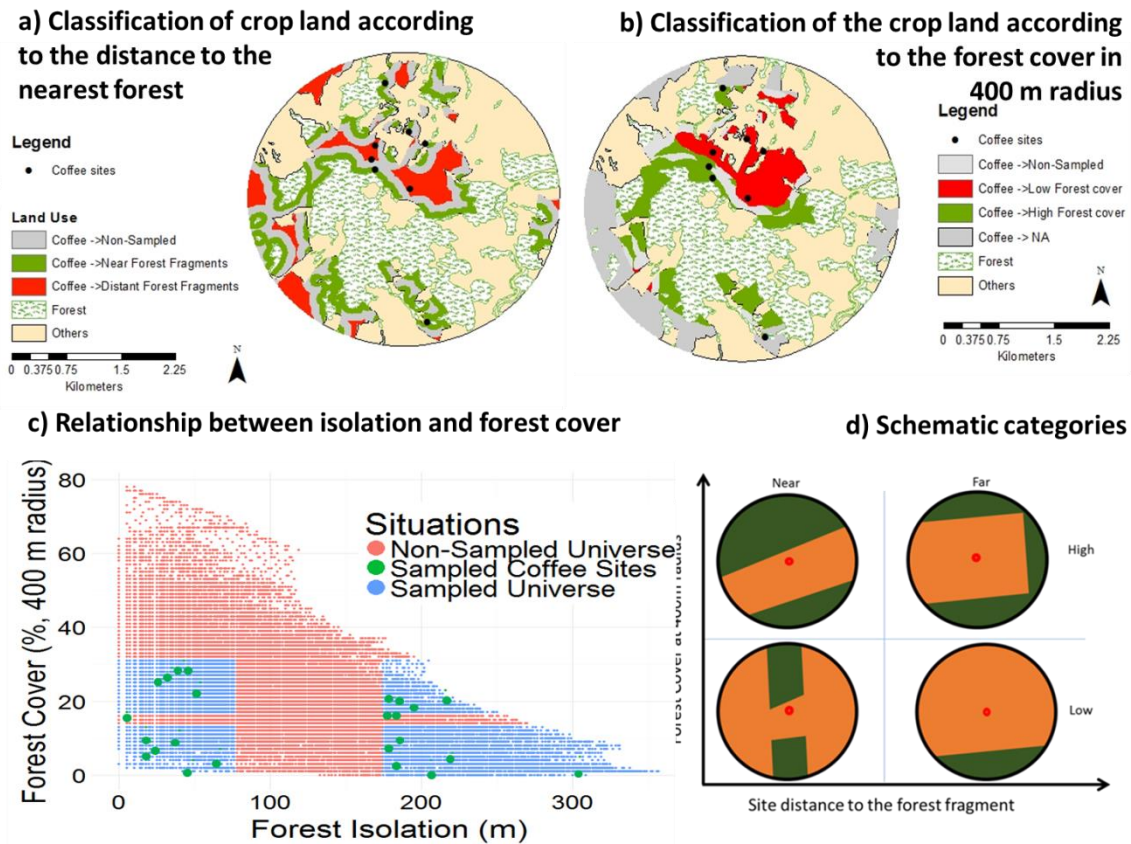


Fig. 3. Schematics representation for defining the local landscapes, strating from the three previously classified landscapes (2 km, radius): a) coffee classification according to the distance to forest fragments (in green near <50m; in red far >175m). b) Classification according to the forest cover in 400 m radius (in green high >20%; in red low <10%). c) the relationship between forest cover (% at 400 m radius) and distance to the nearest forest patch of each coffee pixel in all three 2 km radius landscapes. d) Local landscape representation of the four treatments categories according to the distance to forest fragment and the forest cover at 400 m radius. Each ball is a 400 m local landscape where forest fragments (green) and coffee matrix (orange) varies.

Coffee Visitors

Bee diversity metrics

In each of the 24 experimental sites (local landscapes), we carried bee surveys during the main coffee blooming period (end of September to October of 2014) using entomological nets and pan traps. Net samplings took place along a 50 m transect between coffee lines. Net samplings lasted two minutes

and were carried twice in each experimental site. The first round was conducted in the beginning of the blooming period and the second round, on the third (final) day of the blooming period. To complement the bee assessment, we placed pan traps in each experimental site for 48 hours, (Krug & Alves-dos-Santos 2008) during the same blooming period. Each pan trap sample consisted of three plastic bowls (110 ml), filled with soapy water and sugar, placed along the coffee lines. Two of the bowls were painted blue and yellow colours using a fluorescent ink and the other one was left white. All the collected bees were marked with their respective time and locations. They were brought to the Paulo Nogueira-Neto Entomological Collection at the Bee Lab of University of São Paulo, for identification.

The bee diversity metrics were calculated for each local landscape and were described by: the total amount of bees (abundance) separately for each sampling method (entomological nets and pan traps), total of species (richness) for each sampling method, and the Shannon-Wiener Index (bee diversity). Additionally, we conducted a Non-metric Dimensional Scaling (NMDS) analysis based on a matrix of Bray-Curtis dissimilarities of species abundances and extracted the first two axes as a measure of community composition (Fig. S3, table S1). To interpret the resulting NMDS figure, we correlated species abundances with the ordination axis scores to determine if certain species were associated with different axes (Table S5), and hence with coffee pollination service (Quinn & Keough 2002). NDMS and diversity analysis were only run for bees collected with entomological nets, given that samples for pan traps were too small. The abundance of *Apis mellifera* and stingless bees (Meliponini tribe) were also calculated separately for each local landscape.

Landscape metrics

For each experimental site (local landscape) we calculate the isolation to the nearest forest fragment and the percentage of forest cover (PF) (Table 1). Given that the maximum local forest cover among our 24 samples was 31% (Table 1), we also determined the percentage of each matrix type (coffee, pasture, *Eucalyptus*, young shrubs, human settlements and others), to take into account other components of local landscape covers. The matrix variation among local landscapes was calculated with a Principal Components Analysis (PCA) (Fig. S2). The first axis of the PCA was used as a predictor variable to explain bee diversity (Table S1). This axis explained 36% of the variation among local landscapes, showing a gradient from coffee dominated matrixes to local landscape with more pastures. As both, pasture and coffee cover, were inversely correlated we separately used the percentage of coffee cover and pasture cover to evaluate their effect over bee diversity and coffee fruit set (Table S1).

Table 1. Maximum and minimum values of the landscape metrics, bee diversity variables and coffee pollination indicators.

Variable	Scale	Value range
LANDSCAPE METRICS		
<i>Composition</i>		
Forest cover (%)	400 m	4 – 31
Coffee cover (%)	400 m	13 – 72
Pasture cover (%)	400 m	0 - 61
Matrix composition	400 m	-3.5 – 1.7
<i>Configuration</i>		
Distance to forest fragment (m)		5 - 305
BEE DIVERSITY		
Total Bee Richness	Site	2 - 13
Net bee richness	Site	1 – 9
Pan trap bee richness	Site	0 – 7
Net bee abundance	Site	1 – 19
Pan trap bee abundance	Site	0 – 20
Shannon diversity index	Site	0 – 2.1
NDMS	Site	-1.1 – 0.86
COFFEE POLLINATION		
Number of flowers	Branch	7 – 124
Number of fruit	Branch	0 – 59
Fruit weights (g)	Branch	0 - 43

Coffee Pollination Service

At the local landscape level – exclusion experiment

In each experimental site we measured bee contribution to fruit set on three coffee bushes, by comparing 15 branches (5 per coffee bush) with open access to pollinators with 15 branches (5 per coffee bush) where pollinators were excluded (Fig. 4). To prevent access of any insect we used a fine mesh bag (3 mm), which allowed wind to pass. Fruit set was calculated by branch as the proportion of flowers that became fruit at the harvesting time. We counted the total number of flowers, during the blooming period, for the three nodes closest to the tip of each branch, 1m aboveground. After a week of the blooming period, we removed all bags in order to avoid any effects of the bags on fruit development and marked the branches sampled. At the harvesting period (May 2015) the three nodes previously counted of each branch were harvest and brought to the lab to count the amount of coffee berries formed, and to determine their fresh and dry weight.

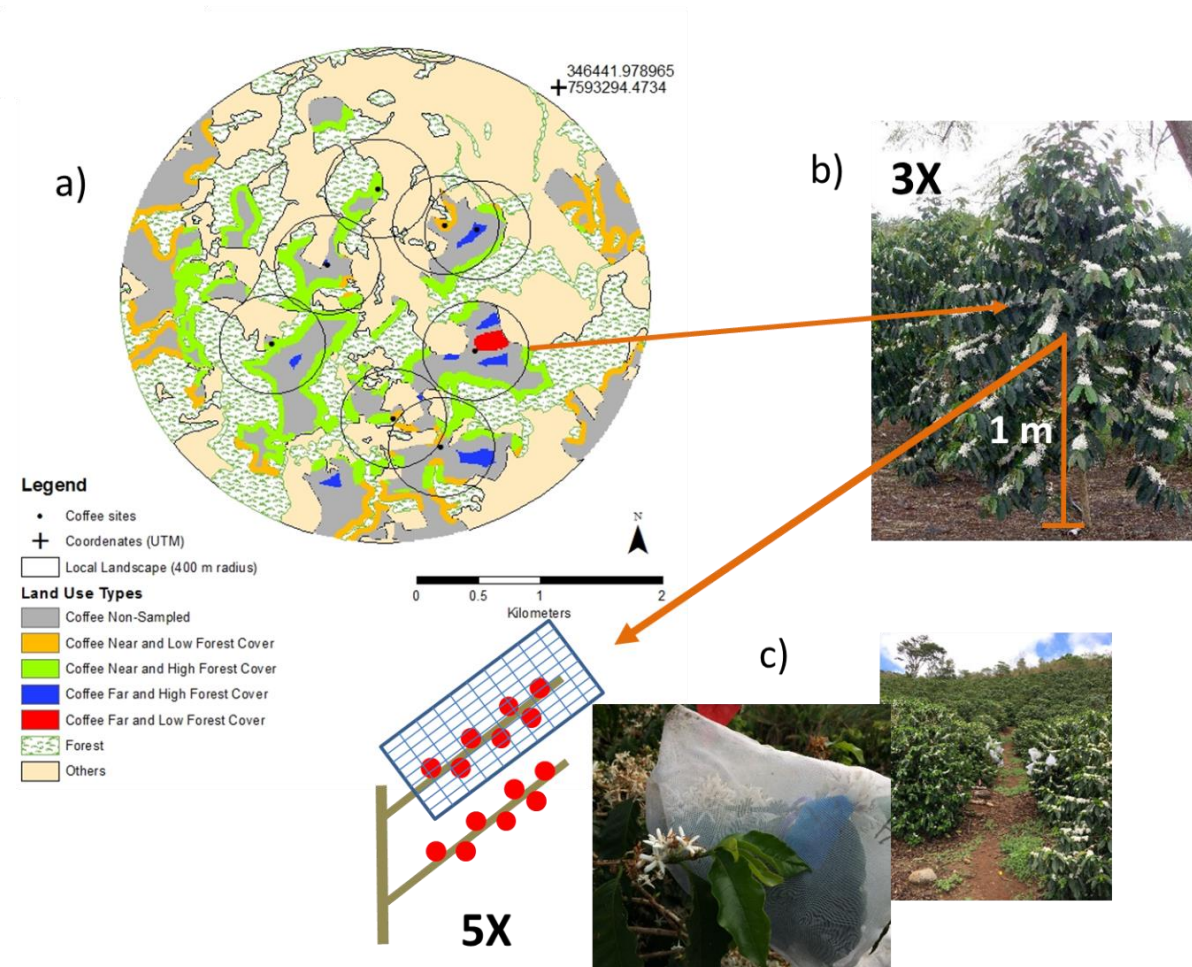


Fig. 4. a) One of the 2-km landscapes with the 8 local landscapes, showing in colours the location of the potential areas according to the distances to forest fragments and forest cover at 400 m radius,. In each coffee site (blue dots) is the centre of the local landscape sampled where (b) three coffee bushes were selected. At 1 meter height in each coffee bush (c), five branches were chosen to be cover with a mesh bag and five were left open to be pollinated by insects.

At the bee species level – Single visit metrics

To assess the contribution of a single visit, of the most abundant bee species (Table S2) to the coffee fruit set, we carried single visit experiments on five of the 24 local landscapes previously chosen, which represent two of the four treatments: high forest cover near to forest fragments (3 sites) and low forest cover distant from forest fragments (2 sites). At each of these five sites, we additionally excluded 30 branches, on other 3 coffee bushes, with the same mesh bags used before. At the beginning of the blooming period, exclusion bags were opened in order to allow a single visit per flower. After the visit, the flower was marked and the mesh bag was closed again until the coffee bloom had finished fruits were then harvest in May 2015. The response variable consisted in final

coffee fruit set after a single visit to the sampled flowers. The predictive variables were, (i) the precedence, whether the bee had visited a flower of the same bush (geitonogamy) or not before visiting the sampled flower (cross pollination); (ii) whether the bee was *Apis mellifera* or a native bee, as not all species were able to be identified. (iii) bees were also separated by their size, in either small or big, accordingly to the intertegular distance (functional classification) (Greenleaf *et al.* 2007).

Statistical Analysis

To test the first hypothesis we evaluated the independent effect of local forest cover and forest isolation on bee diversity. To do so, we used the bee diversity metrics as response variables and local landscape metrics as predictor variables. To test the second hypothesis we evaluated the bee precedence, whether was native or not and bee size on coffee fruit set after single visit using fructification or not after single visit as response variable. To test the third hypothesis we used bee diversity metrics as predictor variables and pollination metrics (fruit set and dry fruit weight) as response variables.

To test the effects of landscape parameters on bee diversity (hypothesis 2), we fitted linear and generalized mixed models with *Poisson* distribution of errors, using the lme4 R package (Bates *et al.* 2014). As we were only interested on the differences among the local landscapes we included the three landscapes of 2km radius as random intercepts. The best random structure was tested by comparing models with identical fixed structure fitted using Restricted Estimated Maximum Likelihood (REML). We then proceeded to select the best fixed structure, using maximum likelihood, and including always a null model (with fixed effect equal to one). Model selection was done using the corrected Akaike information criterion AICc (for models without random effect) or AIC (for models with random effects) (Burnham & Anderson 2002). All models with $\Delta AIC \leq 2$ were considered equally possible. Models comparisons were performed using the *MuMIn* packages (Barton 2015).

To test the third hypothesis that coffee pollination decays as bee diversity decreases, we used generalized linear mixed models with a binomial distribution of errors, and the proportion of flowers that turn to fruit as response. Pollinator exclusion treatment (categorical data) for each branch sampled was included as a fixed effect in the full models along with bee metrics and local landscape. The variation due to the three landscapes, coffee bush and branch was included as random structure as we were interested in assessing the effect of bee diversity and local landscape metrics over pollination service.

The same procedure of generalized mixed models was used for the single visit experiment with only few variations. The response variable consisted on whether the flower turned or not to a fruit after each single visit (binomial distribution). The predictor variables were (1) the precedence of the bees prior to the visit (from the same bush or other bush), (2) whether the bee was native or not and (3) the size of the bee using intertegular distances. For the random effect only variation due to the coffee bush and branches was included as random structure as we were interested in assessing the effect of bee single visit on coffee fruit set.

RESULTS

Bee diversity metrics

During the main coffee blooming period at the end of October 2014, 169 bees were sampled using entomological nets and 67 bees using pan traps. Twenty bee species were collected using entomological nets, mainly belonging to the Meliponini tribe (16 species). Nine of the stingless bees were tree cavity nesters, however of the seven most abundant stingless bees, three were ground nesters (44 individuals), two exposed nester (33 individuals) and two cavities nesters (29 individuals) (Fig. 5a). Pan traps registered 16 morphospecies/species of which only four species were also collected with the nets. The two most abundant morphospecies collected with pan traps belong to the Halictidae family, the genus *Dialictus* (19 individuals) and the *Augochlora* genus (17 individuals) (Fig 5b). *Apis mellifera* was the most abundant species (36 individuals netted and 7 in the pan traps).

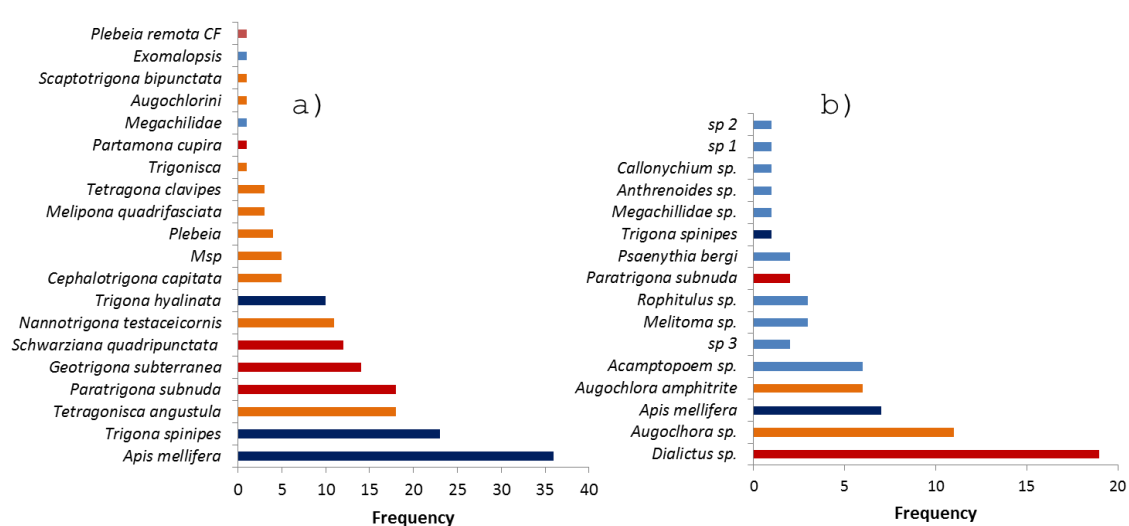


Fig. 5. Bee abundance for the species collected with a) entomological nets and b) pan traps. Colours represent the type of nesting substrate: tree cavities (orange), soil (red), exposed (blue), unknown (light blue).

Single visit

During the twenty-four hours of virgin coffee flowers observations, 149 single visits by 87 bees were registered. Out of the 87 bees that visited the sampled flowers, 32 were honeybees (*Apis mellifera*), which accounted for 50% (n= 75) of the single visits, while the other 50% (n = 74) visits were made by 55 native bees, mainly the Meliponini tribe bees, as only three visit were made by two bee individuals of the *Augochlora* genus (Table S2). Overall 41% of the observed coffee flowers ripened, having only marginal differences between *Apis mellifera* visits (44%) and after native bee visits ($p=0.06$). Bee foraging route was the best variable explaining fruit set after a single visit. There was 49% fruit set when bees came from a different coffee bush and 29% when they came from the same coffee bush ($p=0.002$). Fruit set was higher when honey bees came from a different coffee bush, although the precedence of the bee was a better predictor than whether the bee was native or not (Tables 2, 3).

Table 2. Model selection statistics for single visit fruit set using as predictor variables precedence, native or not and size.

Response	Models	Random	AIC	ΔAIC	Weight
Single Visit Fruit Set	Native, precedence	Bush	176.7	0.00	0.540
Single Visit Fruit Set	Precedence	Bush	178.3	1.58	0.244
Single Visit Fruit Set	Native : Precedence	Bush	178.5	1.83	0.216

Table 3. Summary statistics for the selected models ($\Delta AIC < 2$) for single visit fruit set.

Response	Predictor	Estimate	SE	p -value
Single Visit Fruit Set	Precedence_other bush	1.126	0.4734	0.017
Single Visit Fruit Set	Native bees_Yes	-0.893	0.7193	0.218
Single Visit Fruit Set	Native : Precedence	0.476	1.211	0.697

Landscape effects on bee diversity

Overall bees' richness and abundances were negatively associated to the forest isolation and to the amount of coffee cover in the surrounding (400 m radius) (Fig. 6; Tables 4, S3, S4). The amount of

forest cover at the local landscape was not related to any of the bee metrics measured. *Apis mellifera* abundance was not related to any landscape variable. Neither was the bee diversity index Shannon-Weiner nor both of the community variation axis generated with NMDS related to any landscape variable measured. The Meliponini tribe responded negatively to distance (Tables 4, S3, S4) and the amount the coffee cover in the local landscape (Tables 4, S3, S4 Fig 6a). Decreases in the Meliponini tribe richness and abundance were mainly associated to the absence of small bees and tree cavity nesters in the isolated local landscapes (see *Supporting Information*). The sweet bees (Halictidae) and the rest of the bees collected with pan traps responded only to the coffee cover at the local landscape (Tables 4, S3, S4; Fig. 6b).

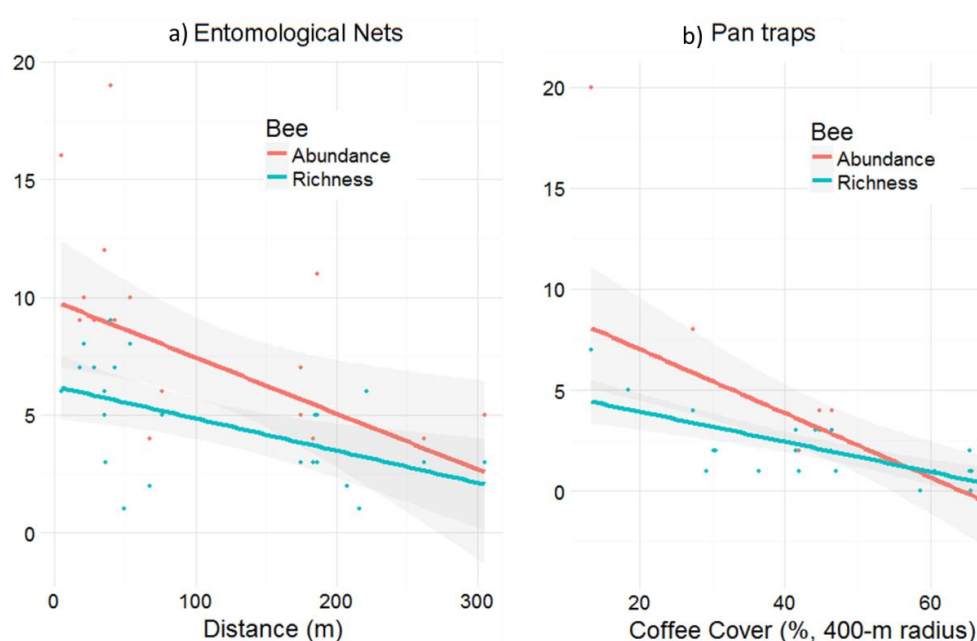


Fig. 6. Relationship between bee richness (blue) and abundance (red) with the predictive variables that best explain the bees sampled with a) Entomological nets and b) Pan traps.

Table 4. Summary statistics for the selected models ($\Delta AICc < 2$) of landscape structure effect on bees.

Response	Predictor	Estimate	SE	p-value
Richness (nets)	Distance (m)	-0.238	0.087	0.011*
	Distance (Categorical)	0.515	0.207	0.019*
Richness (Pantraps)	Matrix variation (PCA – 1st axis)	-0.38764	0.094	0.0001***
	Coffee cover (400-m radius)	-0.62041	0.156	0.0001***
Abundance (nets)	Distance (m)	-0.259	0.087	0.003**
	Coffee cover (400-m radius)	-0.237	0.097	0.014*
Abundance (pantraps)	Coffee cover (400-m radius)	-0.922	0.140	<0.001***

Abundance (Meliponini)	Distance (m)	-0.316	0.126	0.018*
	F2 - Matrix variation	-0.303	0.116	0.014*
	Coffee cover (400-m radius)	-0.274	0.131	0.050*

Bee diversity effects on coffee production

Fruit weight did not respond to neither bee diversity nor to the landscape metrics measured (Table 5). However, fruit set was higher for branches with open access to bee visitors (58%) than from branches without (50%) pollinators (Tables 5, 6), and the difference between pollination treatments increased with bee abundance, with fruit set being higher for open pollinated flowers when the abundance of bees was highest (Fig. 7a). Coffee fruit set also responded to the bee community composition variation (Fig. 7b), being negatively associated to the abundance of five stingless bees (Table S5).

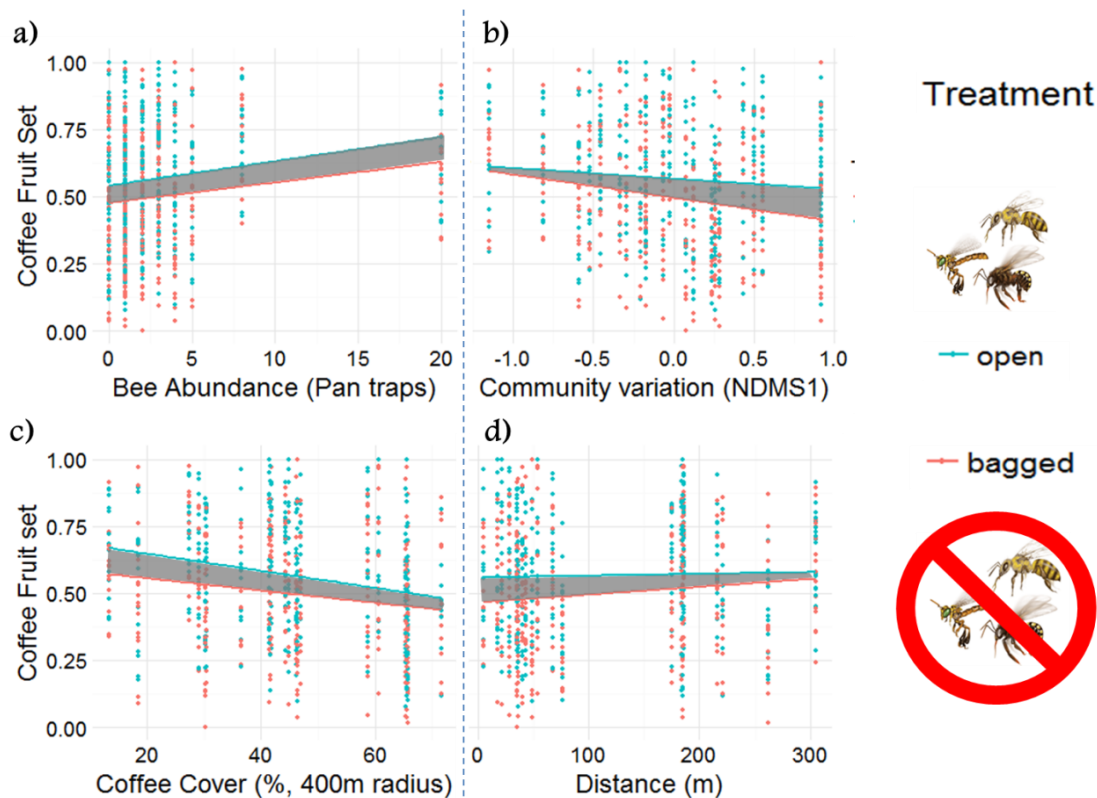


Fig. 7. Coffee fruit set in relationship to: a) pan traps bee abundance, b) community variation, c) coffee cover and d) distance to the nearest forest patch. Each point represents a branch (n=791) of the twenty three experimental sites, and each colour represents one of the exclusion experiments treatments, open to pollinators (blue) and pollinators' excluded (red). The grey area represents the pollination service, the interaction between the exclusion treatments and the predictive variable (x).

Table 5. Model selection statistics for fruit set and fruit weight using as predictor variables both landscape and bee diversity.

Response	Models	Random	AIC	ΔAIC	weight
Fruit Set	Treatment*Pan traps bee abundance, Treatment*Community variation	Landscape, site, bush and coffee variety	7239.7	0.0	0.782
Fruit weight	null	Landscape, site, bush	-741.9	0.00	0.981

Table 6. Summary statistics for the selected models ($\Delta AIC < 2$) for fruit set.

Response	Predictor	Estimate	SE	p-value
Fruit Set	Treatment (open): Pan traps bee abundance	0.149	0.035	<0.001
Fruit Set	Treatment (open): Community Variation	0.218	0.051	<0.001

DISCUSSION

Natural vegetation patches within complex landscapes are known to enhance biodiversity (Tscharntke *et al.* 2005; Batáry *et al.* 2011). However our results show that not all the crop land within such landscapes is equally visit by bees. Coffee sites far away from forest fragments and/or highly surrounded by coffee presented lower bee richness and abundance. The reduction of bee richness and abundances due to isolation and/or to high coffee cover resulted in lower coffee fruit set, as high bee abundances were associated to higher coffee yields. Moreover, no differences were found in coffee fruit set after single visits made by wild bees or by *Apis mellifera*. Together these results support that there is a complementation among species in the service provision. However, not all bee species equally contributed to coffee fruit set, as changes in the community composition negatively affect coffee fruit set, in particular high abundances of bees of the genus *Trigona*. Overall coffee sites nearby forest fragments and/or with low coffee cover had high bee richness and abundances and the highest fruit set. Thus local landscape is mediating the pollination services through changes in bee assemblages. Therefore we suggest that the spatial management of the focal crop could enhance bee diversity within cropland, if the interspersions of cropland within forest patches is maximized. This would maintain a high pollination flow over the cropland, by reducing overall the crop-forest isolation. The local reduction of large coffee extensions would help to guarantee that the pool of pollinators' accounts for the service demand (Fig.8).

Bee assemblage and pollination service

The exclusion experiments showed an overall increase of 8% in fruit set between coffee flowers left open in comparison to the flowers where pollinators were excluded. The increment in coffee fruit set increased up to 12% along with Halictidae bees' abundance (Fig. 7a, S2), although this result seems contradictory as sweat bees (Halictidae) were not found in abundance during the single visit experiment (Table S2). The Halictidae family has been reported to be the most abundant bee group in coffee systems and methodologies like the ones used in this study fail to truly record their abundances (Ngo *et al.* 2013). Moreover, highest coffee fruit set was found at small coffee patches adjacent to forest fragments, where the highest richness and abundance of sweet bees coincided with the highest stingless bees' richness and abundances. Thus these results suggest that both wild bee groups contribute to pollination service.

Even though there is no direct relationship between stingless bees and coffee fruit set, the higher yields found where stingless bee richness and abundance was highest reinforcing that wild bee contribute with pollination service to coffee (Veddeler *et al.* 2008). However not all stingless bees seem to contribute to fruit set, as increments of *Trigona* genus abundance resulted in reduced fruit set. This pattern could be attributed to the damage of flowers buds, that those species may cause, behaviour that has also been reported for other crops (see Saunders *et al.* 2015). *Apis mellifera* was the single most abundant specie found and even though their contribution to coffee yields is widely acknowledged (Roubik 2000, 2002; Ngo, Mojica & Packer 2011), *Apis mellifera* abundance did not explain coffee fruit set variations. This result reinforces that relying on a single species attempts against agroecosystem resilience (Peterson, Allen & Holling 1997; Kremen *et al.* 2007; Winfree *et al.* 2007; Garibaldi *et al.* 2013, 2015; Wilfert *et al.* 2016). Furthermore higher wild bees density and richness have been reported increase honey bee movements between crop plants (Brittain *et al.* 2013), thereby improving the chances of effective cross pollination (Ne'Eman *et al.* 2010; King, Ballantyne & Willmer 2013).

The single visit experiment suggests a complementation among the bees' species in the crop pollination service provision, as no difference was found in fruit set after a single visit made by a wild or a honey bee. Moreover, the lower coffee fruit set found after singles visit in comparison with the exclusion experiment could be attributed to the lack of effective visits, thus reinforcing the key role that bee abundance plays in increasing fruit set (Connelly, Poveda & Loeb 2015). Single visits experiments showed that coffee fruit set was lower when bees visited flowers from the same coffee bush, before visiting the sampled flower, reinforcing that cross pollination by bees causes a

significant increase in fruit set (Klein, Steffan-Dewenter & Tscharntke 2003b). We would therefore expect higher bee richness and abundance to result in higher cross pollination (Brittain *et al.* 2013; Garibaldi *et al.* 2016).

Forest cover vs. forest isolation

Stingless bees were more abundant near forest fragments, but contrary to our expectations bees were not affected by local forest cover. Thus suggesting that proximity to forest fragment, independently of the amount of forest at the local scale, equally contribute to support rich bee assemblages (Table S6) and to the provision of pollination service (Taki, Kevan & Ascher 2007; Taki *et al.* 2011), at least when the landscape forest cover is around 20 -27%. As at sites near forest fragments where fruit set was highest, stingless bees were more abundant and showed greater diversification in nesting sites (tree trunk cavities, exposed nest and ground nesters), size (1-2.8 mm) and foraging behaviour (Ramalho 2004; Brosi *et al.* 2008). It is noteworthy mentioning that lower bee abundances at far sites were associated to the absence of small bees and cavities nesting bees (See *Supporting Information*). Therefore our results reinforce that pollinators' flow is essentially restricted to crop land adjacent to forest fragments (Ricketts 2004b), especially to distances below 175 m in our complex landscapes.

The diverse nesting behaviour of stingless bees found visiting coffee seems to be associated with different response patterns to landscape transformations (Fig. 2). Out of the seven most abundant stingless bees, five were either exposed or ground nesters which have been seen to nest within the coffee crop (*personal observation*). The other two most abundant bees were tree cavity nesters (Fig. 5), which have been reported to benefit from anthropogenic landscapes (Batista, Ramalho & Soares 2003). The low abundance of restricted tree nesters (Fig. 5) might be due to a lack of nesting resources as a result of the landscapes being below the biodiversity loss threshold (Table 1) (Banks-Leite *et al.* 2014). After all the bee assemblages found are dominated by species more tolerant to landscape transformations (Batista, Ramalho & Soares 2003; Jaffé *et al.* 2015) which could alternative explanation why local forest cover did not affect bee diversity. Nonetheless, the non-restricted tree nesters response to isolation (*see Supporting Information*) reinforces that forest fragments provide resources for ground and exposed bee nesters as well (Brosi *et al.* 2008).

The community composition axis strongly associated to *Trigona* genus abundance (Fig. S5) which explained coffee fruit set (Fig 6b) did not respond to any of the landscape variables measured. This lack of association with forest isolation and/or local landscape composition could be attributed to *T. spinipes* exposed nesting behaviour, as they have been reported not to be fully reliant on forest (Jaffé

et al. 2015). Hence, *T. spinipes* could be the species involved in the different effects of native bee community on coffee fruit set at different landscape scales (Saturni *et al.*, *in prep.*). Thus more studies are needed to understand how the stingless bees' community interacts at a landscape level and their association to pollination service.

Coffee cover

The negative relationship between coffee cover and pollination service could be attributed to the dilution effect (Veddeleer, Klein & Tschardtke 2006; Jha & Vandermeer 2009), where the amount of bees cannot account for the amount of flowers to be visited (demand). Given that coffee cover, in our study, varies independently of forest cover and forest isolation, we therefore consider that an excess of service demand (crop extensification) is what is limiting service provision (Mitchell *et al.* 2015). This is consistent with a recent meta-analysis that found higher pollination benefits from increasing bee abundance at small crop fields (Garibaldi *et al.* 2016). The predominance of ground nesters in this complex landscapes also suggests that high local coffee cover is also negatively affecting the establishment of bees within cropland. After all landscape homogenization has been reported to negatively impact bee diversity and pollination service (Connelly, Poveda & Loeb 2015) due to the lack of resources in the surroundings (Benton, Vickery & Wilson 2003). Nonetheless, more studies are needed to understand how other types of cover affect bee diversity and pollination service to coffee.

Implications and final remarks

Our results for complex landscape suggest that: 1) Forest patch size did not affect the supply of bee diversity, within a regional context of intermediate forest cover (20-27%). 2) increasing crop proximity to forest fragments would increment the accessibility and facilitate flow of pollinators to crops. 3) large extension of focal crop results in excessive service demands. We thus provide supporting evidence that fragmentation, within complex landscapes can have positive benefits on pollination service (Mitchell *et al.* 2015), and, as a consequence, that the provision of pollination services is heterogeneously distributed in space (Fig. 8). Once landscape structure affects pollination service, we suggest that if coffee cropland is to be expanded, then it should be done maintaining close distances to forest patches and avoiding large extensions of coffee.

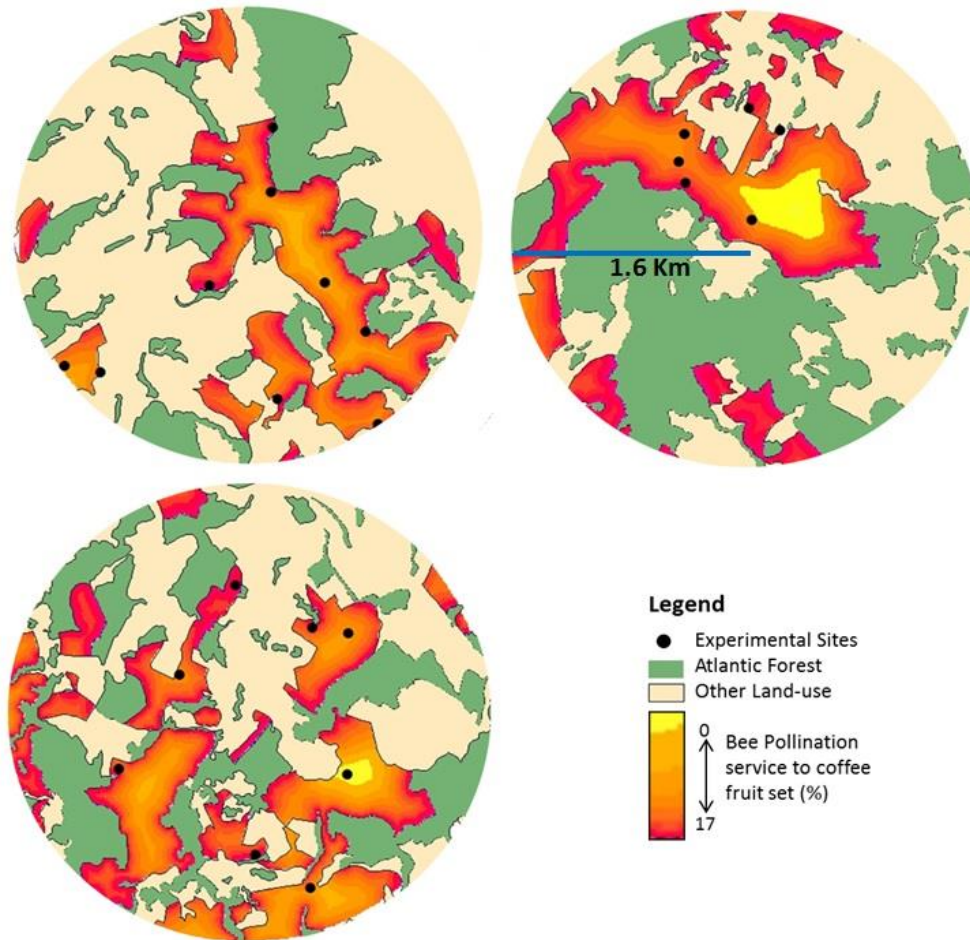


Fig. 8. Extrapolation of yield increments due to coffee bee pollination on the three 2-km landscapes using the best selected model considering distance to forest fragment and local coffee cover.

Our methodological approach using local landscape analysis can help to prioritized areas for management practices that enhance bee diversity, like flowers strip and hedgerows. After all, spatially managing cropland represents an alternative when is not possible (Perfecto & Vandermeer 2010) or unacceptable by farmers (Burton, Kuczera & Schwarz 2008) to increase forest cover. We therefore suggest efforts towards understanding how other land uses and landscape heterogeneity affect biodiversity and service provision, as heterogeneity could be achieved either by more diverse cover types or through a more complex spatial arrangement of cover types (Fahrig *et al.* 2011).

Finally our research have clear conservation implications, because most of the Atlantic forest remaining fragments are small and within private lands (Ribeiro *et al.* 2009), and we found strong evidence that reinforces the important role of any size forest fragments to supply wild pollinators. Therefore we support that landscape management to enhance pollination service could help to increase crop yields where pollination limitation occurs (Garibaldi *et al.* 2016).

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Supporting Information

Bee trait classification

The net sampled bees were classified according to their size using the intertegular distance (ITD) as a proxy for bee size (Cane 1986). Since the size of the intertegular distance of the sampled bees ranged between 1mm to 3.6mm, and only five (5) of the 20 identified morphospecies exhibited an ITD above 2 mm, we grouped bees as small (ITD < 1.64 mm) and medium (ITD > 1.64 mm). Based on the revision on the neotropical bees (Camargo *et al.* 2007), the species were also classified according the most common nesting type cited. Two categories were considered in the analysis: cavities nesting bees vs. non-cavities nesting bees.

This data was not included in the general analysis as there was a zero inflated problem for small and cavity and ground nesting bees, due to their absence in the far experimental sites. Nonetheless for the other classifications analysis were possible: Meliponini tribe, exposed nesting bees (*Trigona spinipes*, *Trigona hyalinata* and *Apis mellifera*), and medium sized bees.

SUPPLEMENTARY FIGURES

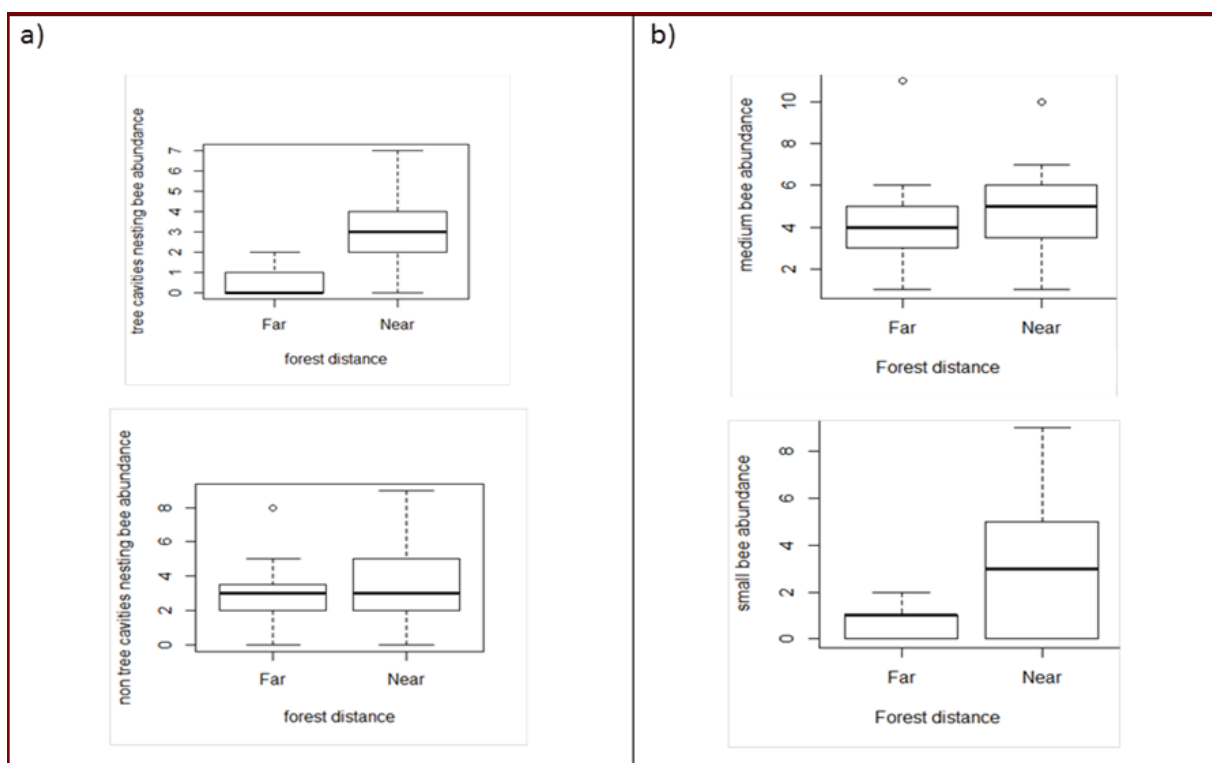


Fig. S1. Effect of distance over two functional categories: nesting behaviour (a) and bee size (b).

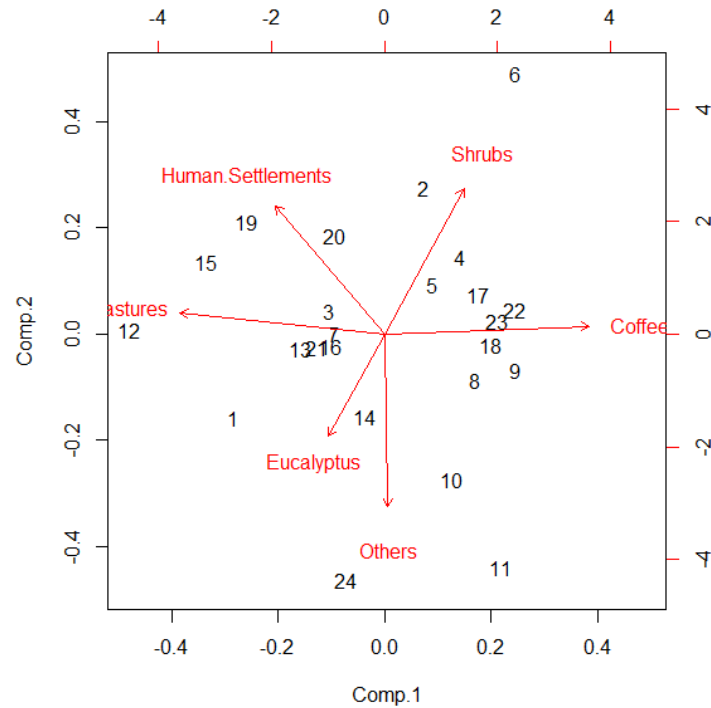


Fig. S2. Principal Component Analysis (PCA) using the percentage of landscape covers of each land use type (matrix composition) on the 24 local landscapes. The first axis explains 36% of the variance.

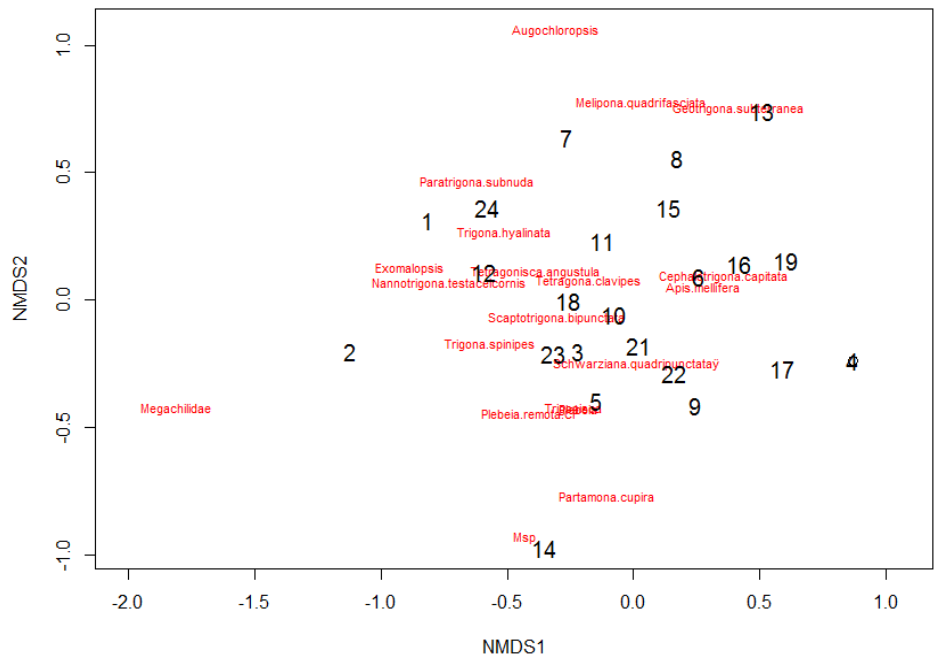


Fig. S3. Community variation analyses with Non-metric Dimensional Scaling (NMDS) using the abundance/presence of visiting species sampled with entomological nets in each of the 24 coffee sites. In red, species names and in black the experimental sites.

SUPPLEMENTARY TABLES

Table S1. Response and predictor variables considered for the analyses.

RESPONSE VARIABLES	PREDICTOR VARIABLES
a) Effect of local landscape variables over bee diversity	
Bee abundance (nets and pan traps) Bee richness (nets, pan traps and total) Shannon Index (nets) Community variation (NMDS)	Distance to forest fragments Percentage of forest cover (400m radius) Percentage of coffee cover (400m radius) Percentage of pasture cover (400m radius) Matrix composition: from more pasture to more coffee (PCA first axis).
b) Effect of bee diversity over coffee production	
Fruit set Fruit weight	Bee abundance (nets and pan traps) Bee richness (nets, pan traps and total) Shannon Index (nets) Community variation (NMDS)
c) Single visit over coffee production	
Fruit set	Bee Precedence (geitonogamy vs. cross pollination) Native vs. <i>Apis mellifera</i> Small vs. medium

Table S2. Number of single visits of a virgin coffee flower, performed by bee species observed in the study sites. Fruit set is the percentage of single visited flowers that ripped. (FC = Forest Cover).

Species	Visits	Same Bush*	Other Bush*	Fruits	Fruit Set (%)	Near & High FC	Far & Low FC
<i>Apis mellifera</i>	73	41	32	32	44	37	36
<i>Plebeia sp.</i>	31	4	27	10	32	31	0
<i>Schwarziana quadripunctata</i>	9	-	-	2	22	9	0
<i>Scaptotrigona</i>	8	1	7	3	38	8	0
<i>Meliponini sp.</i>	5	-	-	3	60	5	0
<i>Plebeia remota</i>	4	0	4	4	100	4	0
<i>Trigona sp</i>	4	1	3	0	0	3	1
<i>Melipona quadrifasciata</i>	3	2	1	1	33	3	0
<i>Jataí</i>	2	0	2	0	0	2	0
<i>Paratrigona subnuda</i>	2	0	2	1	50	2	0
<i>Halictidae sp.</i>	1	0	1	1	100	1	0

Table S3. Results of GGLM model selection for the effect of local landscape variables over bee richness, the likelihood ratio test and LRT *p*-value for the variables of the best model selected using Akaike Corrected criterion.

Response	Models	Random effect	LRT	<i>p</i> -value
Richness (nets)	Distance (m)	Landscape		
	Distance		7.29	0.007**
	Distance (categorical)	Landscape		
	Distance		6.53	0.011*
	Coffee_400, Distance	Landscape		
	Coffee_400		0.01	0.93
	Distance		6.87	0.009**
	Pastures_400, Distance	Landscape		
	Pastures_400		0.01	0.94
	Distance		7.29	0.007**
Richness (Pantraps)	PCA1 - Matrix variation	Landscape		
	Matrix variation		16.77	> 0.001***
	Coffee cover (400-m radius)	Landscape		
	Coffee cover		16.59	> 0.001***

Table S4. Results of GGLM model selection for the effect of local landscape variables over bee abundance, the likelihood ratio test and LRT *p*-value for the variables of the best model selected using Akaike Corrected criterion.

Response	Models	Random effect	LRT	<i>p</i> -value
Abundance (nets)	Coffee_400, Distance (m)	Landscape		
	Coffee_400		5.87	0.015*
	Distance (m)		8.96	0.003**
Abundance (pantraps)	Coffee cover (400-m radius)	Landscape		
	Coffee cover		49.07	> 0.001***
	Coffee_400, Distance	Landscape		
	Coffee cover		46.697	> 0.001***
	Distance		0.27	0.602
Abundance (Meliponini)	Coffee_400, Distance (m)	None		
	Coffee cover		4.86	0.023*
	Distance		6.64	0.010*

Distance (m)	None		
Distance		7.97	0.005**
F2 - Matrix variation	None		
Matrix variation		6.77	0.009**

Table S5. Correlation values, *p-values* and graphs of the species abundances, of the bees correlated, with the first axis of the Non-Dimensional Multi Scale (NMDS). The nesting site and nectar robber behaviour is also presented for each species. *Trigona spinipes*, *Trigona hyalinata*, *Paratrigona subnuda*, *Nannotrigona testicornis*, *Tetragonisca angustula*.

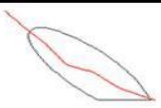

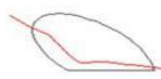
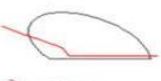

Bee species abundance	Community Composition (First axis)	R ²	<i>p-values</i>	Nesting site	Nectar robbers
<i>T. spinipes</i>		0.81	<0.001	Exposed	Yes
<i>T. hyalinata</i>		0.5	0.014	Exposed	Yes
<i>P. subnuda</i>		0.46	0.004	Ground	No
<i>N. testaceicornis</i>		0.45	0.029	Cavities	No
<i>T. angustula</i>		0.46	0.025	Cavities	No

Table S6. Main sampling characteristics and species composition results of studies that have measured bee diversity during the coffee blooming period, within a variety of shade management (From shaded polyculture to sun coffee production).

Country	Sampling methodology	Sampling effort	Bee richness -> N° Bees	References
Brazil	Entomological nets 2 min sweep-netting - twice	1h 36 min 24 sites	20 species -> 169 bees Figure S6	Our Study
Brazil	Flower observations 9 sessions of 10 min observations per plant	6 hours 4 coffee bush/plants	5 species <i>A. mellifera</i> (89%)	Malerbo-Souza <i>et al.</i> 2003
Brazil - viosa	Observations?	NA	8 species <i>A. mellifera</i> , <i>Dialictus</i> *, <i>M. quadrisfasciata</i> *, <i>T. angustula</i> *, <i>T. spinipes</i> * & <i>Xylocopa</i>	De Marco and Coelho 2004
Ecuador	Flower observations 4 sessions of 15 min	21 hours 21 agroforest	29 morphosps. -> 2733 bees <i>Apis mellifera</i> (42%)	Veddeler <i>et al.</i> 2006
Colombia	Flower observations 10 min session (shrub)	18h 40 min 12 farms -> 112 plants	<i>A. Mellifera</i> (59%); Stingless bees (40%)	Bravo-Monroy <i>et al.</i> 2015
Panamá	Flowers observations Max 3 min per day - 4 days	1h 28min 11 transects.	22 species -> 1926 bees <i>Apis mellifera</i> (73%)	Roubik 2002
Costa Rica	Flowers observations Two sessions of 10 min	9h 20min 12 sites(2001)- 16 sites(2002)	40 morphosp. -> 1041 bees	Ricketts 2004
Costa Rica	Malasia Trap 20 coffee flushes (blooms) 3 days/flush	1,440 hours 9 sites in 3X(shade/sun/follow)	113 morphosp.-> 1012 bees (34 genera) <i>Dialictus</i> (49%), <i>Trigona</i> (11.5%)	Ngo <i>et al.</i> 2013
Mexico	Pan traps 6 sessions of 8 hours once every two weeks (6 before and after the coffee bloom).	10,080 (bowls hours) 30 bowls (of 6 oz = 177 ml) TOTAL: 336 hours (per site)	46 species -> 648 bees 72.2% Halictidae and Apidae 27.8%	Jha & Vandermeer 2010
Brazil	Pan Traps 3 bowls (110 ml) per site. During 48 h	3,456 (bowl hours) (1728h of day) 24 sites	16 species -> 67 bees Figure S6	Our Study
México	Flower observation 4 sessions (shrub) of 25 min	26h 40 min 4 farms -> 4 sites per farm	7 species → 550 bees <i>A. mellifera</i> (87%); <i>Scaptotrigona</i> (7%)	Vergara <i>et al.</i> 2008
México	Flowers observtions 10 minutes sessions per plant	5 hours 30 plants	5 species -> 55 bees <i>Trigona</i> (47%); <i>A. mellifera</i> (12.7%)	Philpott <i>et al.</i> 2006
Mexico	Flower observations 15 min sessions	31 hours 124 sessions	17 species -> 499 bees	Jha & Vandemeer 2009
India	Flower observation 15 min sessions -> looking at 5 branches	176 h 15 min 149 sites -> 5 bushes/site TOTAL: 10575 min	15 species -> 5658 bees <i>A. mellifera</i> (81.4%); <i>Tetragonula</i> (18%)	Krishnan <i>et al.</i> 2012
Indonesia	Flower observations 15 min sessions on 7 coffee bush per system	7 h 30 min 10 coffee systems TOTAL: 450 min	22 sps → 510 bees 7 sp socias -> 312 ind 15 sp solitary -> 198 ind	Klein 2002
Indonesia	Flower observations 3 sessions (days) of 25 min	15 sites(18h 45 min) 24 sites (30 hours)	33 sp -> 2269 bees (<i>C. canephora</i>) 29 sp. -> 2038 bees (<i>C. arabica</i>)	Klein <i>et al.</i> 2003