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RESEARCH ARTICLE - BEES

Bee diversity responses to forest and open areas in heterogeneous Atlantic Forest

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Abstract

Agriculture driven landscape changes have caused worldwide forest loss and fragmentation, severely affecting biodiversity and ecosystem services, amongst which pollination is remarkably important. Bees are an essential pollinator group for forest plant populations and food production in tropical landscapes. They are also dependent on forested environments which are essential to maintaining their diversity and pollination services. We analysed bee diversity in forest patches and adjacent open areas to evaluate if bees can use complementary environments in heterogeneous altered tropical landscapes. The effect of landscape level heterogeneity and forest amount on bee diversity was also assessed. Our hypothesis was that bee communities will be richer and more diverse in highly forested and heterogeneous landscapes when compared to areas dominated by few human-made environments, but due to supplementary foraging behaviors, they will be more abundant in open areas where flower availability is higher. We actively sampled bees visiting flowers within forest patches and in surrounding open areas between the Cantareira and Mantiqueira mountain ranges in São Paulo, Brazil. We found both higher bee richness and diversity in open areas than in forest patches, partially denying our initial hypothesis but supporting that bees are more abundant in open areas. We found strong indication that landscapes with a higher amount of forest and environmental heterogeneity can provide more resources for bees through resource complementation processes, maintaining their diversity in the landscape. The presence of forest patches close to crop and open areas is of utmost importance for the conservation of bees and pollination services with important consequences for land management in tropical environments.

Introduction

Over the years, human activity has modified about 43% of Earth's land surface (Barnosky et al., 2012) by converting natural areas for several human activities, among them agriculture and urbanization (Lambin et al., 2001). In Brazil, this process is even harsher, with about a third of all land being converted, mostly for agriculture and cattle production (Sparovek et al., 2010), endangering most, if not all, of the Brazilian biomes (Ferreira et al., 2012). The Atlantic Forest is one of these biomes, having lost more than 85% of its area (Ribeiro et al., 2009) due to exploitation of forest resources and land use activities for agriculture, pasture, forestry and urban expansion (Dean & Ferro, 1996), up to the point of being considered one of the 25 most endangered biodiversity hotspots of the world (Myers et al., 2000). Human driven land use changes can cause forest loss and fragmentation, changing landscape structure and leading to severe consequences for biodiversity and ecological processes (Andrén, 1994; Fahrig, 1998), compromising essential ecosystem services. One of the most threatened ecosystem services is crop pollination (Potts et al., 2016), for habitat loss limits available resources for pollinators and fragmentation forces pollinators to change their foraging patterns, altering the topology of plant-pollinator

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interaction networks and consequently plant reproduction (Brosi et al., 2008; Van Geert et al., 2010; Moreira et al., 2015).

Bees are considered one of the most crucial pollinator groups, being undoubtedly related to the maintenance of plant diversity in tropical forests as well as food production in agroecosystems (Bawa, 1990). Pollination performed by bees also contributes to the world economy and human health, since this process is essential for at least 35% of the world's food production (Klein et al., 2007) and being responsible for providing different nutrients for human populations (Eilers et al., 2011). For bees, habitat loss and fragmentation can increase the isolation of individuals and populations, affecting dispersion and foraging capacity (Brosi et al., 2008; Ferreira et al., 2015; Boscolo et al., 2017). This isolation compromises bees' chances to find mating partners, food, and nesting resources, with negative effects on population sizes and genetic diversity. When most populations are hindered like this, sharp decreases in abundance and richness of bee communities are expected (Tonhasca et al., 2003; Brosi et al., 2008; Ferreira et al., 2015). Habitat loss and fragmentation are being thus recognized as one of the top determinant factors for the general worldwide decline of bee populations detected during the last few years (Potts et al., 2016).

However, the magnitude of the impact of land use changes on bees can vary depending on the characteristics and requirements of each species (Aizen & Feisinger, 1994). The presence at the landscape level of enough natural areas such as forests is an important factor for the maintenance of bee diversity and pollination (Brosi et al., 2008). Landscapes with higher proportions of forest cover have a positive effect on bees species diversity (Aizen & Fiesinger, 1994; Morato et al., 1999; Tonhasca et al., 2003; Brosi et al., 2008; Brosi, 2009; Ferreira et al., 2015; Boscolo et al., 2017). The maintenance of forest patches in agricultural landscapes can even increase the diversity of flower visiting bees, especially of species considered flower and nesting specialists (Carvalheiro et al., 2010).

However, some species, such as social ground-nesting bees, may be able to nest and explore resources both in the forest and in open areas (Ferreira et al., 2015), being less sensitive to environmental modifications. That plasticity in resource acquisition allows bees living in heterogeneous landscapes to explore resources in a wide range of environment, what must be especially true if additional food and nesting sites are available in non-native patches, such as in unmanaged pastures and open areas (Steffan-Dewenter et al., 2002). Empirical studies have shown that in tropical regions altered by human activity, the maintenance of several different environments, instead of a single dominant anthropic land cover type, can favour many pollinator species (Moreira et al., 2015; Boscolo et al., 2017). Depending on the requirements of each species, high landscape heterogeneity, namely the equitable presence of different types of land use and occupation, can increase the range of different environments used as habitat or source of complementary resources for bees (Dunning et al., 1992; Moreira et al., 2015, 2017). This complementation process is more likely to occur when different types of environments are near each other (Lindgren et al., 2017), facilitating bee movements among these areas and consequently their ability to obtain resources, potentially increasing their fitness and population sizes (Brosi et al., 2008). If this is the case, this opens a new range of environmental management possibilities to guarantee long term bee preservation along with human activities with associated ecosystem services in tropical environments.

In order to develop strategies to conserve and increase bee abundance and diversity in altered landscapes, it is necessary to understand not only the requirements of these species regarding floral and nesting resources but also how landscape structure can affect their presence in different environments**.** Our objective was to assess the influence of forest cover and landscape heterogeneity on the abundance and diversity of bees foraging within the forest and in adjacent open areas, which can be used as complimentary habitat in the face of forest loss. We hypothesize that bee communities will be richer and more diverse in highly forested and heterogeneous landscapes when compared to areas dominated by a few human-made environments with low forest cover. Also, due to supplementation foraging behaviors, we expect bee abundance to be higher in open areas, where flowers are more abundant, than inside the forest. We expect to aid in the development of guidelines and strategies for the management of agricultural areas dependent on pollination services in order to reconcile the productivity of these areas with the preservation of more diverse pollinator communities, thus allowing the land occupation to be more sustainable.

Material and Methods

Study area

This study was developed at the region between Cantareira and Mantiqueira mountain ranges (São Paulo, Brazil), at the rural areas spanning from the city of Itatiba (23º 01' 00" S 46º 50' 00" W) to Igaratá (23º 12' 00" S 46º 09' 00" W) (Fig 1). Since 1994, the Cantareira region belongs to the "São Paulo city green belt" UNESCO Biosphere Reserve, being a key region to develop novel conservation approaches and sustainable development (Jaeger, 2005). The region also contributes to water supply, providing to the most important water source for the São Paulo city metropolitan region (Whately & Cunha, 2007). During the period of data sampling – November 2015 to March 2016 and November 2016 to March 2017 – the monthly precipitation at the region varied from 194.26 mm/month to 281.16 mm/month (DAEE) with a mean annual temperature varying between 15-18 °C.

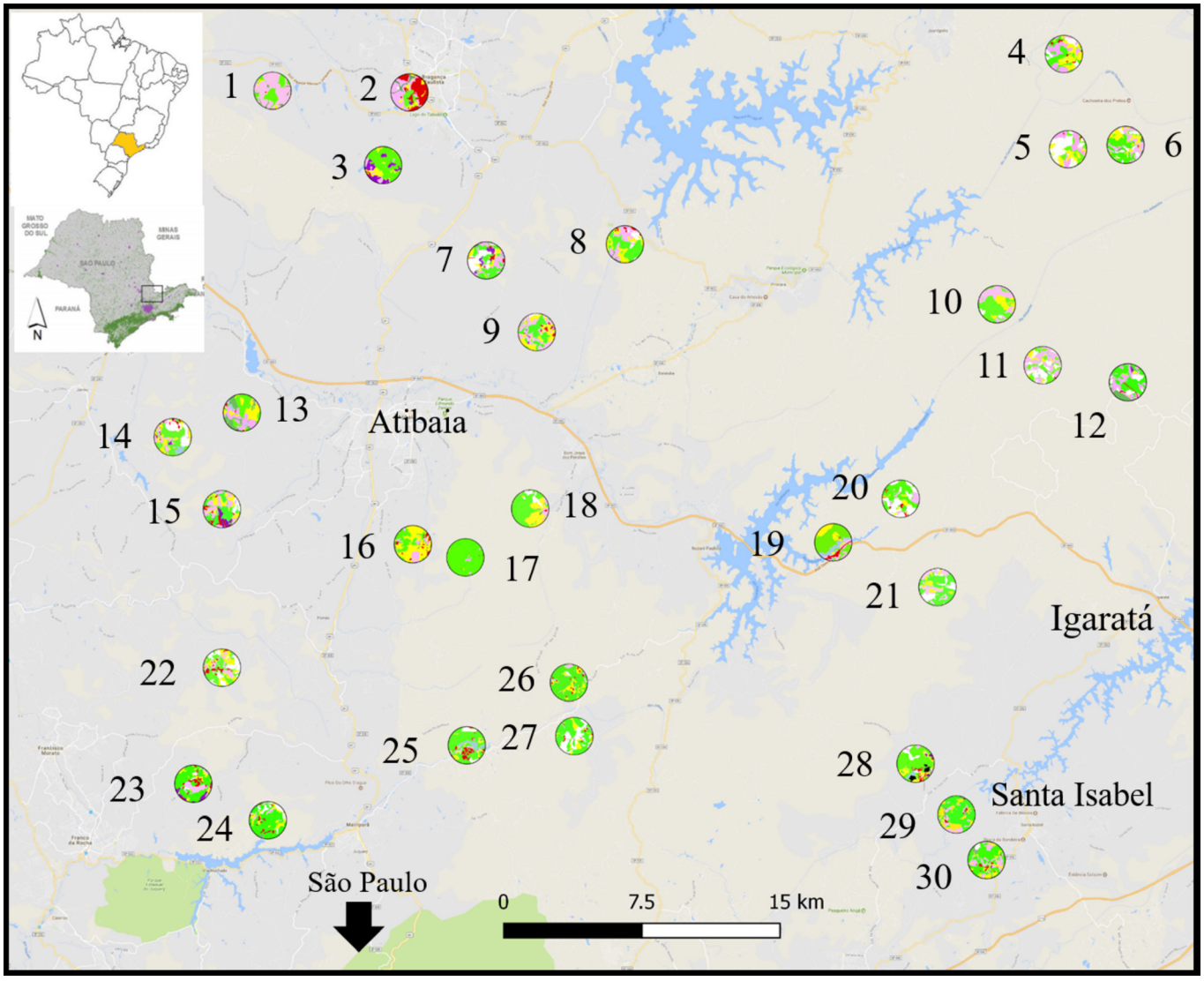


Fig 1. Map of Cantareira-Mantiqueira mountain range region, São Paulo State, Brazil. The circles show the landscapes of 1 km radius with their respective types of environments indicated in Figure 2.

The region is included within the Atlantic Forest biome and known to hold a great diversity of landscape structures with different degrees of anthropic intervention and forest fragmentation (Ribeiro et al., 2009). Land cover is very heterogeneous, including several types of forests, crops, commercial tree plantations, open areas and urbanized environments at different intensity levels (IBGE, 1992). Its complex of different heterogeneous landscape structures generates several levels of permeability and varying resource availability for bees, influencing the interaction between plants and these floral visitors. Specifically, we focused on studying bees in both forest patches and adjacent open areas. Sampled forests were composed of second growth dense ombrophilous forests in intermediate regeneration state (SIFESP, 2009), presenting trees of up to 25m tall with a shrub understory (Veloso et al., 1991). Open areas encompassed unmanaged grassy pastures with only scattered trees, with the presence of Asteraceae, Poaceae and other herbaceous plants (S.1). All collected plant vouchers were deposited at the herbarium at FFCLRP-USP.

Bee sampling

To compare bee diversity in different environments, we sampled bees inside forest patches and in surrounding adjacent open areas. Floral visiting bees were sampled actively with entomological nets. To delimit our search area, we installed inside each selected forest patch (see patch selection details below) a hexagonal plot with 25 meters sides, totalling 0.06 hectare sampled per forest site. To reduce edge effects all hexagons were installed at least 50 meters away from the forest edge. Concurrently we delimited a region of similar area at the closest available open field surrounding the patch. In both environments we conducted recursive walks searching for flower visiting bees. Within each hexagon, sequential 15 min of observations were made in all open flowers (up to two meters above ground) in sunny, hot days (20-31 °C), from 7:30 h to 14:00 h. We also sampled bees in open areas surrounding forest with the same searching method. Bees were identified with the aid of experts to the most specific taxonomic level possible.

We conducted fieldwork at the season of the year in which flowering plants were most likely to be found (Morelato LPC, personal communication), namely between November and February of 2015-16 and 2016-17. In each site, we sampled, at least, three times in each season. The use of these periods increased the chances of sampling a higher richness and abundance of flower visiting bees (Nielsen & Bascompte, 2007).

Sampling points selection and landscape pattern analysis

Land cover maps of the study area were generated from high resolution satellite images (Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo and GIS User community) through remote sensing (RS) within geographic information systems (GIS), using both manual and supervised classification at a scale of 1:5000 (executed by the Spatial Ecology and Conservation Laboratory-LEEC, UNESP). The study region was classified into nine categories: water, forest, shrub, agriculture, forestry, open areas, wetland and anthropic (urban) areas (Fig 2). Subsequently, these areas were checked in the field to correct mapping errors so that in the end more than 90% of the region was correctly classified. From these maps, we selected 30 forest patches, with areas ranging between 15 and 25 ha and 24 open areas ranged from 0.73 to 26 ha. These forests were surrounded by several distinct anthropogenic environments (citrus, coffee, pasture, forestry, urban areas, etc.), with consequent variation in local vegetation structure that could influence local bee communities in different degrees. We purposely selected these 30 forest patches so that chances of high correlation between the amount of overall surrounding forest and landscape heterogeneity were reduced. Bees were sampled both inside forest patches and in immediately adjacent open areas.

To evaluate the influence of the composition of the surrounding landscape on flower visiting bees, we calculated two descriptive landscape metrics, forest cover and landscape heterogeneity. These measures were done within circular areas of varying radius surrounding sample plots. Landscape pattern analysis was conducted with Fragstat v.4 program (McGarigal et al., 2012) to calculate forest cover and landscape heterogeneity (Shannon-Wiener index). The Shannon-Wiener index considers the number of different types of environments and its proportion in each landscape. If two landscapes are covered by exactly the same types of environments, that with the highest Shannon-Wiener value will be the one with the highest category evenness (McGarigal et al., 2012).

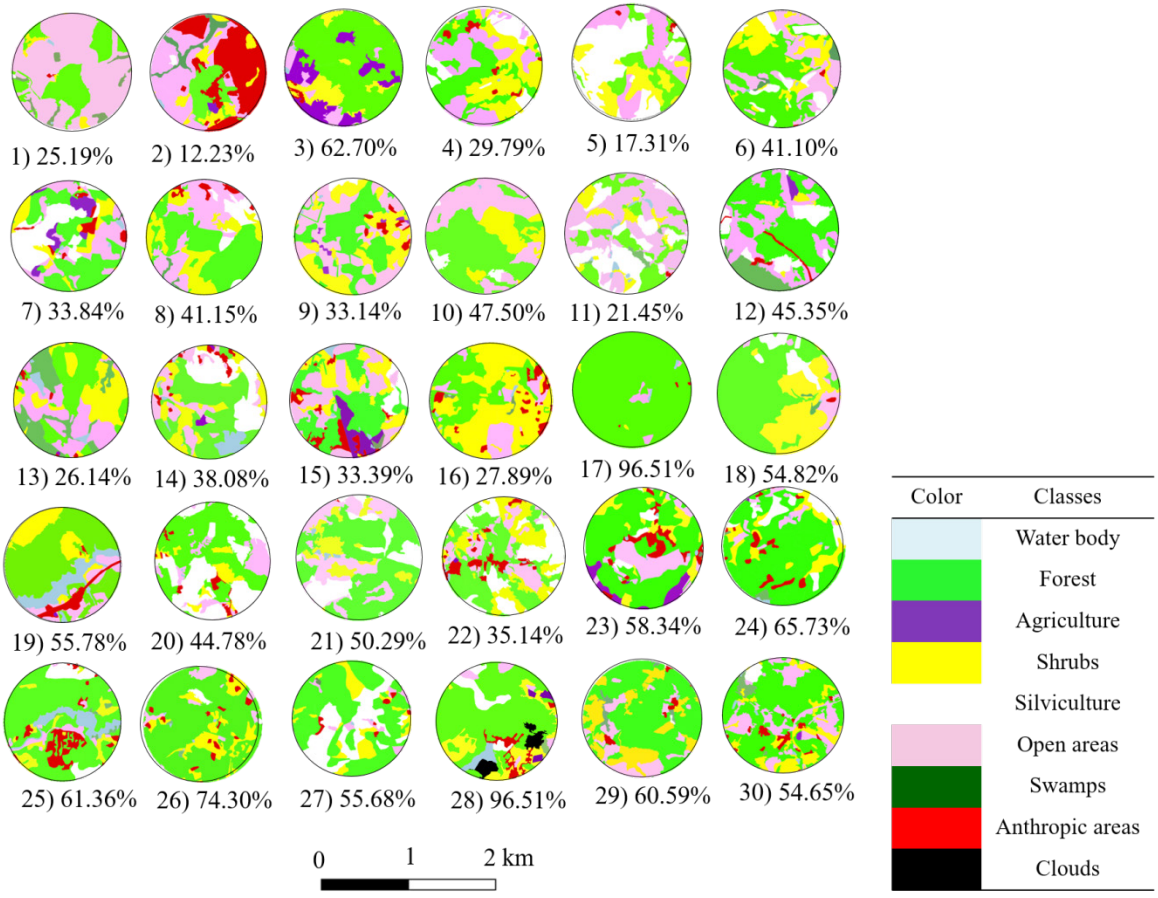


Fig 2. Mapped 1km radius landscapes. Each colour represents an environment as indicated in the legend (complete class descriptions can be found in Table S.2). Percentages indicate the remaining amount of forest in each landscape.

Data analysis

For each site of forest or open area, we estimated three bee community level variables: richness (number of species), abundance (total bee amount), from which we could also calculate the Shannon diversity index. We calculated this index with the function *diversity* from the *vegan* package in R environment (Team, 2017). The Shannon index is defined as $H' = - \sum_i p_i \, Ln \, p_i$, where p_i is the proportional abundance of species *i* and *Ln* is the natural logarithm (Oksanen et al., 2017). This index increases proportionally to the overall community diversity, being the sites with the highest species richness and equitability the most diverse and therefore represented by the highest index values.

Analysis of the effects of landscape patterns on bee diversity

To evaluate the effects of landscape composition on bee diversity, we determined the spatial scale (landscape radius) in which linear models provided the best explanation of the response variables (Steffan-Dewenter et al., 2002). For that we considered buffers with a radius varying from 250m to 1000m in 250m intervals (Steffan-Dewenter et al., 2002; Winfree et al., 2008) and then analysed it using simple linear regressions for each scale, having either forest cover or landscape heterogeneity as explanatory variables and each bee community descriptor as response variables. From these regressions, we obtained the R^2 values with their respective p-values (e.g., Pearson, 1993; Bergin et al., 2000; Steffan-Dewenter et al., 2002; Moreira et al., 2015). The highest observed R^2 among all four scales for a given explanatory variable indicated the scale of effect to be used for each biological variable.

After finding the scale of effect, we evaluated the influence of forest cover and landscape heterogeneity on bee richness, abundance, and diversity using simple linear regressions at the best selected scale for each variable. We used p values to check if the observed relationships were significant at a 0.05 alpha level and checked whether the parameters values were positive or negative to interpret the effect of landscape factors on biological variables. We then generated scatter plots for each response variable containing the observed data and model fit lines for both forest and open area sampling sites. This allowed us to directly compare the landscape effects on the communities observed in these two environments and check if they were the same. To effectively compare if the two sampling groups (forest and open areas) were significantly different from each other, we also conducted an Analysis of variance for each bee community descriptor. We did all analyses in the R environment version 3.4.3.

Results

We sampled 206 bee individuals within 54 species and morphotypes inside forest patches and 1875 bee individuals within 161 species and morphotypes in open areas surrounding these patches, totalling 2081 bee individuals in 176 species and morphotypes (Table S. 3) with 39 common species between forest and open areas distributed within 4 of the 5 sampled families. These results show that in open areas we found about threefold the bee richness observed inside the forest.

As expected for the selection of the scale of effect, the best explanation was found to be related to different scales for each response variable. Bee community variables (Shannon diversity index, richness, and abundance) inside the forest responded to forest cover in the scale of 750 m. In open areas, the best scale for these variables was at the 1000 m radius. For landscape heterogeneity, bee diversity best responded at the scale of 750 m for open areas and 1000 m for forest patches (Fig 3). On the other hand, bee abundance responded to landscape heterogeneity at the 500 m, the smallest selected scale among all tested relationships (Table S.4).

Table 1. Linear regression results for bee richness, abundance and diversity (Shannon index) inside the forest and in adjacent open areas. The table shows only the models selected with the highest R^2 results after landscape scale selection for the proportion of forest in landscape (F. Cover) and Landscape Heterogeneity (L. Heterogeneity) measured with the landscape shannon index. The letters "a" to "f" corresponds to the graphics of figure 2 with the same letters. Significant p values are marked with *.

Models	R^2	p
Forest Cover		
a) Bee Shannon index in the Forest ~ Forest Cover_750	0.05971	0.1931
a) Bee Shannon index in Open areas ~ Forest Cover_1000	0.0964	0.1398
b) Bee Richness in the Forest ~ Forest Cover_750	0.0252	0.4021
b) Bee Richness in Open areas ~ Forest Cover_1000	0.1326	0.08018
c) Bee abundance in the Forest ~ Forest Cover_1000	0.03959	0.2918
c) Bee abundance in Open areas ~ Forest Cover_1000	0.1871	0.03476*
Landscape Heterogeneity		
d) Diversity in the Forest ~ L. Heterogeneity_1000	0.0217	0.4372
d) Diversity in Open areas ~ L.Heterogeneity_750	0.01128	0.6213
e) Richness in the Forest ~ L. Heterogeneity_1000	0.002946	0.7758
e) Richness in Open areas ~ L. Heterogeneity_750	0.01714	0.542
f) Abundance in the Forest ~ L. Heterogeneity_750	0.04273	0.2731
f) Abundance in Open areas ~ L. Heterogeneity_500	0.06063	0.2461

Using these variables at its best explanatory power, bee richness, abundance and diversity in open areas responded positively to forest cover. This response was more intense for bee richness and abundance than for diversity. However, we found the opposite response for bee diversity and richness inside the forest, with a negative effect of forest amount on these variables, which was more intense for bee diversity (Fig 3 a, b). Bee abundance did not respond to forest cover. Differently, bee communities in open areas responded negatively to landscape heterogeneity for all three response variables, but more strongly for bee abundance (Fig 3 f). The only positive effect of landscape heterogeneity was on bee diversity sampled within the forest (Fig 3 d), indicating that landscapes with more different available environments increases bee diversity inside the forest, but not outside. Furthermore, the Analysis of Variance revealed that forest and open area sites were significantly different from each other for all three bee community variables, namely richness ($F = 57.33$, $p < 0.0001$), abundance ($F = 59.86$, $p < 0.0001$) and diversity ($F = 47.78$, $p < 0.0001$), with all variables having higher mean values always in open areas in comparison to forest interior.

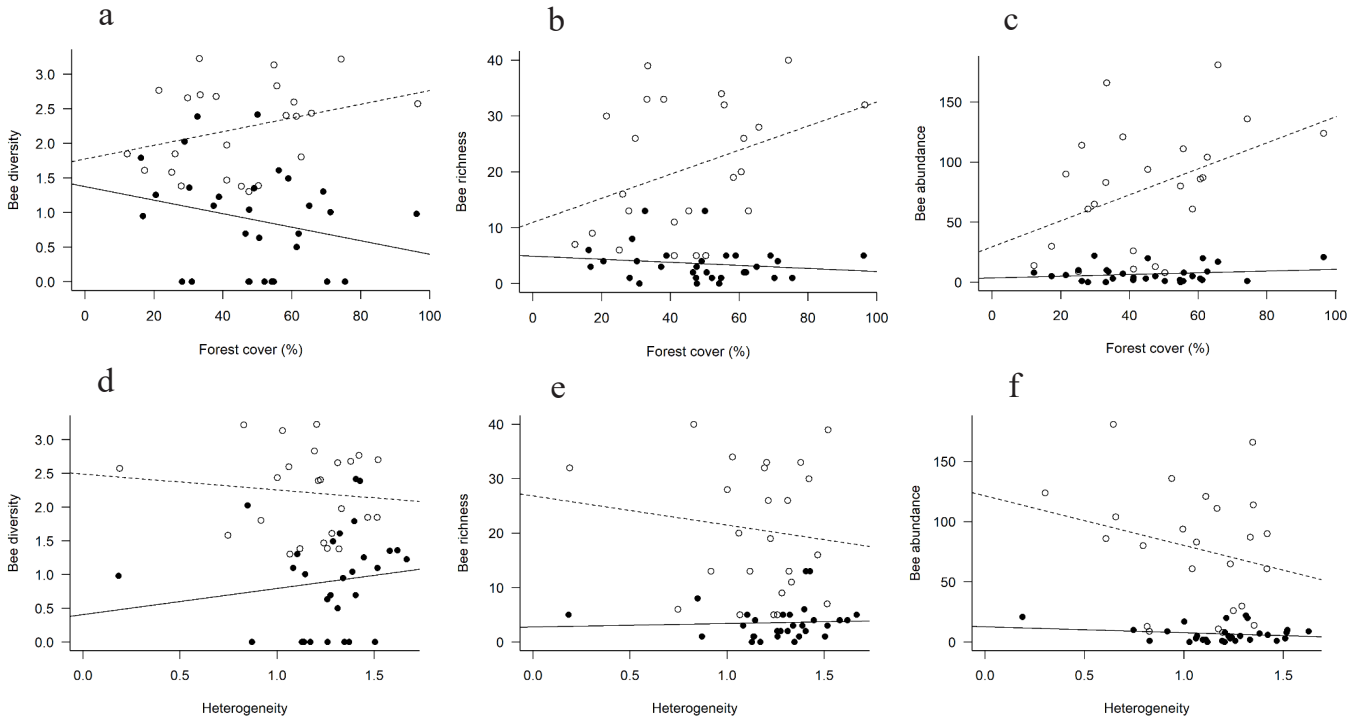


Fig 3. Linear regression plots. Dashed lines and hollow points are for open areas adjacent to forests and continuous line and black points correspond to forest patches. Response for bee shannon index (bee diversity) in "a" and "d"; Response for bee richness in "b" and "e"; and for bee abundance in "c" and "f". Graphs "a" and "b" show the effect of forest cover on bee richness at 750 m inside the forest and 1000 m in open areas. In "c" it is shown the forest cover effect on bee abundance at 1000 m for forest patches and open areas. However, "d" and "e" show the effect of landscape heterogeneity on bee diversity and richness at 1000 m in forest patches, and at 750 m in open areas, respectively. Graph "f", represents the effect of landscape heterogeneity on bee abundance at 750 m in forest patches and at 500 m in open areas. Graphs "a" and "b" show that bee diversity is directly related to forest cover in open areas and is inversely related to forest cover in forest fragments. In "d" and "e", bee diversity and richness were inversely related to increases in landscape heterogeneity in open areas, even though in forest fragments bee diversity increase when landscape heterogeneity is high. In "c" and "f" forest cover had a positive effect on bee abundance for both open areas and forest patches. Landscape heterogeneity had a negative effect on this same response variable, for both open areas and forest patches.

Discussion

We observed a distinct response pattern of bee communities between those sampled inside forest fragments and in surrounding open areas. Most surprisingly was that, independently of the landscape context, open areas present more diverse and rich bee communities than those found inside the forest, with three times more species visiting flowers in the non-forested environment. These results deny our initial hypothesis for bee diversity and richness but corroborate it for their abundance. Partially, the low levels of bee richness and diversity found inside the forest may be related to the sampled forest strata used in the current study. Since we sampled bees that were foraging on flowers, the response depends directly on blooming intensity in the understory. However, flower abundance is known to be lower in the understory of mature forests, which usually presents reasonably closed canopy with little light input, hindering the growth and blooming of shrubs and herbaceous species closer to the ground (Terborgh, 1985), where we were sampling. Thus, sampling flower visitors in the understory of forest patches may indicate low species diversity, while in fact, sampling only this stratum may not

allow forest bee communities to be fully assessed. In mature forests, blooming may be significantly higher in the well-lit canopy, according to the flowering season of the trees, and bees may be drawn there to forage (Ramalho, 2004). To overcome this limitation, novel methods to sample flower visiting bees in the canopy for a wide range of trees must be developed. However, even with this limitation, the results for bee communities within and outside forest patches remain entirely comparable and have ecological significance and management value at the landscape level.

What we found when considering landscape composition is that this higher overall bee diversity in open areas tends to increase along with higher amounts of surrounding forest at broader landscape scales (mainly 750 and 1000 m radius). This relationship between open areas and forest cover in the landscape can be understood as an effect of bees using open areas as an alternative, complementary habitat type (Dunning et al., 1992; Boscolo et al., 2017; Lindgren et al., 2017). The hypothesis of habitat complementation, or likewise habitat supplementation, arises from the fact that open areas adjacent to forest fragments may offer a great amount of feeding resources, mainly due to a more constant and higher availability of flowers (e.g., Asteraceae, Myrtaceae) than in the understory of forest patches (Moreira et al., 2015). Thus, bees may leave the forest to forage in these adjacent areas. The presence of bees in these areas is a significant indication that, even though they are initially forest dwelling species, these animals also use the resources available outside the forest (Brosi et al., 2008). For many Atlantic Forest bees, the forest is considered a high-quality habitat and has an essential role as source environment (Brosi et al., 2008; Tscharntke et al., 2012; Ferreira et al., 2015), as it may offer a higher amount of adequate nesting sites. The availability of other kinds of resources, on the other hand, may be lower in the understory when compared to open areas. This attracts bees nesting in the forest to use alternative human made environments to fulfil their needs. Species that nest above the ground, for instance, are highly dependent on forested areas for nesting and end up being more susceptible to forest loss when compared to species that nest in the ground (Ferreira et al., 2015). For these species, the presence of forested habitat within foraging ranges is important to supply their needs, mainly due to enhanced nesting opportunities within the available forest patches (Brosi et al., 2008).

Our results corroborate studies that elucidate the importance of maintaining high levels of forest quantity in the landscape in order to maintain biodiversity (Fahrig et al., 2011; Lindgren et al., 2017). Open areas present different climatic conditions from forest patches, being drier and hotter than the forest understory (Baudena et al., 2015). This may be a problem for species that are more sensitive to extreme climatic conditions (Hilário et al., 2001). For these sensitive species, foraging outside the forest may be challenging, even if feeding resources are attractive in open areas, which are exposed to more light and have a higher amount of flower resources (Terborgh, 1985; Wender et al., 2004). In this scenario, higher amounts of forest in the landscape leads to lower isolation of remaining forest patches (Fahrig, 2003), being extremely important for the maintenance of more sensitive bee species (Brosi et al., 2008), for it reduces the distance and time needed to access open areas, making foraging there less demanding and more efficient (Jha & Vandermeer, 2010).

Landscapes composed of enough close by forest and open areas are then an advantageous situation for both sensitive species and those that can endure open areas conditions. Resilient bees may be even more efficient in using both environments, exploring forest to forage and nest and adjacent open areas to forage for food. For bees that nest in the ground, open areas may even mean a source of nesting resources along with food (see Ferreira et al., 2015). Landscape configuration, i.e., the spatial distribution of forest patches and open areas, is thus of utmost importance for the conservation of bee diversity and abundance in the landscape (Moreira et al., 2015; Boscolo et al., 2017). This also means that the maintenance of forest and bee friendly non-forest environments in the landscape is favourable to plant pollination within forest patches and also for the provision of pollination ecosystem services for plants outside the forest, for example in agricultural areas (Jha & Vandermeer, 2010; Moreira et al., 2015; Boscolo et al., 2017; Hipólito et al., 2018).

Highly forested landscapes may also be of ecological importance to provide other ecosystems services, such as climatic and water regulation and soil formation, among others (Asner et al., 2004). For pollinators and pollination, the increase we found on species number not necessarily represents an improvement of environmental quality or ecosystem service provision. For example, the fragmentation of forest creates edges that receive a significant amount of sunlight and is an interesting environment for bees to forage due to more diversity of herbaceous flower resources (Chacoff & Aizen, 2006). However, that also favors the invasion of opportunistic and or exotic species (Aizen et al., 2008). In the first moment the presence of these species increases richness, but in the long term these opportunistic species may be very competitive and represent a negative impact for forest communities and pollination within the remaining forest patches. Likewise, the current rates of tropical forest replacement for anthropic open areas, mostly with agricultural purposes (Gibbs et al., 2010), imposes an important challenge for the scientific argument of the need to maintain heterogeneous pollinator friendly landscapes.

The economic pressure to acquire short term profits that dominates tropical landscape change processes usually leads to land management directives that hinder long-term maintenance of bees and associated pollination services. Current agribusiness model tends to favor high yield but low durability or sustainability of the crops in tropical environments (Landy et al., 1990), moving over

native environments when production decreases due to environmental degradation. This constant movement of crop areas generates highly homogenized landscapes where pollination services will be lower due to pollinators debt. The yield of pollinator dependent crops has already been shown to be higher and to produce greater value for the landowner when the landscape has a more interspersed structure with native environments being closer and spatially alternated with crops (Ricketts et al., 2004; Klein et al., 2007; Hipólito et al., 2018). This effects of the nearness between crops and native environments corroborates the idea that the presence of forest patches near crops can increase pollination (Brosi et al., 2008). Also, the presence of forests may favor the permanence of more sensitive species, which can offer specific more efficient pollinators for a particular crop or native plant species. In this scenario, our results give an important argument towards the ecological intensification of altered landscapes. We have strong indication that landscapes that have higher amount of forest and higher levels of environmental bee friendly heterogeneity can provide more food and nesting resources for bees, being more interesting for the maintenance of bee species and the ecological service of pollination they provide.

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Supplementary Material

Link: https://periodicos.uefs.br/index.php/sociobiology/article/view/3472/10405

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