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Landscape Structure Effects on Bee and Wasp Assemblages in a Semiarid Buffer Zone

Abstract

Understanding the effects of anthropogenic changes on groups that perform key ecosystem services, such as pollination and pest control, is essential for conservation and maintenance of these groups in landscapes. We aimed to understand how landscape heterogeneity and the natural vegetation loss affect the diversity of bees, wasps and their parasitoids in a resource limited semiarid environment. We sampled bees and wasps that nest in pre-existing cavities in 20 landscapes, for two years, in Ubajara National Park, in northeastern of Brazil. We recorded eleven species of bees, nine of wasps and six of parasitoids in 657 trap-nests. Landscape heterogeneity had different effects on bees, wasps and their parasitoids. Landscape configuration had stronger effect than composition. Bee abundance decreased according to the complexity of the spatial arrangement of landscape units, while wasp abundance increased. Our study shows that in semiarid regions some species may have different responses to landscape structure from those found in other regions. The spatial patterns described here have important implications for conservation of these essential biological groups, indicating that conservation actions for these groups should associate both landscape composition and configuration to increase the provision of resources and to facilitate the access to resources throughout the year.

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1 Introduction

In In the last decades, several studies have warned about the decline of bee and wasp populations around the world (Tscharntke et al. 1998; Roubik 2001; Klein et al. 2002; Gallai et al. 2009; Potts et al. 2010). Various factors have been listed as potential causes for this decline, but farms with high impact local management have been identified as one of the main causes (Hipólito et al. 2018). Simplification of native habitat structure, on a local scale, may also be an important factor that reduces species richness and modifies species composition of solitary bee and wasp assemblages (Flores et al. 2018). However, since bees and wasps may not be confined to a single environment type, they can be affected also by the conditions of their surrounding landscape (Holzschuh et al. 2010; Moreira et al. 2015).

The widespread conversion of natural vegetation into extensive agriculture results in landscape homogenization, and many species of bees and wasps may become endangered due to the reduced availability of food and nesting sites (Williams & Kremen 2007; Charman et al. 2010; Flores et al. 2018). In contrast, heterogeneous landscapes that include agricultural habitats may provide a greater diversity of resources for wasps and bees (Klein et al. 2002; Winfree et al. 2007; Moreira et al. 2015; Boscolo et al. 2017). This occurs, for example, in landscapes that facilitate the movements of bees and wasps through functionally connected habitats (Kennedy et al. 2013; Boscolo et al. 2017). Thus, when essential resources are lacking in a certain environment, these insects can seek alternative resources available in other nearby patches. This cannot occur in homogeneous landscapes with large modified areas where different environments tend to be too far from each other to allow efficient foraging strategies (Schüepp et al. 2011; Moreira et al. 2015; Boscolo et al. 2017; Hipólito et al. 2018).

Also, bees and wasps are responsible for important ecosystem services (Loyola & Martins 2008). Bees are the main group of pollinators of cultivated and non-cultivated plant species (Didham et al.1996; Ashmann et al. 2004; Klein et al. 2007; Loyola & Martins 2008; Potts et al. 2010), while wasps are important predators and parasitoids of other arthropods, and can act in agricultural pest control (Gould & Jeanne 1984; Penagos & Williams 1995; Symondson et al. 2002). Therefore, analyzing the effects of human activities on biological groups that provide ecosystem services, such as bees and wasps, is essential for planning actions aimed at minimizing the loss of such services (Morandin & Winston 2006; Ricketts et al. 2008; Krewenka et al. 2011).

Responses of bee and wasp species to anthropogenic changes in their surrounding environments are quite varied, even in closely related taxonomic groups or within a guild (Ricketts 2001; Antongiovanni & Metzger 2005; Happe et al. 2018). Solitary species of bees and wasps seem to be even more sensitive to human disturbance than their social counterparts (Tscharntke et al. 1998; Kennedy et al. 2013; Happe et al. 2018). From 5 to 10% of solitary species build a nest in pre-existing cavities above ground and can be found in most terrestrial ecosystems (Krombein 1967; Falk & Lewington 2015). These insects build their nests in hollow branches or cavities in tree trunks (Krombein 1967; O'Neill 2001), thus being strongly dependent on different plant species to obtain both food and nesting resources, making them very sensitive to landscape changes (Batra 1984).

Bees and wasps can be affected by changes of both landscape composition and configuration (Kennedy et al. 2013; Steckel et al. 2014; Hipólito et al. 2018). Holzschuh et al. (2010), for example, showed that the diversity of cavity-nesting bees increases with the diversity of habitat types at the landscape level (a measure of landscape composition). On the other hand, richness and abundance of wasps increased with edge length between different habitats (a measure of configuration). Hence, it is important that studies focusing on bee and wasp conservation consider both compositional and configurational aspects of landscape structure.

Understanding the effects of landscape structure on solitary bees and wasps can be even more important in semiarid regions, where resources are limited and very seasonal (Schwinning et al. 2004). During the dry season, the availability of water, plant biomass and flowers is extremely limited for most bees and wasps (Melo & Zanella 2012). Hence, even in landscapes with a large proportion of natural vegetation, individuals may be forced to forage in nearby alternative environments, such as small agricultural areas (Goodell 2003; Dingle & Drake 2007).

To ensure the services provided by bees and wasps and mitigate or reverse biodiversity declines, it is crucial to understand how these insects respond to landscape changes (Chapin et al. 2000; Metzger 2001). Thus, our goal was to investigate how landscape heterogeneity and the loss of natural vegetation affect the assemblages of cavity-nesting bees and wasps in semiarid forests. We hypothesized that species richness and abundance of bees, wasps, and their parasitoids increase with (1) compositional heterogeneity (landscape diversity); (2) configurational heterogeneity and (3) decrease with the loss of natural vegetation. Additionally, we predicted that landscapes with a large proportion of natural vegetation combined with high environmental diversity should have high richness and abundance of bees and wasps because they can provide a greater variety of environments that can act in the complementarity of resources.

2 Material and Methods

2.1 Study area

Sampling was carried out at the Ubajara National Park (UNP) (3°46’S, 40°54’W) and its surrounding areas. Ubajara National Park is a federal conservation area in the Ibiapaba mountain range in the State of Ceará, northeastern Brazil. Although within the semiarid climatic domain, the UNP has a humidity gradient resulting from an altitudinal range from 400 to 900 m a.s.l. (Figueiredo 1988). In the lower areas (400 m a.s.l.), the average annual rainfall is 947 mm, with rains concentrated between January and May, and the average annual temperature is 28.2°C (FUNCEME 2015, historical data from 1982-2014). In the higher areas (900 m a.s.l.), the average temperature is 27°C, and the average rainfall is 1,487 mm annually (concentrated between January and June) (FUNCEME 2015, historical data from 1982-2014). Though the precipitation is high for semiarid patterns, the potential evapotranspiration (PET) is greater than precipitation, indicating that water loss is greater than water input. Hence, the climate is classified as DdA’a’ semiarid with little or no surplus water, with high PET throughout the year (Thornthwaite 1948) (Fig. 1). Combined with its topographic heterogeneity and microclimate variation, there are three types of vegetation in the UNP: Deciduous Thorny Savanna (DS) and Deciduous Seasonal Forest (DF) in the lower parts of the mountain range, and Evergreen Seasonal Forest (ESF) in areas of higher altitude (Araújo et al. 2005). The UNP surroundings are characterized by small agricultural areas and subsistence farming. In the lower areas, the main types of land use are silviculture, annual crops (e.g., corn and beans), and irrigated banana crops. In the higher areas, the land use is mainly characterized by pasture and perennial fruit crops (Araújo et al. 2017).

2.2 Trap-nests

Solitary bees and wasps that nest in pre-existing cavities, as well as their parasitoids, were sampled using trap-nests (Krombein 1967). This method enables the capture of reproductively active species, excluding those that are only transiting through the site (Morato & Martins 2006). Trap-nests were standardized and built according to the methods described in Tscharntke et al. (1998) and Tylianakis et al. (2005). Each trap-nest was made of a 22 cm long Polyvinyl chloride (PVC) tube with a diameter of 15 cm and containing 75 bamboo internodes with a length of 20 cm and diameters ranging from 2 to 20 mm. A broad range of diameters allows to capture a greater diversity of species, since the cavity diameter is correlated to the body size of the females building the nest. In all the trap-nests we inserted ten bamboo internodes with 2-4 mm, 30 with 5-10mm, 30 with 11-15mm and 5 with 16-20 mm of diameter. A larger number of internodes with a diameter between 5 and 15 mm was used since this is the preferred size range of many species (Fricke 1991; Tylianakis et al. 2005; Nascimento & Garofalo 2014; Rubene et al. 2015; Nether et al.

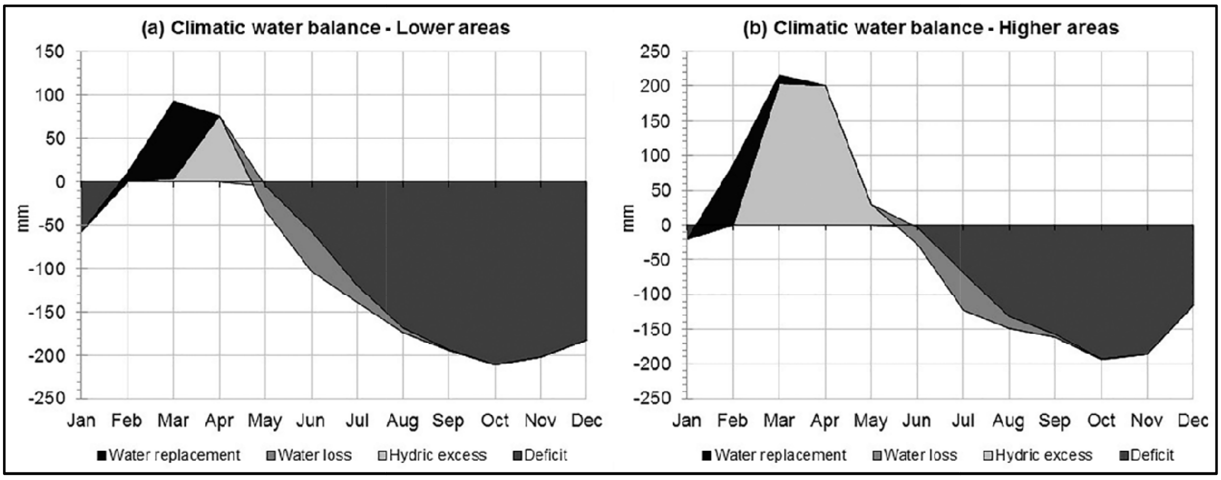

Figure 1: Climatic water balance: (a) lower areas of the Ibiapaba mountain range (FUNCEME 2015, Frecheirinha station, historical data of 1982–2014; annual rainfall: 947 mm, annual evapotranspiration: 2065mm, annual water deficit: 1197mm); (b) higher areas (FUNCEME 2015, Ubajara station, historical data of 1982–2014; annual rainfall: 1487mm, annual evapotranspiration: 1928 mm, annual water deficit: 875mm). Thornthwaite Water Balance (BHidrico GD 4.0 – 2004)

2019). Three trap-nests were placed at each of two sampling points in each landscape (see details in the section bellow), always under a tree for protection against sun and rain. Each set of three trap-nests was tied with a metal wire to a wooden pole or tree branch, 1.5 m above the ground. The metal wire was covered with automotive grease to avoid ant attacks (Tylianakis et al. 2005; Flores et al. 2018). Trap-nest occupation was checked every 45 days for two years, from January 2013 to December 2014. At each visit, the occupied nests were removed and replaced with new bamboo internodes of the same diameter. The occupied nests were placed individually in Polyethylene terephthalate (PETE) bottles and, taken to the laboratory and kept at room temperature (27°C) until adult emergence.

2.3 Landscape data

We used 5 m resolution satellite images, obtained in February 2012 by the WorldView-2 satellite, to produce a map of land use of the UNP and its surroundings within a 10km buffer (Fig. 2). To prepare this map, images were subjected to a segmentation process using the method of growing regions with similarity index of one and minimum area of 500 pixels (Câmara et al. 1996). Images were subjected to the „Bhattacharya“ supervised classifier (using prior knowledge of the study area), with an acceptance threshold of 99%, using ArcMap 10.3.1.Land cover types were then classified into Deciduous Thorny Savanna (DS); Deciduous Seasonal Forest (DF); Evergreen Seasonal Forest (ESF); DS secondary; DF secondary; ESF secondary; agriculture/pasture; exposed soil/road; urban area and water.

Within the mapped area we selected 20 landscapes, 10 in the lower area and 10 in the higher area of the park (Fig 2). A pair of sampling points was used in each landscape, one 100 m outside the border of the UNP and another 100 m within the border. Considering a foraging distance of 600 m or less for many species of solitary bees and wasps (Gathmann & Tscharntke 2002; Klein et al. 2004; Zurbuchen et al. 2010), a one-kilometer buffer around the midpoint between the two sampling points was used to define each landscape. The mid-points of adjacent landscapes were at least 2 km apart from each other to avoid landscape overlap. The spatial autocorrelation was evaluated using Moran's Index to ensure the spatial independence of the landscapes.

We calculated landscape heterogeneity within these 20 landscapes using Shannon Landscape Diversity Index (SHDI) (Fahrig et al. 2015; Boscolo et al. 2017). SHDI is calculated as minus the sum of the total landscape proportion covered by each land-cover type multiplied by that proportion. It increases when the number of different land-cover types increase and/or the proportional areas of these patch types become more even (McGarigal et al. 2012; Boscolo et al. 2017). We chose SHDI because it is more sensitive to rare types of environments than other indices (e.g.

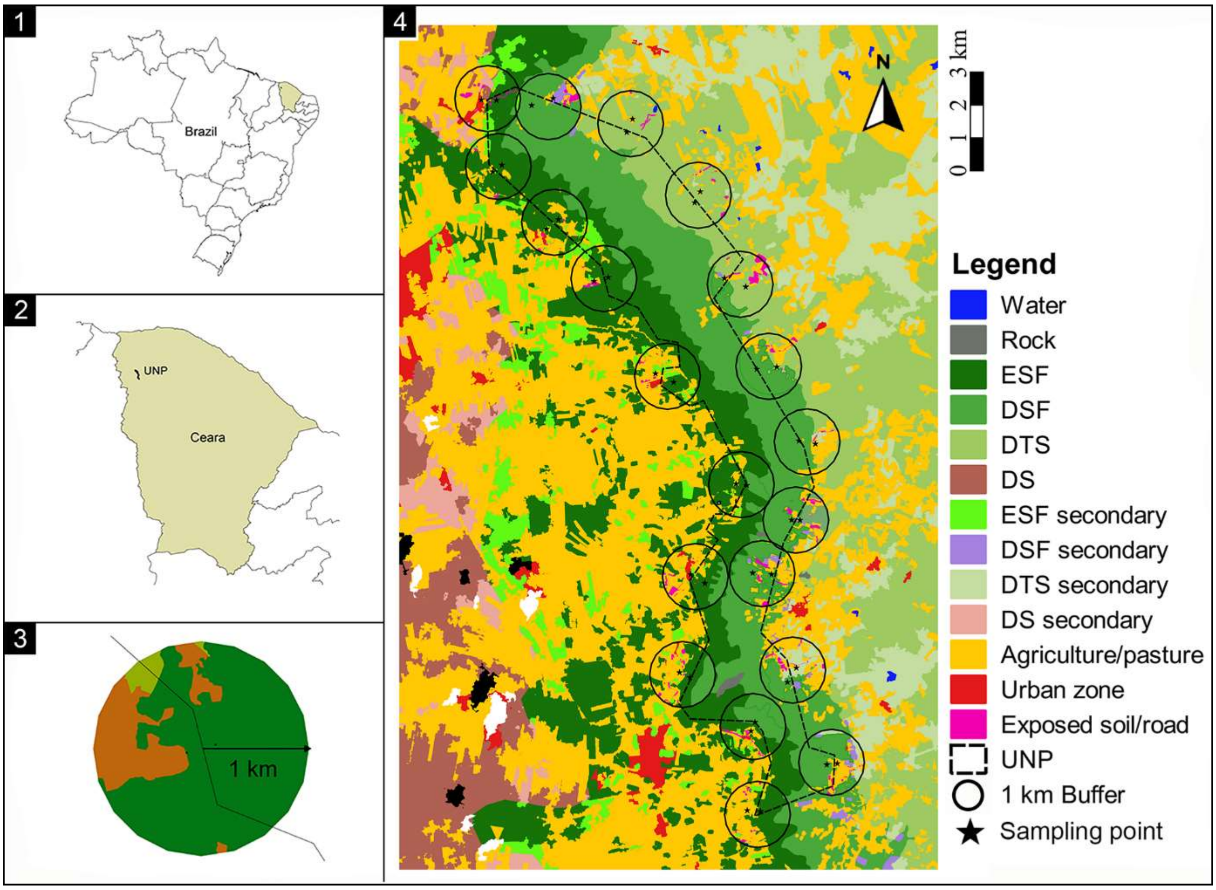

Figure 2: Location of the study area: (1) Brazil and the state of Ceará, in gray; (2) the state of Ceará and the Ubajara National Park, in black (UNP); (3) example of a selected landscape with a 1 km buffer; (4) UNP and surrounding area, and the arrangement of the 20 sampling units. ESF = Evergreen Seasonal Forest; DSF = Deciduous Seasonal Forest; DTS = Deciduous Thorny Savanna; DS = Dry Shrubland; UNP = Ubajara National Park

Simpson Index), as it measures both the amount and evenness of types of environments in the landscape (McGarigal et al. 2012). However, because one of the sampling points in each landscape was within the UNP, the landscapes were always composed of a large proportion of natural vegetation (> 50%) and linked to the same large continuous area of natural vegetation that could be a source of species to the surroundings of the UNP. Therefore, we used the proportion of agriculture (PA) to measure the loss of natural vegetation. The landscapes had a gradient of agricultural cover varying between 9 and 47% of the total area of each landscape (see supplementary material 1). We also measured the landscape configuration of each landscape and of all agricultural areas in each landscape. The landscape configuration was measured through the mean Shape Index among all patches in the landscape (SHAPE-MN). The Shape Index of each patch is equal to the patch edge length divided by the square root of the patch area, multiplied by a constant to adjust for a square standard (McGarigal et al. 2012). SHAPE-MN increases as the patches of all environments in the landscape become more irregular. To measure agriculture configurational heterogeneity, we used the Splitting Index (SPLIT-A). The SPLIT-A was calculated using the total landscape area squared divided by the sum of patch area squared, summed across all agriculture patches (McGarigal et al. 2012). SPLIT-A is equal to one when the landscape is formed by a single patch and increases as the agricultural patches become smaller and more dispersed in the landscape (McGarigal et al. 2012). All mapping was performed with QGis 2.18.4 and ArcMap 10.3.1. The landscape metric calculations were executed with Fragstats 4.2.1. (McGarigal et al. 2012).

2.4 Statistical analysis

Generalized Linear Models (GLM), assuming a negative binomial error distribution, were used to analyze the effects of landscape structure on abundance and species richness of bees and wasps. We considered each of the 20 landscapes as a sampling unit, i.e., data from the two sampling points in each landscape were combined. A set of GLMs was used for each of the following eight response variables (Tab.1): (1) bee richness, (2) wasp richness, (3) parasitoid richness, (4) complete assemblage species richness, (5) bee abundance, (6) wasp abundance, (7) parasitoid abundance and (8) overall abundance. The landscape metrics SHDI, PA, SPLIT-A, and SHAPE-MN were used as explanatory variables for all sets of models. We did not put correlated variables (r≥0.7) in the same model. Additionally, for the analyses of parasitoid richness and abundance, richness and abundance of host species were also added as explanatory variables. Since the number of available cavities to one group (bees or wasps) decreases when the other group is occupying them, bee abundance was included as an explanatory co-variable in models with wasp richness and abundance as response variables. Likewise, wasp abundance was added as an explanatory co-variable in the models of bee abundance and richness. Considering that higher and lower areas of the UNP have different rainfall regimes and that the precipitation is the same for the ten landscapes in each area, we also used two categories of average annual rainfall (high and low) as a co-variable in the models. We also used null models, in which no explanatory variables were taken into account (Burnham & Anderson, 2002; Ferreira et al. 2015). We used Akaike‘s Information Criterion with second-order bias correction for small samples (AICc) to compare models for each response variable (Burnham & Anderson 2002). To interpret the results, we considered both ΔAICc and Akaike’s weight (w) of each model. Models with the lowest AICc values in the set were considered the most plausible ones. The models with a AICc difference to the best model (ΔAICc) lower than 4.0 were interpreted as having the most substantial support. Akaike’s weight (*w*) represents the probability that the selected model is the best in the set (Burnham & Anderson 2002), and we used that to aid our interpretation of the AICc values. All statistical analyses were done in R version 3.5.3 (R Core Team, 2019) using the *glm.nb* function in MASS package (Venables & Ripley 2002) and *model.sel* function in *MuMIn* package (Barton 2019).

3 Results

Altogether, out of the 9000 available traps, 657 were occupied. Trap-nests were occupied in all sampling sites. We recorded nine species of wasps (532 nests and 1574 individuals) belonging to the families *Crabronidae*, *Pompilidae*, *Sphecidae* and *Vespidae*; eleven species of bees (111 nests and 432 individuals) of the families *Apidae* and *Megachilidae*; and six cleptoparasitic/parasitoid species (35 parasitized nests and 48 individuals of parasitoids) belonging to the families *Apidae*, *Chrysididae*, *Ichneumonidae* and *Leucospidae*.

Table 1: Competing models used to analyze the effects of landscape structure on the species richness and the abundance of bees and wasps that nest in pre-existing cavities. SHDI = Shannon Diversity Index; PA = proportion of agriculture; SPLIT-A = Splitting Index for agriculture; SHAPE_MN = Shape Index mean.

Models	Explanatory variables	Hypothesis
1	SHDI	Composition of landscape
2	PA	Habitat loss
3	SPLIT-A	Agriculture configuration
4	SHAPE_MN	Configuration of landscape
5	SHDI + PA	Habitat loss combined with compositional heterogeneity
6	Null	No effects of explanatory variables

Overall, both landscape composition and configuration were important in explaining the assemblage of bees and wasps that nest in pre-existing cavities (Fig. 3). Total species richness was explained mainly by the Shape Index (*w* = 41%; Tab.2). Species richness decreased when the patches of all land-cover types in the landscape became more irregular. The second best model, containing the Splitting Index, had similar plausibility to the first model (ΔAICc <4, *w* = 21%). According to this second model, total species richness slightly increased in landscapes with small and dispersed agricultural areas. Although with lower probability, the landscape composition models also explain the species richness, which decreased both with increasing SHDI (*w* = 15%) and PA (*w* = 14%). The rainfall co-variable had a slightly positive effect on species richness.

When we separated the assemblages into bees, wasps, and their parasitoids, no landscape effects were found for parasitoid species. Configurational heterogeneity was also found to be very important for bees and wasps, however with different effects

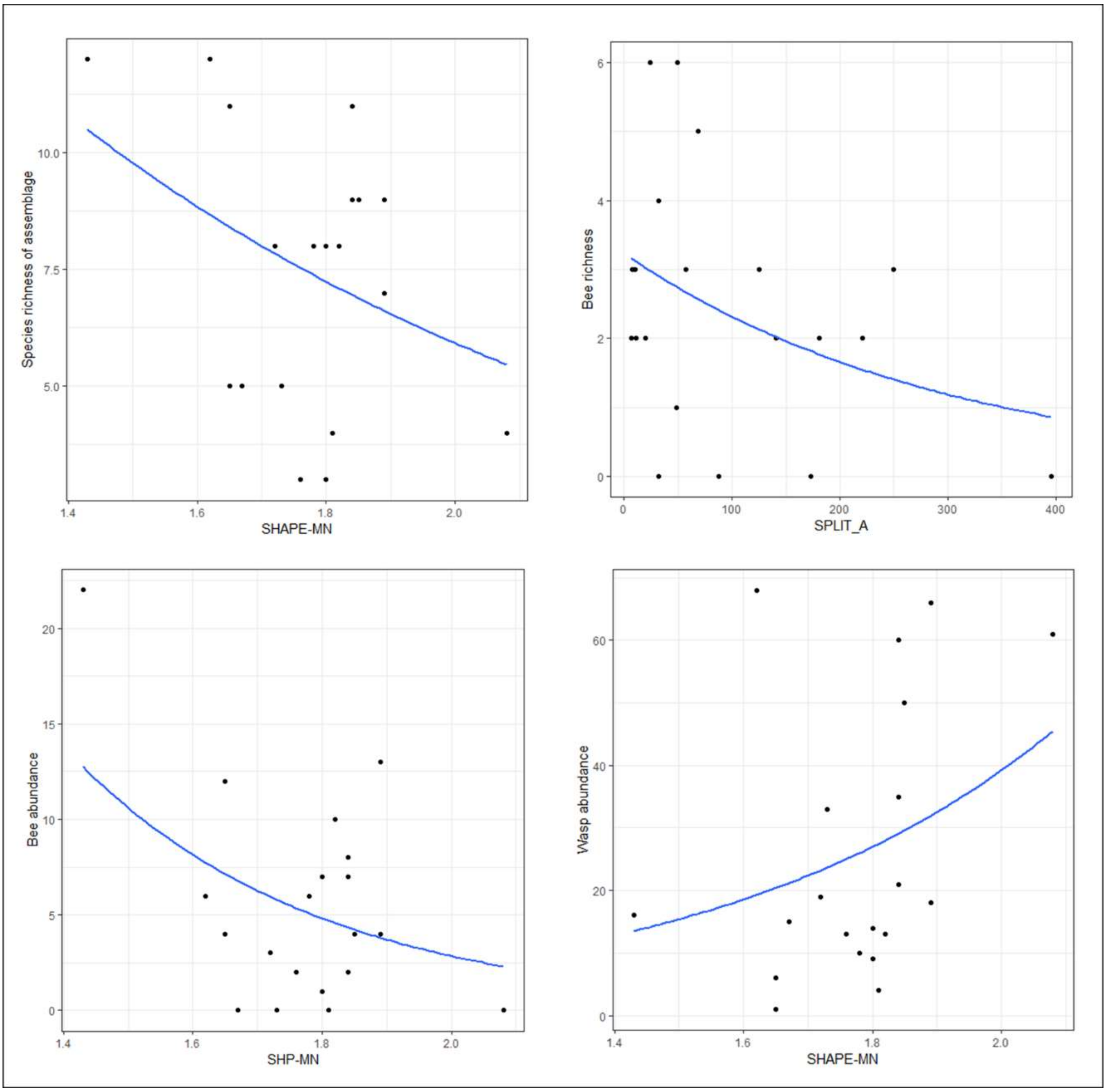

Figure 3: Effects of the explanatory variables on species richness of complete assemblage and abundance of bees and wasps separately. SHAPE-MN = Shape Index for landscape; SPLIT_A= Splitting Index for agriculture.

on them. Configurational heterogeneity had a negative effect on bee abundance and richness. According to the best model, bee richness decreased in landscapes with small and dispersed agricultural areas (SPLIT-A, *w* = 70%).For abundance, the model containing the Shape Index had higher support (*w* = 67.5%), and bee abundance decreased as landscape configuration became more intricate. The second best model showed that bee abundance decreased when agricultural areas were small and dispersed (SPLIT-A, *w* = 15.7%). For both bee abundance and species richness, wasp abundance and rainfall co-variables had a positive effect.

Wasp abundance was higher in landscapes with more irregular patches (*w* = 36.2%). With lower weight of evidence than the first model (*w* = 20.2%) but with substantial support (ΔAICc <4), the second ranked model showed that more intricate configuration of agricultural areas had a slightly positive effect on wasp abundance, which increased with the Splitting Index. Bee abundance and rainfall co-variables respectively had a slight positive and negative effect on wasp abundance. For wasp richness, the null model was between the most plausible models, bringing considerable uncertainty to the landscape effects on the number of wasp species.

Table 2: Model selection results for all significant response variables (total species richness, bee richness, bee and wasp abundance) according to the Akaike's Information Criterion corrected for small samples (AICc) and Akaike's weight (w). ΔAICc is the difference to the best model. Only models with ΔAICc < 4 are presented. Estimate for each variable of the model. SE = Standard error of estimate. SHAPE = Shape Index mean; SPLIT = Splitting Index for agriculture; PA = Proportion of agriculture; SHDI = Shannon Landscape Diversity Index; WA = wasp abundance; BA = bee abundance; Rf = rainfall.

Models	**df**	**AICc**	**ΔAICc**	***w* (%)**	**Estimate**	**SE**	**p**
Total species richness							
SHAPE + Rf	4	177.4	0	41.17	SHAPE= -0.93 Rf= 0.79	SHAPE= 0.11 Rf= 0.28	SHAPE= 0.04 Rf= 0.004
SPLIT + Rf	4	178.72	1.32	21.28	SPLIT= 0.001 Rf= 0.64	SPLIT= 0.002 Rf= 0.32	SPLIT= 0.6 Rf= 0.04
SHDI + Rf	4	179.34	1.94	15.61	SHDI= -0.73 Rf= 0.44	SHDI= 0.65 Rf= 0.39	SHDI= 0.26 Rf= 0.26
PA + Rf	4	179.53	2.13	14.19	PA= -0.14 Rf= 0.73	PA= 1.45 Rf= 0.31	PA= 0.92 Rf= 0.02
Bee richness							
SPLIT + WA + Rf	5	78.10	0	70.40	SPLIT= -0.01 WA= 0.04 Rf= 1.13	SPLIT= 0.003 WA= 0.01 Rf= 0.54	SPLIT= 0.04 WA= 0.04 Rf= 0.03
Bee abundance							
SHAPE + WA + Rf	5	109.5	0	67.5	SHAPE= -0.01 WA= 0.05 Rf= 2.07	SHAPE=0.003 WA= 0.01 Rf= 0.61	SHAPE= 0.02 WA < 0.001 Rf < 0.001
SPLIT + WA + Rf	5	112.4	2.91	15.7	SPLIT= -1.81 WA= 0.04 Rf= 2.12	SPLIT= 1.18 WA= 0.01 Rf= 0.58	SPLIT= 0.12 WA= 0.004 Rf <0.001
Wasp abundance							
SHAPE + BA + Rf	5	168.3	0	36.2	SHAPE= 0.88 BA= 0.06 Rf= -1.44	SHAPE= 1.2 BA= 0.03 Rf= 0.31	SHAPE= 0.04 BA= 0.05 Rf <0.001
SPLIT + BA + Rf	5	169.5	1.17	20.2	SPLIT= 0.02 BA= 0.06 Rf= -1.22	SPLIT= 0.001 BA= 0.03 Rf= 0.33	SPLIT= 0.27 BA= 0.04 Rf <0.001
SHDI + BA + Rf	5	169.7	1.36	18.4	SHDI= -0.6 BA= 0.05 Rf= -1.13	SHDI= 0.63 BA= 0.03 Rf= 0.42	SHDI= 0.34 BA= 0.08 Rf= 0.01
PA + BA + Rf	5	169.8	1.45	17.5	PA= 1.04 BA= 0.06 Rf= -1.54	PA= 1.44 BA= 0.03 Rf= 0.35	PA= 0.47 BA= 0.05 Rf < 0.001

4 Discussion

Our study has shown that both landscape composition and configuration have effects on the assemblages of bees and wasps that nest in pre-existing cavities. For bees, landscape configuration played a greater role in determining their richness and abundance than did landscape composition. Richness decreased with increasing agriculture configurational heterogeneity (SPLIT-A) and abundance decreased with increasing patch shape complexity (Shape Index).In previous studies, landscape configuration (e.g., mean shape, interpatch connectivity and aggregation of landscape patches) had a positive effect or no effect on bee assemblages (Kennedy et al. 2013; Moreira et al. 2015). Although those studies indicated that configurational heterogeneity is associated with increased connectivity, facilitating bee foraging movements across the landscape, most of them were conducted in agriculture-dominated areas (Holzschuh et al. 2010; Kennedy et al., 2013). This is not the case in our area, where the landscapes had a high proportion of natural land cover types, in addition to being connected to a very large protected reserve (UNP). Thus, increases in configurational heterogeneity tend to lead to the fragmentation of large continuous natural vegetation patches (Fahrig 2017), causing bees to respond negatively to landscape configuration.

Although the landscapes with simpler configuration had higher species numbers, these landscapes were also the ones with the highest proportion of evergreen forest (ESF; see supplementary material 1). In semiarid regions, this type of vegetation is located in areas of greater rainfall. Due to the greater water availability, these evergreen forests have less seasonal bloomings, providing floral resources to bees throughout the year (Rodal et al. 2005; Schwinning et al. 2004; Abrahamczyk et al. 2011). This allows bees to access a greater availability of adequate resources, being less dependent on resources provided by other environments (Aguiar et al. 2005; Abrahamczyk et al. 2011). Since most crops in the Brazilian semiarid regions are annual, even if bee richness and abundance is affected by landscape configuration, they are also indirectly affected by land cover types (landscape composition), since annual crops only provide complementary floral resources during a short period of the year.

Unlike bees, wasp abundance increased with greater patch shape complexity (Shape Index). Landscapes with high configurational heterogeneity have more edges between the different cover types, and many species of wasps build nests in edges or other more open environments (Taki et al. 2008; Holzschuh et al. 2010; Fahrig et al. 2011; Pereira-Peixoto et al. 2014; Hoffmann et al. 2018). More complex landscape configuration may favor the flow of wasps across the landscape and allow the use of resources from different environments within their foraging range (Klein et al. 2004; Holzschuh et al. 2010). Landscapes with a higher division of agriculture in smaller patches also had greater abundance of wasps. In the Brazilian semiarid region, small agricultural areas are typically temporary crops. These habitats are usually more open and have little or no tree species. Other studies also found higher wasp abundance in landscapes with a larger proportion of open habitats, such as grasslands or agricultural areas (Fye 1972; Jennings & Howseweart 1984; Buschini & Wolff 2006; Holzschuh et al. 2010; Schüepp et al. 2011; Hoffmann et al. 2018). They suggested that these land cover types have plentiful light penetration, where wasp preys (e.g., spiders, cockroaches and Lepidoptera larvae) may be more abundant and accessible. Although the lack of trees in the areas of temporary agriculture decrease the nesting cavities availability, and the disperse spatial distribution of these areas facilitate the flux of wasps across the landscape and allow the wasps nesting in natural habitats to forage in agricultural areas.

This increased access to different feeding resources is important in semiarid regions, where food can be seasonal, especially for solitary bees and wasps with lower foraging efficiency than their social counterparts (Gathmann & Tscharntke 2002; Morato & Martins 2006). From an agricultural perspective, complex landscapes can also be beneficial because they favor wasp movement, thereby increasing their potential to control pests within crop fields (Franklin & Forman 1987; Dale et al.2000). Hipólito et al. (2018), for example, showed that farms close to areas with natural vegetation and low management intensity produce 30% more while maintaining the biodiversity of floral visitors, including bees and wasps.

Contrary to expectations, we found no effects of native vegetation loss, landscape composition or landscape configuration on richness and abundance of parasitoids. Because they belong to higher trophic levels, parasitoids usually are expected to be affected by landscape changes and by the richness and abundance of their hosts (Thies et al. 2003; Holzschuh et al. 2010; Ebeling et al. 2012; Steckel et al. 2014). However, according to Schüepp et al. (2011), effects of landscape changes may be smaller for generalist parasitoids. This can explain our findings, as the most abundant parasitoids were known generalists and were found in all environments and in the nests of different species (see Flores et al. 2018).

Overall, for the complete assemblage, landscape configuration has a more evident effect, with hymenopteran richness increasing in simpler spatial arrangements. The stronger effect of landscape configuration may be due to the high proportion of natural vegetation in the UNP (>50%). According to Pardini et al. (2010) and Fahrig et al. (2011), however, effects of landscape composition are evident when the percentage of native vegetation cover is low or intermediate (30-40%). Conversely the increase of one cover type in the landscape necessarily reduces other types, high natural vegetation proportion results in a low landscape diversity (SHDI) and a simpler configuration with less fragmentation (SHAPE) (see supplementary material 1; Fahrig et al. 2011). Therefore, the higher species number in these more homogeneous landscapes is potentially due to a great amount of natural cover, provided and maintained by the UNP.

5 Conclusions and implications for conservation and management

The different responses to landscape structure found for bees and wasps may have important implications for both the productivity of crops and conservation of native vegetation. Bees were negatively affected by landscape configuration and may benefit from environments that provide higher abundance and diversity of flowering plants throughout the year, such as the native forests. On the other hand, wasps may benefit from open habitats due to a higher abundance of prey (Tscharntke et al. 1998; Schmidt et al. 2005). Since bees are pollinators of many crops and wasps are predators of a vast number of arthropods, it is important to promote landscape patterns that benefit both groups.

In these semiarid regions, where small agricultural areas are mainly annual crops, the floral resources supply for bees are limited to a short period of the year while for wasps, these areas may provide higher constant prey abundance (Fye 1972; Jennings & Howseweart 1984; Fabian et al. 2013). The two groups can benefit from associating temporary crops with irrigated permanent crops interspersed with native patches. This association may provide flowers for bees throughout the year, prey for wasps and nesting sites for both. Therefore, to develop effective conservation strategies, assessing only landscape diversity may not be adequate. It is also necessary to evaluate the type of agriculture, associated with landscape configuration in order to increase the supply of resources and to facilitate access to these resources throughout the year.

Although many conservationists see agriculture as the main cause of biodiversity loss, Perfecto et al. (2009) state that managed environments also contain a fraction of the biodiversity and it is a mistake to ignore them. According to these authors, it is not habitat conversion but rather the type and shape of these modified environments that determine whether regional biodiversity is preserved. Therefore, just as important as properly managing protected areas, it is essential to employ adequate landscape management. This is especially important in semiarid regions, where the surroundings of the protected areas can provide alternative resources during the dry season for some species. Appropriate landscape management may allow the surrounding area to act as a filter to external aggressions against nearby protected areas while providing essential ecosystem services, such as pollination and pest control. Thus, composition and configuration must be associated in landscape planning, aiming at the maintenance of these different taxonomic groups, especially in areas close to natural reserves, where the conversion of natural vegetation must be carefully done. This will enable both the maintenance of biodiversity and the better use of ecosystem services provided by them.

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References

Abrahamczyk, S.; Kluge, J.; Gareca, Y.; Reichle, S. & Kessler, M. 2011. The influence of climatic seasonality on the diversity of different tropical pollinator groups. *PLoS ONE* 6(11), 1-9. DOI: 10.1371/journal.pone.0027115

Aguiar, C.M.L.; Garófalo, C.A. & Almeida, G.F. 2005. Trap-nesting bees (Hymenoptera, Apoidea) in areas of dry semideciduous forest and caatinga, Bahia, Brazil. *Revista Brasileira de Zoologia* 22, 1030-1038. DOI: 10.1590/S0101-81752005000400031

Antongiovanni, M. & Metzger, J.P. 2005. Influence of matrix habitats on the occurrence of insectivorous bird species in Amazonian forest fragments. *Biological Conservation* 122(3), 441-451. DOI: 10.1016/j.biocon.2004.09.005

Araujo, F.S.; Menezes, M.O.T.; Barbosa, L.S.; Oliveira, V.M.R.; Nogueira Rafaella, S.; Menezes, B.S.; Souza, B.C.; Carvalho, E.C.D.; Silveira, A.P.; Flores, L.M.A. & Zanette, L.R.S. 2017. Efetividade da zona de amortecimento de unidades de conservação federais do estado do Ceará: Parque Nacional de Ubajara e Estação Ecológica de Aiuaba. In: W. Mantovani, R.F. Monteiro, L. Anjos & M.O. Cariello (eds.): Pesquisas em unidades de conservação no domínio da caatinga: subsídios à gestão. Edições UFC – Fortaleza.

Araújo, F.S.; Rodal, M.J.N.; Barbosa, M.R.V. & Martins, F.R. 2005. Repartição da flora lenhosa no domínio da Caatinga. In: F.S. Araújo, Rodal, M.J.N. & Barbosa, M.R.V. (eds.): Análise das Variações da Biodiversidade do Bioma Caatinga: Suporte a Estratégias Regionais de Conservação. Ministério do Meio Ambiente – Brasília.

Ashman, T.L.; Knight, T.M.; Steets, J.A.; Amarasekare, P.; Burd, M.; Campbell, D.R. & Wilson, W.G. 2004. Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. *Ecology* 85(9), 2408–2421. DOI: 10.1890/03-8024

Barton, K. 2019. MuMIn: Multi-Model Inference. R package version 1.43.6. https://CRAN.R-project.org/package=MuMIn (Date: 20.06.2019)

Batra, S.W. 1984. Solitary bees. *Scientific American*, 250, 86-93. DOI: 10.1038/scientificamerican0284-120

Boscolo, D.; Tokumoto, P.M.; Ferreira, P.A.; Ribeiro, J.W. & Santos, J.S. 2017. Positive responses of flower visiting bees to landscape heterogeneity depend on functional connectivity levels. *Perspectives in Ecology and Conservation* 15, 18–24. DOI: 10.1016/j.pecon.2017.03.002

Burnham, K.P. & Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. second ed., Springer, New York, USA.

Buschini, M.L.T. & Wolff, L.L. 2006. Notes on the biology of Trypoxylon (Trypargilum) opacum Brèthes (Hymenoptera; Crabronidae) in southern Brazil. *Brazilian Journal of Biology* 66(3), 907-917. DOI: 10.1590/S1519-69842006000500017

Câmara, G.; Souza, R.C.M.; Freitas, U.M. & Garrido, J. 1996. SPRING - Integrating remote sensing and GIS by object-oriented data modelling. *Computers & Graphics* 20, 395-403. DOI: 10.1016/0097-8493(96)00008-8

Chapin III, F.S.; Zavaleta, E.S.; Eviner, V.T.; Naylor, R.L.; Vitousek, P.M.; Reynolds, H.L. & Díaz, S. 2000. Consequences of changing biodiversity. *Nature* 405(6783), 234-242. DOI: 10.1038/35012241

Charman, T.G.; Sears, J.; Green, R.E. & Bourke, A.F. 2010. Conservation genetics, foraging distance and nest density of the scarce Great Yellow Bumblebee (Bombus distinguendus). *Molecular Ecology* 19(13), 2661-2674. DOI: 10.1111/j.1365-294X.2010.04697.x

Dale, V.H.; Brown, S.; Haeuber, R.A.; Hobbs, N.T.; Huntly, N.; Naiman, R.J.; Riebsame, W.E.; Turner, M.G. & Valone, T.J. 2000. Ecological principles and guidelines for managing the use of land. *Ecological Applications* 10(3), 639-670. DOI: 10.1890/1051-0761(2000)010[0639:EPAGFM]2.0.CO;2

Didham, R.K.; Ghazoul, J.; Stork, N.E. & Davis, A.J. 1996. Insects in fragmented forests: a functional approach. *Trends in Ecology & Evolution* 11, 255-60. DOI: 10.1016/0169-5347(96)20047-3

Dingle, H. & Drake, V.A. 2007. What is migration? *BioScience* 57(2), 113-121. DOI: 10.1641/B570206

Ebeling, A.; Klein, A.M.; Weisser, W.W. & Tscharntke, T. 2012. Multitrophic effects of experimental changes in plant diversity on cavity-nesting bees, wasps, and their parasitoids. *Oecologia* 169, 453-65. DOI: 10.1007/s00442-011-2205-8

Fabian, Y.; Sandau, N.; Bruggisser, O.T.; Aebi, A.; Kehrli, P.; Rohr, R.P.; Naisbit, R.E. & Bersier, L.F. 2013. The importance of landscape and spatial structure for hymenopteran-based food webs in an agro-ecosystem. *Journal of Animal Ecology* 82, 1203–1214. DOI: 10.1111/1365-2656.12103

Fahrig, L. 2017. Ecological responses to habitat fragmentation per se. *Annual Review of Ecology, Evolution, and Systematic*s 48(1), 1-23. DOI: 10.1146/annurev-ecolsys-110316-022612

Fahrig, L.; Baudry, J.; Brotons, L.; Burel, F.G.; Crist, T.O.; Fuller, R.J.; Sirami, C.; Siriwardena, G.M. & Martin, J.L. 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters* 14(2), 101-112. DOI: 10.1111/j.1461-0248.2010.01559.x

Fahrig, L.; Girard, J.; Duro, D.; Pasher, J.; Smith, A.; Javorek, S. & Tischendorf, L. 2015. Farmlands with smaller crop fields have higher within-field biodiversity. *Agriculture, Ecosystems & Environment* 200, 219-234. DOI: 10.1016/j.agee.2014.11.018

Falk, S. & Lewington, R. 2015. Field Guide to the Bees of Great Britain and Ireland. British Wildlife Publishing Lt. – London.

Ferreira, P.A.; Boscolo, D.; Carvalheiro, L.G.; Biesmeijer, J.C.; Rocha, P.L. & Viana, B.F. 2015. Responses of bees to habitat loss in fragmented landscapes of Brazilian Atlantic Rainforest. *Landscape Ecology* 30(10), 2067-2078. DOI: 10.1007/s10980-015-0231-3

Figueiredo, M.A. 1988. As serras úmidas no Ceará e a produção alimentar para o semi-árido cearense. *Coleção Mossoroense* 353, 1-15.

Flores, L.M.A.; Zanette, L.R.S. & Araújo, F.S. 2018. Effects of habitat simplification on assemblages of cavity nesting bees and wasps in a semiarid neotropical conservation area. *Biodiversity and Conservation* 27, 311–328. DOI: 10.1007/s10531-017-1436-3

Franklin, J.F. & Forman, R.T. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. *Landscape Ecology* 1(1), 5-18. DOI: 10.1007/BF02275261

Fricke, J.M. 1991. Trap-nest bore diameter preferences among sympatric Passaloecus spp. (Hymenoptera: Speci¬dae). Great Lakes Entomology 24, 123-125.

FUNCEME 2015. Fundação Cearense de Meteorologia e Recursos Hídricos. http:/www.funceme.br (Date: 03.05.2015).

Fye, R.E. 1972. The effect of forest disturbances on populations of wasps and bees in northwestern Ontario (Hymenoptera: Aculeata). *The Canadian Entomologist* 104(10), 1623-1633. DOI: 10.4039/Ent1041623-10

Gallai, N.; Salles, J.M.; Settele, J. & Vaissière, B.E. 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological economics* 68(3), 810-821. DOI: 10.1016/j.ecolecon.2008.06.014

Gathmann, A. & Tscharntke, T. 2002. Foraging ranges of solitary bees. *Journal of Animal Ecology* 71, 757–764. DOI: 10.1046/j.1365-2656.2002.00641.x

Goodell, K. 2003. Food availability affects Osmia pumila (Hymenoptera: Megachilidae) foraging, reproduction, and brood parasitism. *Oecologia* 134(4), 518-527. DOI: 10.1007/s00442-002-1159-2

Gould, W.P. & Jeanne, R.L. 1984. Polistes wasps (Hymenoptera: Vespidae) as control agents for lepidopterous cabbage pests. *Environmental Entomology* 13, 150–56. DOI: 10.1093/ee/13.1.150

Happe, A.K.; Riesch, F.; Rösch, V.; Gallé, R.; Tscharntke, T. & Batáry, P. 2018. Small-scale agricultural landscapes and organic management support wild bee communities of cereal field boundaries. *Agriculture, Ecosystems & Environment* 254, 92–98. DOI: 10.1016/j.agee.2017.11.019

Hipólito, J.; Boscolo, D. & Viana, B.F. 2018. Landscape and crop management strategies to conserve pollination services and increase yields in tropical coffee farms. *Agriculture, Ecosystems & Environment* 256, 218-225. DOI: 10.1016/j.agee.2017.09.038

Hoffmann, U.S.; Jauker, F.; Lanzen, J.; Warzecha, D.; Wolters, V. & Diekötter, T. 2018. Prey-dependent benefits of sown wildflower strips on solitary wasps in agroecosystems. *Insect Conservation and Diversity* 11, 42–49. DOI: 10.1111/icad.12270

Holzschuh, A.; Steffan-Dewenter, I. & Tscharntke, T. 2010. How do landscape composition and configuration organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? *Journal of Animal Ecology* 79(2), 491–500. DOI: 10.1111/j.1365-2656.2009.01642.x

Jennings, D.T. & Houseweart, M.W. 1984. Predation by eumenid wasps (Hymenoptera: Eumenidae) on spruce budworm (Lepidoptera: Tortricidae) and other lepidopterous larvae in spruce-fir forests of Maine. *Annals of the Entomological Society of America* 77(1), 39-45. DOI: 10.1093/aesa/77.1.39

Kennedy, C.; Lonsdorf, E.; Neel, M.C.; Williams, N.M.; Ricketts, T.H.; Winfree, R.; Bommarco, R.; Brittain, C.; Burley, A.L.; Cariveau, D.; Carvalheiro, L.G.; Chacoff, N.P.; Cunningham, S.A.; Danforth, B.N.; Dudenhöffer, J.; Elle, E.; Gaines, H.R.; Garibaldi, L.A.; Gratton, C.; Holzschuh, A.; Isaacs, R.; Javorek, S.K.; Jha, S.; Klein, A.M.; Krewenka, K.; Mandelik, Y.; Mayfield, M.M.; Morandin, L.; Neame, L.A.; Otieno, M.; Park, M.; Potts, S.G.; Rundlöf, M.; Saez, A.; Steffan-Dewenter, I.; Taki, H.; Viana, B.F.; Westphal, C.; Wilson, J.K.; Greenleaf, S.S. & Kremen, C. 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters* 16(5), 584–599. DOI: 10.1111/ele.12082

Klein, A.M.; Steffan-Dewenter, I. & Tscharntke, T. 2004. Foraging trip duration and density of megachilid bees, eumenid wasps and pompilid wasps in tropical agroforestry systems. *Journal of Animal Ecology* 73, 517–525. DOI: 10.1111/j.0021-8790.2004.00826.x

Klein, A.M.; Steffan-Dewenter, I.; Buchori, D. & Tscharntke, T. 2002. Effects of land-use intensity in tropical agroforestry systems on flower-visiting and trap-nesting bees and wasps. *Conservation Biology* 16(4), 1003–1014. DOI: 10.1046/j.1523-1739.2002.00499.x

Klein, A.M.; Vaissière, B.E.; Cane, J.H.; Steffan-Dewenter, I.; Cunningham, S.A.; Kremen, C. & Tscharntke T. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society B: *Biological Sciences* 274: 303-13, 2007. DOI: 10.1098/rspb.2006.3721

Krewenka, K.M.; Holzschuh, A.; Tscharntke, T. & Dormann, C.F. 2011. Landscape elements as potential barriers and corridors for bees, wasps and parasitoids. *Biological Conservation* 144(6), 1816-1825. DOI: 10.1016/j.biocon.2011.03.014

Krombein, K.V. 1967. Trap-nesting wasps and bees: life histories, nests, and associates. Smithsonian Press – Washington DC.

Loyola, R.D. & Martins, R.P. 2008. Habitat structure components are effective predictors of trap-nesting Hymenoptera diversity. *Basic and Applied Ecology* 9, 735-742. DOI: 10.1016/j.baae.2007.06.016

McGarigal, K.; Cushman, S.A. & Ene, E. 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts – Amherst.

Melo, R.R. & Zanella, F.C. 2012. Dinâmica de fundação de ninhos por abelhas e vespas solitárias (Hymenoptera, Aculeta) em área de caatinga na Estação Ecológica do Seridó. *Revista Brasileira de Ciências Agrárias* 7, 657-662. DOI: 10.5039/agraria.v7i4a1966

Metzger, J.P. 2001. O que é ecologia de paisagens? *Biota Neotropica* 1, 1-9. DOI: 10.1590/S1676-06032001000100006

Morandin, L.A. & Winston, M.L. 2006. Pollinators provide economic incentive to preserve natural land in agroecosystems. Agriculture, *Ecosystems & Environment* 116(3), 289-292. DOI: 10.1016/j.agee.2006.02.012

Morato, E.F. & Martins, R.P. 2006. An overview of proximate factors affecting the nesting behavior of solitary wasps and bees (Hymenoptera: Aculeata) in preexisting cavities in wood. *Neotropical Entomology* 35(3), 285-98. DOI: 10.1590/S1519-566X2006000300001

Moreira, E.F.; Boscolo, D. & Viana, B.F. 2015. Spatial heterogeneity regulates plant-pollinator networks across multiple landscape scales. *PLoS ONE* 10(4), e0123628. DOI: 10.1371/journal.pone.0123628

Nascimento, A.L.O. & Garófalo, C.A. 2014. Trap-nesting solitary wasps (Hymenoptera: Aculeata) in an insular landscape: Mortality rates for immature wasps, parasitism, and sex ratios. *Sociobiology* 61(2), 207-217. DOI: 10.13102/sociobiology.v61i2.207-217

Nether, M.C.; Dudek, J., & Buschini, M.L.T. 2019. Trophic interaction and diversity of cavity-nesting bees and wasps (Hymenoptera: Aculeata) in Atlantic forest fragments and in adjacent matrices. *Apidologie* 50(1), 104-115. DOI: 10.1007/s13592-018-0623-x

O‘Neill, K.M. 2001. Solitary wasps: behavior and natural history. Cornell University Press – Ithaca.

Pardini, R.; Bueno, A.A.; Gardner, T.A.; Prado, P.I. & Metzger, J.P. 2010. Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. *PLoS ONE* 5(10), e13666. DOI: 10.1371/journal.pone.0013666

Penagos, D.I. & Williams, T. 1995. Important factors in the biology of heteronomous hyperparasitoids (Hym: Aphelinidae): Agents for the biological control of whiteflies and scale insects. *Acta Zoológica Mexicana* 66, 31–57.

Pereira-Peixoto, M.H.; Pufal, G.; Martins, C.F. & Klein, A.M. 2014. Spillover of trap-nesting bees and wasps in an urban–rural interface. *Journal of Insect Conservation* 18(5), 815-826. DOI: 10.1007/s10841-014-9688-7

Perfecto, I.; Vandermeer, J. & Wright, A. 2009. Nature's matrix: linking agriculture, conservation and food sovereignty. Earthscan – London.

Potts, S.G.; Biesmeijer, J.C.; Kremen, C.; Neumann, P.; Schweiger, O. & Kunin, W.E. 2010. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution* 25(6), 345-353. DOI: 10.1016/j.tree.2010.01.007

R Core Team 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing – Vienna. URL https://www.R-project.org/ (Date: 20.06.2019)

Ricketts, T.H. 2001. The matrix matters: effective isolation in fragmented landscapes. *The American Naturalist* 158(1), 87-99. DOI: 10.1086/320863

Ricketts, T.H.; Regetz, J.; Steffan-Dewenter, I.; Cunningham, S.A.; Kremen, C.; Bogdanski, A.; Gemmill-Herren, B.; Greenleaf, S.S.; Klein, A.M.; Mayfield, M.M.; Morandin, L.A.; Ochieng, A. & Viana, B.F. 2008. Landscape effects on crop pollination services: are there general patterns? *Ecology Letters* 11(5), 499–515. DOI: 10.1111/j.1461-0248.2008.01157.x

Rodal, M.J.N.; Sales, M.F.; Silva, M.J. & Silva, A.G. 2005. Flora de um Brejo de Altitude na escarpa oriental do planalto da Borborema, PE, Brasil. *Acta Botanica Brasilica* 19(4), 843-858. DOI: 10.1590/S0102-33062005000400020

Roubik, D.W. 2001. Ups and downs in pollinator populations: when is there a decline? *Conservation Ecology* 5, 1-22.

Rubene, D.; Schroeder, M. & Ranius, T. 2015. Diversity patterns of wild bees and wasps in managed boreal forests: effects of spatial structure, local habitat and surrounding landscape. *Biological Conservation* 184, 201-208. v

Schmidt, M.H.; Roschewitz, I.; Thies, C. & Tscharntke, T. 2005. Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders. *Journal of Applied Ecology* 42(2), 281-287. DOI: 10.1111/j.1365-2664.2005.01014.x

Schüepp, C.; Herrmann, J.D.; Herzog, F. & Schmidt-Entling, M.H. 2011. Differential effects of habitat isolation and landscape composition on wasps, bees, and their enemies. *Oecologia* 165(3), 713–721. DOI: 10.1007/s00442-010-1746-6

Schwinning, S.; Sala, O.E.; Loik, M.E. & Ehleringer, J.R. 2004. Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems. *Oecologia* 141(2), 191–193. DOI: 10.1007/s00442-004-1683-3

Steckel, J.; Westphal, C.; Peters, M.K.; Bellach, M.; Rothenwoehrer, C.; Erasmi, S.; Scherber, C.; Tscharntke, T. & Steffan-Dewenter, I. 2014. Landscape composition and configuration differently affect trap-nesting bees, wasps and their antagonists. *Biological Conservation* 172, 56-64. DOI: 10.1016/j.biocon.2014.02.015

Symondson, W.O.C.; Sunderland, K.D. & Greenstone, H.M. 2002. Can generalist predators be effective biocontrol agents? *Annual Review of Entomology* 47, 561–594. DOI: 10.1146/annurev.ento.47.091201.145240

Taki, H.; Viana, B.F.; Kevan, P.G.; Silva, F.O. & Buck, M. 2008. Does forest loss affect the communities of trap-nesting wasps (Hymenoptera: Aculeata) in forests? Landscape vs. local habitat conditions. *Journal of Insect Conservation* 12(1), 15-21. DOI: 10.1007/s10841-006-9058-1

Thies, C.; Steffan-Dewenter, I. & Tscharntke, T. 2003. Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos* 101(1), 18-25. DOI: 10.1034/j.1600-0706.2003.12567.x

Thornthwaite, C.W. 1948. An approach toward a rational classification of climate. *Geographical Review* 38, 55–94. DOI: 10.2307/210739

Tscharntke, T.; Gathmann, A. & Steffan-Dewenter, I. 1998. Bioindication using trap-nesting bees and wasps and their natural enemies. *Journal of Applied Ecology* 35(5), 708-719. DOI: 10.1046/j.1365-2664.1998.355343.x

Tylianakis, J.M.; Klein, A.M. & Tscharntke, T. 2005. Spatiotemporal variation in the diversity of hymenoptera across a tropical habitat gradient. *Ecology* 86(12), 3296-3302. DOI: 10.1890/05-0371

Venables, W.N. & Ripley, B.D. 2002. Modern Applied Statistics with S. Fourth Edition. Springer – NewYork.

Williams, N.M. & Kremen, C. 2007. Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecological Applications* 17(3), 910–921. DOI: 10.1890/06-0269

Winfree, R.; Griswold, T. & Kremen, C. 2007. Effect of human disturbance on bee communities in a forested ecosystem. *Conservation Biology* 21(1), 213-223. DOI: 10.1111/j.1523-1739.2006.00574.x

Zurbuchen, A.; Landert, L.; Klaiber, J.; Müller, A.; Hein, S. & Dorn, S. 2010. Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biological Conservation* 143(3), 669–676. DOI: 10.1016/j.biocon.2009.12.003

Supplementary material 1: Correlogram with results of Pearson Correlation test. Variables were correlated when r ≥ 0.7. SHAPE_MN = Shape Index mean; SPLIT_A = Splitting Index for agriculture; PA = Proportion of agriculture; SHDI = Shannon Landscape Diversity Index; PNV = Proportion of natural vegetation.