

Effects of habitat simplification on assemblages of cavity nesting bees and wasps in a semiarid neotropical conservation area

Lilian M. A. Flores¹  · Lorenzo R. S. Zanette¹ · Francisca S. Araujo¹

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Abstract Habitat complexity is directly correlated to insect diversity in most natural environments. Structural complexity reflects an increase in vertical stratification and plant diversity and often leads to a greater availability of floral resources and nesting sites. Efficient conservation strategies require understanding of how changes in habitat structure affect insects that provide essential ecosystem services. We analyzed how the diversity and species composition of bees and wasps that nest in pre-existing cavities is affected by habitat complexity. Our study was developed in the semiarid region of northeastern Brazil, in the Ubajara National Park and surrounding area. Four types of habitats within two physiognomies were sampled for two consecutive years. We used 120 trap-nest (9000 cavities) distributed in 40 sample points. Overall, 657 cavities were occupied by 11 species of bees, nine of wasps, and six of cleptoparasitic/parasitoids. Bees and wasp diversity increases with habitat complexity. While species richness was higher in more complex physiognomies, abundance was higher in disturbed areas. Species composition also varied with habitat structure. Habitat simplification has adverse effects on the diversity and composition of assemblages. These effects are stronger in more complex habitats indicating that conservation of humid habitats within semiarid areas is essential to maintain bee and wasp regional diversity.

Keywords Environmental heterogeneity · Hymenoptera · Trap-nest · Ecosystem services · Beta diversity

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✉ Lilian M. A. Flores
liufrpe@yahoo.com.br

¹ Graduate Course of Ecology and Natural Resources, Department of Biology, Federal University of Ceará – UFC, Av Mister Hull, 000, Fortaleza-Ceará 60440-900, Brazil

Introduction

An important issue for both ecology and conservation studies is to understand why areas with different habitat structures support different numbers of species and different patterns of diversity (Ebeling et al. 2012; Rubene et al. 2014, 2015). According to the theory of environmental heterogeneity, habitats with high structural complexity provide greater diversity of resources, more niches and therefore have greater species diversity than simplified habitats (MacArthur and MacArthur 1961; MacArthur et al. 1962). Habitat structural complexity can be defined as the heterogeneity in the horizontal and vertical structure of the habitat (Stein et al. 2014). A reduction in vegetation structural heterogeneity necessarily reduces also the amount of habitat (August 1983; Stein et al. 2014). Hence, any decrease in the number of different land cover types (horizontal structure) or stratification of the vegetation (vertical structure) will result in habitat simplification (Stein et al. 2014). Empirical evidence indicates that habitat simplification reduces the diversity and changes the community composition of different taxonomic groups, e.g. birds (MacArthur and MacArthur 1961), mammals (August 1983) and bees and wasps (Ebeling et al. 2012; Antonini et al. 2016). In a meta-analysis, Stein et al. (2014) confirmed these results and showed that habitat structural complexity is a universal driver of species richness and has a greater effect than climatic or topographic variation.

Human activities can modify vegetation structure and can result in habitat simplification and species loss at higher trophic levels (Cadenasso et al. 2003; Fahrig 2003; Harper et al. 2005; Ebeling et al. 2012). Logging and conversion to agriculture, for example, can severely reduce tree and shrub diversity, simplifying habitat structure and reducing the availability of food sources and natural cavities that are nesting sites for many species (Oliveira 2001; Morato and Martins 2006; Cadenasso et al. 2003; Fahrig 2003; Harper et al. 2005).

In addition to human activities, habitat complexity is strongly affected by rainfall in arid and semiarid ecosystems (Sampaio et al. 1981). Areas with greater water availability can support higher plant density and vertical stratification (Sampaio et al. 1981; Rodal et al. 2005). Moreover, during the rainy season precipitation can be variable, unpredictable and sporadic, and this strongly affects flowering onset (Schwinning and Sala 2004; Amorim et al. 2009; Abrahamczyk et al. 2011). Therefore, precipitation can indirectly affect resource availability for many groups, including rodents (Ernest et al. 2000), spiders (Polis et al. 1998) bees and wasps (Tylianakis et al. 2005; Spengler et al. 2011).

Bees and wasps are very sensitive to habitat simplification and are globally in decline due to environmental changes (Dobson et al. 2006; Morato and Martins 2006; Pauw and Hawkins 2011). Bees are the main group of pollinators of the angiosperms (Klein et al. 2007; Potts et al. 2010). Wasps, in turn, are important predators and parasitoids of a very large number of arthropod species (Gould and Jeanne 1984; Symondson et al. 2002). Among solitary bees and wasps, 5–10% of species nest in pre-existing cavities above ground (Krombein 1967; Falk and Lewington 2015). Due to their strong dependence on the presence of natural cavities in the vegetation, these bees and wasps can be very sensitive to changes in habitat structure and, hence, good indicators of environmental quality, (Krombein 1967; Oliveira 2001; Kreyer et al. 2004; Zanette et al. 2005; Klein et al. 2006; Loyola and Martins 2006). The negative effects of habitat simplification on the diversity of these insects can have a strong effect on the key ecosystem services they provide (Kearns et al. 1997; Lassau and Hochuli 2005; Morandin and Winston 2006; Isaacs et al. 2009). Hence, strategies to maintain the diversity of these cavity-nesting insects should be a conservation priority.

Developing efficient conservation strategies requires knowledge of the spatial patterns of diversity (Jost et al. 2010; Socolar et al. 2016). Studies of beta diversity can help to quantify biodiversity loss and to identify priority areas for conservation (Wiersma and Urban 2005; Jewitt et al. 2016; Socolar et al. 2016). To understand spatial patterns of biodiversity, beta diversity must be partitioned into two components, nestedness and spatial turnover (Baselga 2010). Nestedness occurs when a community is a subset of another community and reflects a non-random process of species loss due to any factor that promotes the ordered disaggregation of communities, such as human activities (Baselga 2010; Hill et al. 2011; Solar et al. 2015). Habitat fragmentation and deforestation, for example, can act as environmental filters that select a subset of the original community (Pineda and Halffter 2004; Püttker et al. 2015). Turnover reflects the replacement of species as a result of historical and spatial constraints, is correlated to the proportion of endemic and specialist species of a certain habitat type (Baselga 2010). Turnover often occurs between different physiognomies or areas with dissimilar biogeographic histories (Pineda and Halffter 2004; Baselga 2008; Solar et al. 2015). High nestedness indicates that one or a few sites with greatest richness should be prioritized, while high spatial turnover indicates that many different sites should be preserved, not necessarily the ones with highest species richness (Baselga 2010).

Our aim was to analyze the effect of habitat structure on the species diversity of bee and wasp assemblages nesting in pre-existing cavities across a structural gradient, including different disturbance levels, in the semiarid region of Brazil. We explored the following hypotheses: (i) habitat simplification reduces the occupation rate of cavities, species richness and diversity, and modifies species composition, (ii) beta diversity patterns between physiognomies with different habitat structures are explained mainly by species replacement (spatial turnover), (iii) beta diversity patterns between disturbed and undisturbed areas are explained by nestedness.

Materials and methods

Study area

Our study was conducted in the Ubajara National Park (UNP, 3°46'S, 40°54'W) and surrounding area (Fig. 1). UNP is a federal protected area, covering an area of 6288 ha in the Ibiapaba mountain range in the state of Ceará, Brazil. The park is in the Brazilian semiarid climatic domain with altitudes ranging from 400 to 900 m above sea level, which results in a humidity gradient (Figueiredo 1988). In the areas below 500 m, the average annual rainfall is 943 mm, and the average annual temperature is 28.2 °C, while in the areas above 800 m, the average annual rainfall is 1487 mm and the average temperature is 27 °C (FUNCEME 2015—data from 1982 to 2014, Online Resource 1).

The park is located in a heterogeneous region formed by a mosaic of habitats with different levels of structural complexity and vegetation cover. Two main types of vegetation are found in the park and its immediate surroundings: Deciduous Thorny Woodland (DTW) and Evergreen Seasonal Forest (ESF), which differ in structure and composition (Tavares et al. 2000; Araujo et al. 2007; Fabricante and Andrade 2007; Rodal et al. 2008; Costa and Araujo 2012). ESF occurs in areas of the park between 800 and 900 m, and is exposed to less rainfall seasonality (due to fog formation and greater rainfall), while DTW is found at lower altitudes (below 500 m) and is exposed to high rainfall seasonality

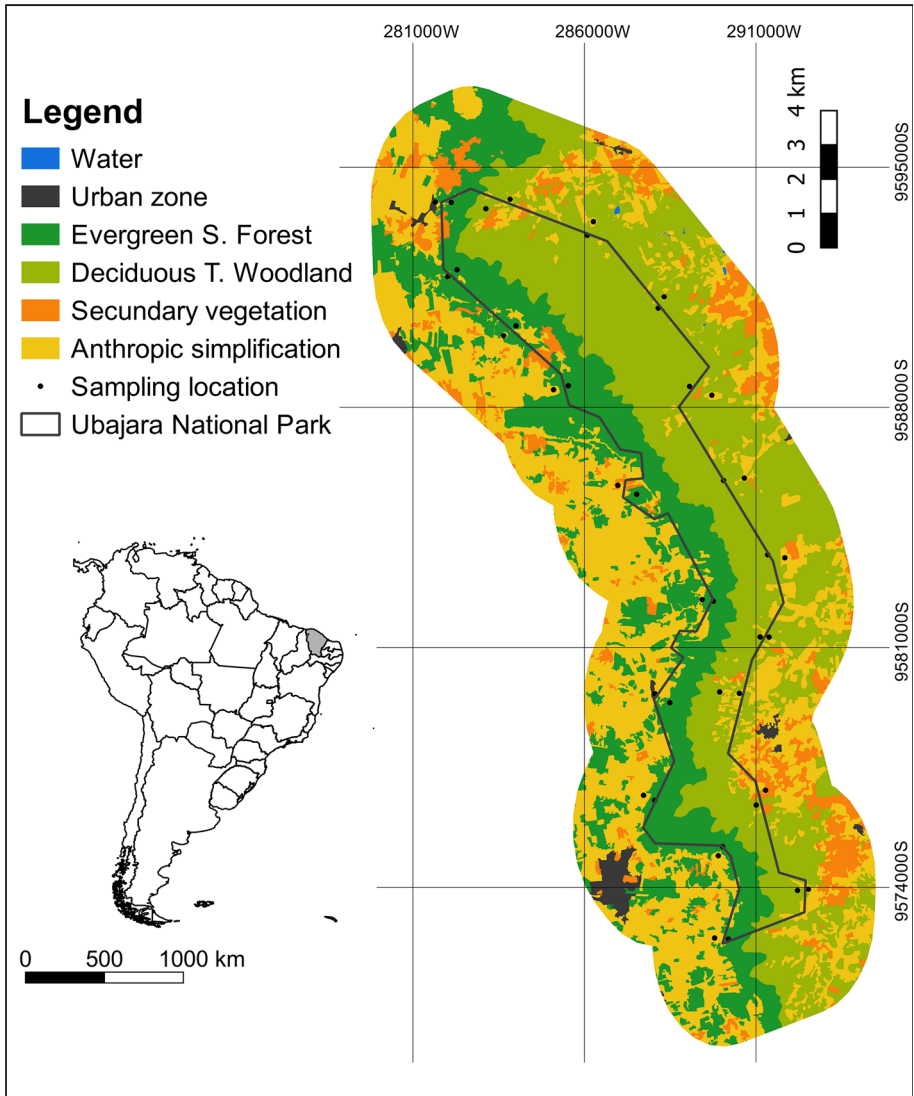


Fig. 1 Location of the study area: Brazil and the state of Ceará, in gray (on the left); the Ubajara National Park (UNP) and the 3 km surrounding area (on the right). The UNP covers an area of 6288 ha in a humidity gradient resulting of an altitudinal gradient of 400–900 m above sea level (altitude decrease from left to right). Two principal types of vegetation form the UNP: Deciduous Thorny Woodland (DTW) and Evergreen Seasonal Forest (ESF), which differ in structure and composition. Black dots represent sample points. In some places, the UNP boundary does not represent the real boundary between disturbed and undisturbed areas. In such cases, we consider the border between disturbed and undisturbed areas to establish our sample points

(Figueiredo 1988). ESF has more tree species than DTW ($S_{ESF} = 99.25 \pm 18.8$; $S_{DTW} = 25 \pm 2.4$) and the trees in ESF have a larger basal area ($BA_{ESF} = 28.8 \pm 12.6 \text{ m}^2/\text{ha}$; $BA_{DTW} = 25.5 \pm 7.1 \text{ m}^2/\text{ha}$) and a higher canopy (maximum height, $MH_{ESF} = 22 \pm 8.9 \text{ m}$; $MH_{DTW} = 11.67 \pm 1.2 \text{ m}$; Tavares et al. 2000;

Araujo et al. 2007; Fabricante and Andrade 2007; Rodal et al. 2008; Costa and Araujo 2012). Hence, ESF has greater variation in vertical stratification and is structurally more complex. To account for seasonal variations in rainfall within each physiognomy we measured the total precipitation every 45 days over 2 years (16 measurements), from one meteorological station in the ESF and another in the DTW (FUNCEME 2015).

Sampling points

To evaluate the effect of habitat simplification and rainfall seasonality on bee and wasp assemblages, depending on vegetation type, we selected 10 pairs of sampling points in the ESF and 10 pairs in the DTW along the edge of the UNP using remote sensing images.

All sampling points were at least 1000 m away from major roads, and 100 m away from trails and open fields to avoid exposure to sun and wind. Each pair consisted of one sampling point 100 m outside the park (disturbed area) and one sampling point 100 m inside the park (undisturbed area). Each pair of sampling points was 2.5–3.5 km away from any other pair to ensure spatial independence (assuming a maximum foraging distance of 600 m for solitary bees and wasps; Gathmann and Tschardt 2002; Klein et al. 2004; Zurbuchen et al. 2010).

Trap-nests

Bees and wasps that nest in pre-existing cavities were sampled using trap-nests, thereby avoiding the sampling of transient individuals (Krombein 1967; Morato and Campos 2000). Each trap-nest was made of 75 bamboo internodes 20 cm long with diameters ranging from 2 to 20 mm, each with a single opening. All 75 internodes were placed with their entrances facing a single direction in a PVC tube (15 × 22 cm). Three trap-nests were placed at every sample point, each facing a different direction (ca. 120° between them), always under a tree for increased sun and rain protection. Each set of three trap-nests was tied horizontally to a single wooden stake or tree branch, 1.5 m above the ground. The metal wire used to tie the nests was covered in automotive grease to prevent ant attacks (Tschardt et al. 1998; Tylianakis et al. 2005). Thus, 225 cavities were available at each sample point and a total of 9,000 cavities were available in the study area (75 cavities × 3 trap-nests × 40 sampling points).

Sample points were visited every 45 days, from January 2013 to December 2014. At each visit, all occupied cavities were removed and replaced by new ones of equal diameter. The occupied cavities were taken to the laboratory and kept at room temperature (27 °C) until the adult emerged.

Habitat complexity

Four levels of structural habitat complexity were defined (listed in order of decreasing complexity): Non-simplified Evergreen Seasonal Forest (N-ESF; undisturbed forest in the park); Simplified Evergreen Seasonal Forest (S-ESF; disturbed forest outside the park); Non-simplified Deciduous Thorny Woodland (N-DTW; undisturbed woodland in the park); Simplified Deciduous Thorny Woodland (S-DTW; disturbed woodland outside the park). To control for potential effects of land use within each level of complexity, sampling points were also categorized by land use: (1) conserved vegetation, (2) secondary

vegetation and (3) agriculture, using WorldView-2 satellite images obtained in February/2012, with 5 m of spatial resolution.

To confirm the categories of structural habitat complexity, we measured the normalized difference vegetation index—NDVI (Rouse et al. 1973). NDVI can be used to spatialize vegetation structure through remote sensing (Boscolo et al. 2016). The value of NDVI is directly related to vegetation biomass, providing an indirect measure of vegetation growth and habitat vertical structure/complexity (Riera et al. 1998; Lassau et al. 2005; Lassau and Hochuli 2008; Turner et al. 2001; Wood et al. 2012; Gamarra et al. 2016). For each sampling point, we calculated the NDVI mean and standard deviation in a buffer of 100 m radius around each sampling point (Wood et al. 2012). NDVI was calculated from RapidEye satellite images obtained in September 2012, with 5 m resolution, available in the database of the Brazilian Environment Ministry (<http://geocatalogo.mma.gov.br/>). We defined a 100 m radius to avoid the overlap between points within each pair of sampling points. After the atmospheric correction of the images, we calculated the NDVI through the QGIS 2.18.0 program and obtained the NDVI values for each of the four habitat types (Fig. 2).

Statistical analysis

Linear mixed models (LMMs) were used to analyze how the assemblages of bees and wasps are affected by habitat simplification. The total abundance (given by the number of occupied cavities) and species richness (including and excluding clepto/parasitoid species) at every sampling point, for each 45 day period, were used as response variables in two separate sets of LMMs (40 sampling points \times 16 sampling events). The explanatory variables (fixed effects) for both sets of models were: physiognomy (forest/woodland); habitat simplification by human disturbance (simplified/non-simplified); land use (conserved vegetation, secondary vegetation or agricultural) and all two-way interactions. Rainfall (total rainfall every 45 days) was used as a covariable to account for temporal variations in precipitation. An additional set of LMMs replacing all categorical explanatory variables by NDVI mean, NDVI standard deviation and their interaction was used to

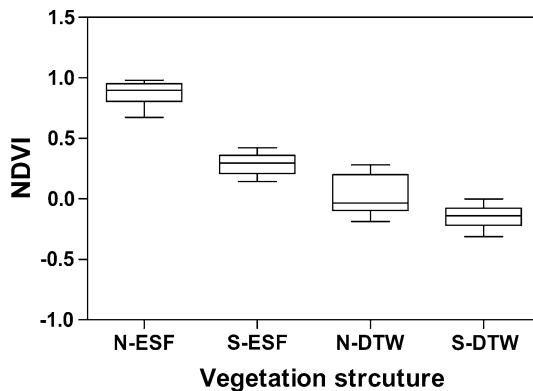


Fig. 2 The boxplot with median of normalized difference vegetation index (NDVI) in a buffer of 100 m radius around the trap-nests of the 10 plots by environmental type. *N-ESF* Non-Simplified Evergreen Seasonal Forest (NDVI = 0.87 ± 0.10), *S-ESF* Simplified Evergreen Seasonal Forest (NDVI = 0.29 ± 0.09), *N-DTW* Non-Simplified Deciduous Thorny Woodland (NDVI = 0.04 ± 0.18), *S-DTW* = Simplified Deciduous Thorny Woodland (NDVI = -0.15 ± 0.10)

confirm the effects of habitat simplification on abundance and species richness. Considering that sampling points within each pair were only 200 m apart, we used pair identity as a random intercept effect in all sets of models and because every sampling point was visited 16 times, the identity of each point was also used as a random intercept effect, nested within pair identity (Crawley 2007). The minimal model was found by stepwise removal of fixed effect variables followed by deviation analyses (Crawley 2007). All LMMs were done using the *lme4* package (Bates et al. 2015) on R v3.3.1 (R Core Team 2016).

The diversity of bees and wasps species was estimated through the Hill numbers of order $q = 1$, for each complexity level (Chao et al. 2014). Differences in diversity between the four environments were tested using paired t tests. The efficiency of sampling and estimation of species richness was analysed with a rarefaction curve for each environment using PAST (Hammer et al. 2001).

Moran's Index was used to evaluate the spatial autocorrelation between sampling points using presence/absence data (Legendre and Legendre 1998; Socolar et al. 2016). No significant spatial autocorrelation was found (Moran's $I = 0.54$, $p = 0.33$). Composition dissimilarity between environments was evaluated using Non-metric Multidimensional Scaling (NMDS) with two dimensions ($k = 2$) using a binary matrix of Sørensen dissimilarity (Kruskal and Wish 1978). Complexity level was also added as a factor variable to the NMDS. We used an Analysis of Similarity (ANOSIM) and a Permutational Analysis of Dispersion (PERMDISP) to test whether there is a significant difference in the composition between the four complexity levels (Clarke and Green 1988). The Indicator Species Analysis (IndVal) was used to assess the occurrence of each species in the assemblages using the R package *indicspecies* (De Cáceres and Legendre 2009). The NMDS and ANOSIM analysis were run using the software PRIMERV7 (Clarke and Gorley 2015). The R package *betapart* was used to calculate beta diversity, spatial turnover and nestedness, computing *pair-wise* and *multiple-site* dissimilarities (Baselga 2010; Baselga et al. 2013).

Results

Overall, out of the 9000 available cavities, 657 were occupied (7.3%). We recorded 13 species of wasps (532 cavities and 1605 individuals) belonging to the families: Crabronidae, Pompilidae, Sphecidae, Vespidae, Chrysididae, Ichneumonidae and Leucospidae; 13 species of bees (116 cavities and 449 individuals) of the families Apidae and Megachilidae. Of these, four species of wasps (31 individuals) and two of bees (17 individuals) were parasitoid/cleptoparasitic (Tables 1, 2).

Megachilidae and Apidae, excluding cleptoparasitic bees, were the families with the highest number of species, each with six species, 46% of the total number of species. While wasps from the Crabronidae and Sphecidae occupied most of the cavities (247 and 151 respectively), 59% of all occupied cavities. Wasps were more abundant than bees ($N = 40$; Mann–Whitney = -7.99 ; $p < 0.001$).

Bee and wasp diversity decreased with habitat complexity (Table 2): N-ESF > S-ESF ($t = 5.05$, $p < 0.001$, d.f. = 157.37), S-ESF > N-DTW ($t = 5.46$, $p < 0.001$, d.f. = 303.04), N-DTW > S-DTW ($t = 2.73$, $p = 0.006$, d.f. = 392.59). A larger number of species was found in the forest than in the woodland (Table 3; Fig. 3). In both physiognomies, richness was significantly higher during the periods of high rainfall (Table 3). Bee and wasp abundance was significantly affected by habitat simplification and rainfall

Table 1 Bees, wasps, and parasitoid species sampled with trap-nests in Ubajara National Park and surrounding area, Ceará—Brazil

Group	Family	Species	Local			
			N-ESF	S-ESF	N-DTW	S-DTW
Bee	Apidae	<i>Centris analis</i>	x		x	
		<i>Eufriesea nordestina</i>	x		x	
		<i>Euglossa nanomelanotricha</i>	x			
		<i>Tetrapedia diversipes</i>	x	x	x	x
		<i>Xylocopa (Neoxylocopa) grisescens</i>	x		x	
		<i>Xylocopa (Neoxylocopa) suspecta</i>	x			
		<i>Coelioxoides waltheriae</i> *			x	
	Megachilidae	<i>Dicranthidium arenarium</i>	x	x	x	
		<i>Hypanthidium</i> sp. 1	x	x	x	x
		<i>Hypanthidium</i> sp. 2	x	x	x	x
		<i>Megachile</i> sp. 1	x			
		<i>Megachile</i> sp. 2	x	x		x
		<i>Austrostelis maranhensis</i> *			x	
Wasp	Crabronidae	<i>Trypoxylon</i> sp. 1	x	x	x	x
		<i>Trypoxylon</i> sp. 2	x	x	x	x
	Pompilidae	<i>Auplopus militaris</i>	x			
		<i>Priochilus</i> sp.	x			
	Sphecidae	<i>Isodontia costipennis</i>	x			
		<i>Podium</i> sp. 1	x	x	x	x
	Vespidae	<i>Monobia</i> sp. 1		x		x
		<i>Pachodynerus</i> sp. 1	x	x	x	x
		<i>Pachodynerus</i> sp. 2	x	x	x	x
	Chrysididae	<i>Chrysis intricata</i> Brullé*	x	x	x	x
	Ichneumonidae	<i>Ichneumonidae</i> sp.*				x
	Leucospidae	<i>Leucospis</i> sp.*		x		
	Indet	Indet*	x			

Out of the 9000 available cavities, 657 were occupied for 13 species of bees and 13 species of wasps, including cleptoparasites and parasitoids

N-ESF Non-simplified Evergreen Seasonal Forest, *S-ESF* Simplified Evergreen Seasonal Forest, *N-DTW* Non-Simplified Deciduous Thorny Woodland, *S-DTW* Simplified Deciduous Thorny Woodland

* Cleptoparasitic and parasitoid species

(Table 4; Fig. 3). Excluding clepto/parasitoids, species richness was also affected by habitat simplification. A larger number of species was found in non-simplified areas (Table 3). In both physiognomies, abundance was significantly higher during the periods of high rainfall. The highest abundance was recorded in the simplified woodland area.

The rarefaction curve for each environment reached an asymptote, except for the non-simplified forest. Species composition was significantly affected by habitat structural complexity (PERMDISP: $F = 4.12$, $p = 0.01$, Fig. 4). The stress value of 0.16 is adequate for the interpretation of assemblage data (Clarke 1993). The main species shared between the four environments were wasps: *Trypoxylon* sp. 2 (IndVal = 0.69, $p > 1$), *Podium* sp. (IndVal = 0.79, $p > 1$) and *Hypanthidium* sp. 1 (IndVal = 0.55, $p > 1$). The partitioning

Table 2 Species richness, abundance (given by the number of occupied cavities) and Hill Number of order $q = 1$ (Hill Numb.) of bees, wasps, and cleptoparasitic/parasitoids sampled in 657 pre-existing cavities of four environmental complexity level in Ubajara National Park and surrounding area, Ceará—Brazil

	Richness		Abundance		Hill Numbers	
	T	X ± SD	T	X ± SD	T	X ± SD
Non-simplified forest (N-ESF)	21	6.75 ± 1.6	105	10.78 ± 4.4	10.6	4.61 ± 2.09
Simplified forest (S-ESF)	15	4.57 ± 2.07	129	12.4 ± 9.3	9.4	3.71 ± 1.46
Non-simplified woodland (N-DTW)	13	4.0 ± 1.69	187	18.7 ± 15.3	5.85	3.14 ± 1.29
Simplified woodland (S-DTW)	12	3.87 ± 2.1	257	29.78 ± 20.1	6	2.82 ± 1.05

T total number, X ± SD mean ± standard deviation

Table 3 Result of the LMM testing the habitat simplification effects on species richness of all bees and wasps, and excluding cleptoparasitic and parasitoid species, in two separate sets models: (1) physiognomy (Deciduous Thorny Woodland × Evergreen Seasonal Forest), habitat simplification (simplified × non-simplified), land use (agriculture × conserved vegetation × secondary vegetation) and rainfall; (2) NDVI mean and NDVI standard deviation

	Richness					Richness excluding clepto/parasitoids				
	D	d.f.	p	E	SE	D	d.f.	p	E	SE
Physiognomy	580.0	1	0.01	0.295	0.114	523.6	1	0.01	0.311	0.116
Habitat simplification	573.5	1	0.29			517.7	1	0.03	0.204	0.099
Land use	572.4	2	0.52			514.6	2	0.71		
Rainfall	580.4	1	0.008	0.001	<0.001	520.7	1	0.03	0.001	<0.001
NDVI										
Standard deviation	579.4	1	0.70			523.76	1	0.27		
Mean	589.57	1	0.001	0.486	0.145	529.9	1	0.01	0.395	0.150

The not significant interactions were removed

D difference residue after removal of the variable, d.f. degrees of freedom, p associated p value, E estimate (for significant variables), SE standard error

of beta diversity for all environments ($\beta_{SOR} = 0.45$), showed that turnover ($\beta_{SIM} = 0.29$) accounted for a larger fraction of beta diversity than nestedness ($\beta_{NES} = 0.16$). Since the N-ESF did not reach an asymptote in the species collection curve, we also analyzed beta diversity without N-ESF, and we found that it decreased from $\beta_{SOR} = 0.45$ to $\beta_{SOR} = 0.40$ and turnover and nestedness had similar contributions ($\beta_{SIM} = 0.21$, $\beta_{NES} = 0.19$, respectively). This reduction in beta diversity indicates that N-ESF was potentially responsible for the increase in species richness in the region.

Significant differences in species composition were found between non-simplified forest and simplified forest (N-ESF vs. S-ESF; $t = 3.01$, $p = 0.01$) and between simplified forest and simplified woodland (S-ESF vs. S-DTW; $t = 3.17$, $p = 0.009$). In N-ESF vs. S-ESF, turnover ($\beta_{sim} = 0.27$) was larger than nestedness ($\beta_{nes} = 0.12$), and ten species were lost in the simplified forest (six bees and four wasps including a parasitoid). Four of these ten species were replaced by four new species (turnover), two cleptoparasitic bees (*Austrostelis maranhensis* and *Coelioxoides waltheriae*), one parasitoid wasp (*Leucospis* sp.) and one carpenter wasp (*Monobia* sp.). Excluding the cleptoparasitic and parasitoid species of the analysis, nestedness component was greater than turnover ($\beta_{nes} = 0.24$, $\beta_{sim} = 0.09$).

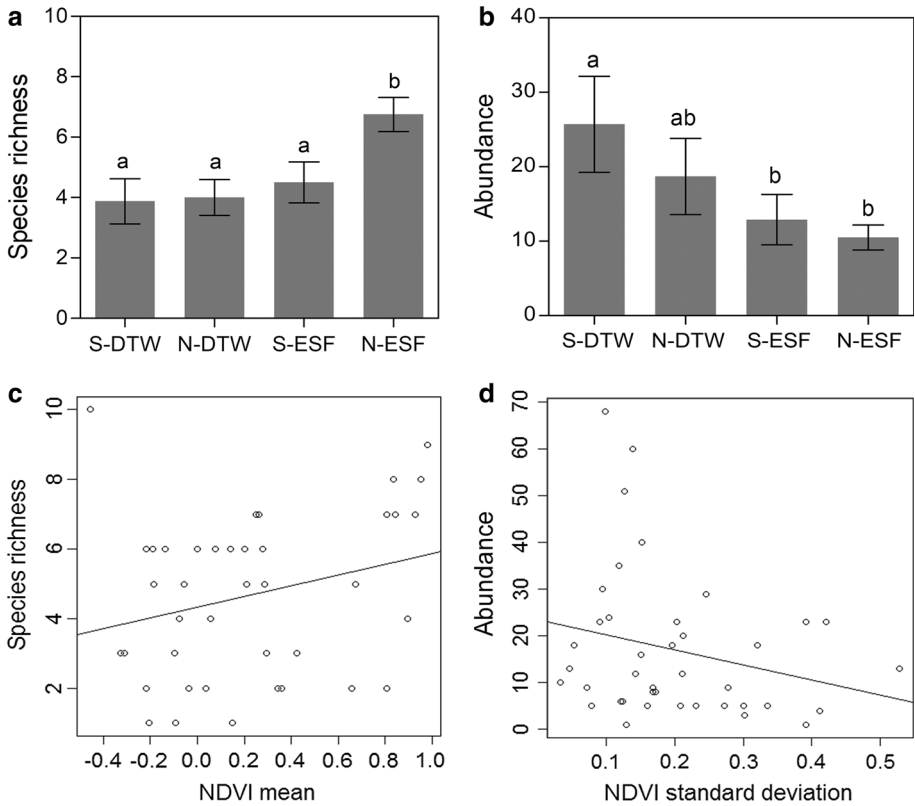


Fig. 3 Distribution of mean **a** species richness and **b** abundance of bees and wasps that nest in pre-existing cavities in four environments with different complexity levels. Bar represent standard error of the mean, different letters above the bars indicate significant differences in a Tukey post hoc test ($p < 0.03$). **c** Species richness and **d** abundance in function of NDVI. *S-DTW* Simplified Deciduous Thorny Woodland, *N-DTW* Non-Simplified Deciduous Thorny Woodland, *S-ESF* Simplified Evergreen Seasonal Forest and *N-ESF* Non-Simplified Evergreen Seasonal Forest

When comparing only simplified environments (*S-ESF* and *S-DTW*), beta diversity was relatively low ($\beta_{\text{sor}} = 0.18$), and nestedness and turnover contributed equally to beta diversity ($\beta_{\text{nes}} = 0.10$, $\beta_{\text{sim}} = 0.08$, respectively). In this case, these composition changes were due to the loss of one bee species (*Dicranthidium arenarium*) and two cleptoparasitic bees (*Austrostelis maranhensis*, *Coelioxoides waltheriae*) and one parasitoid wasp (*Leucospis* sp.) and their replacement by a parasitoid Ichneumonidae.

Discussion

Overall, the rate of cavity occupation (7.3%) was relatively low when compared to that found in similar neotropical physiognomies (14–21%) (Aguar et al. 2005; Loyola and Martins 2008; Garófalo et al. 2004). Nevertheless, we found higher species richness and diversity than previously reported, indicating that semiarid physiognomies may support less dense but diverse assemblages, and be relevant for biodiversity conservation.

Table 4 Result of the LMM testing the habitat simplification effects on abundance of all bees and wasps, and excluding cleptoparasitic and parasitoid species, in two separate sets models: (1) physiognomy (Deciduous Thorny Woodland × Evergreen Seasonal Forest), habitat simplification (simplified × non-simplified), land use (agriculture × conserved vegetation × secondary vegetation) and rainfall; (2) NDVI mean and NDVI standard deviation

	Abundance					Abundance excluding clepto/parasitoids				
	D	d.f.	p	E	SE	D	d.f.	p	E	SE
Physiognomy	1163.4	1	0.49			1161.4	1	0.55		
Habitat simplification	1173.0	1	0.001	-1.561	0.461	1171.3	1	0.002	-1.588	0.464
Land use	1163.1	2	0.8			1161	2	0.87		
Rainfall	1169.7	1	0.009	0.005	0.002	1166.4	1	0.02	0.005	0.002
NDVI										
Standard deviation	1179	1	0.04	-4.328	2.046	1175.7	1	0.03	-4.584	2.045
Mean	1173	1	0.13			1175.1	1	0.045	-1.267	0.612

The not significant interactions were removed

D difference residue after removal of the variable, *d.f.* degrees of freedom, *p* associated *p* value, *E* estimate (for significant variables), *SE* standard error

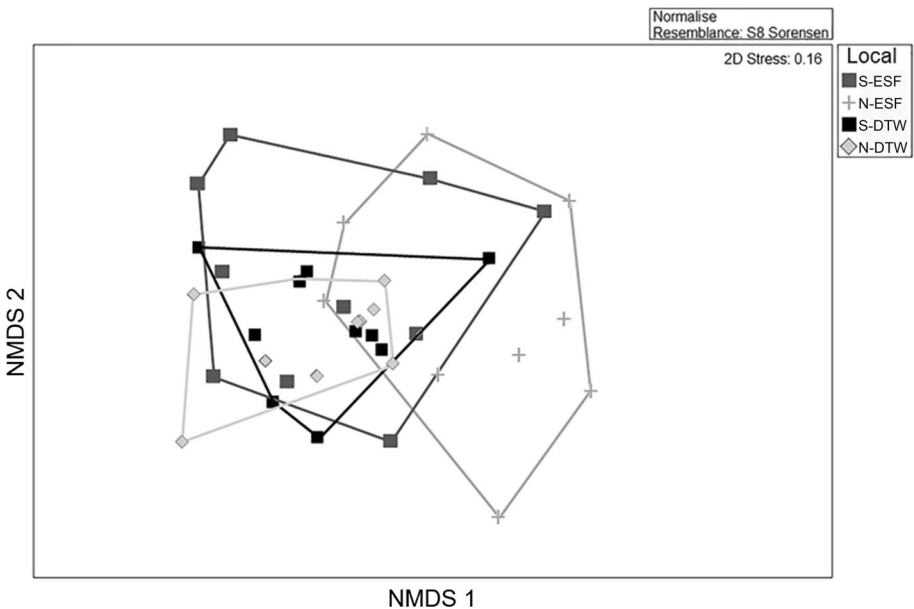


Fig. 4 Non-metric multidimensional scaling (NMDS) based on Sørensen dissimilarity of four environments complexity levels. *N-ESF* non-simplified Evergreen Seasonal Forest, *S-ESF* simplified Evergreen Seasonal Forest, *N-DTW* non-simplified Deciduous Thorny Woodland and *S-DTW* simplified Deciduous Thorny Woodland

Our results indicate that the diversity of bees and wasps decreases with habitat simplification. This is likely to be caused by a reduction of plant diversity that leads to a decrease in the variety of food resources and nesting sites available (August 1983; Tilman

2000; Ebeling et al. 2012; Antonini et al. 2016). However, species richness and abundance seem to be regulated by different factors. The greater abundance of bees and wasps was found in the simplified areas. Studies in tropical and temperate agricultural systems have also found a higher abundance of bees and wasps in simplified environments, due to an increase in the abundance of generalist species. Indeed, generalist hymenopteran species are less sensitive to environmental disturbance and habitat loss (Klein et al. 2002; Williams et al. 2010; Taki et al. 2013), which could explain the higher nest occupancy in the more disturbed sites in this present study. Furthermore, in highly simplified environments, the availability of artificial nesting sites can further increase the abundance of insects that nest in pre-existing cavities (Steffan-Dewenter and Schiele 2008).

Wasps were more abundant than bees, especially in simplified habitats. Previous trap-nest studies also found that wasps are more abundant than wild bees (Loyola and Martins 2006; Sobek et al. 2009; Schüepp et al. 2011; Ebeling et al. 2012; Araujo et al. 2017). Although bees and wasps that nest in pre-existing cavities rely on woody structures for nesting, habitat simplification can increase prey availability for some wasp species, increasing their abundance (Schüepp et al. 2011). Species in the two most abundant wasp genera in this study *Trypoxylon* and *Pachodynerus* exhibit such preference for open habitats (Fye 1972; Jenning and Howsewart 1984; Schüepp et al. 2011; Ebeling et al. 2012; Araujo et al. 2017). Open habitats have more light and more plants in the understory, where the spiders hunted by *Trypoxylon* and Lepidoptera larvae hunted by *Pachodynerus* may become more accessible (Fye 1972; Jenning and Howsewart 1984; Schüepp et al. 2011; Ebeling et al. 2012). In addition, some species of these wasp genera are flexible in their choice of prey and can be opportunistic in using different prey species (Sears et al. 2001; Schüepp et al. 2011). In contrast, many species of solitary bees have species-specific pollen preference, e.g. many oligolectic species of Megachilidae (Villanueva-Gutiérrez and Roubik 2004), and species like *T. diversipes* and *C. analis* (Dorea et al. 2010) that, although polylectic, are very selective as to the type of pollen and anther (Wcislo and Cane 1996; Schlindwein 2004). This could explain why bees were less abundant than wasps in simplified areas, despite their known preference for open habitats (Klein et al. 2002). Although the use of bees and wasps that nest in pre-existing cavities as indicators of environmental change has been frequently suggested, bees appear to be more affected by changes than wasps, hence, more suitable as bioindicators (Noss 1990; Tschartke et al. 1998; Tylianakis et al. 2004).

Contrasting with the data on abundance, we found greater species richness of bees and wasps in the more complex physiognomy (ESF). The difference in species number between forest and woodland can be explained by the structural dissimilarity between these two physiognomies, which is independent of their geographical proximity. Although species richness increased with NDVI, it did not vary between undisturbed areas and adjacent disturbed areas, when we considered the clepto/parasitoids species, indicating that only large structural changes may have an effect on species richness. In addition, this also suggests that undisturbed areas within UNP may act as a source of non-parasitic species for adjacent simplified areas, considering that bees and wasps can easily move between the two environments (Goodell 2003; Dingle and Drake 2007; Moreira et al. 2015). However, it is not possible to ascertain the provenance of many cleptoparasitic and parasitoid species found in the disturbed areas outside the park.

The assemblage composition varied between levels of habitat complexity within and between physiognomies and the non-simplified forest was responsible for the largest increase of species in the region. Although on the largest spatial scale rainfall influenced the number of species and their abundance, the assemblage composition varied between

adjacent forest areas with the same precipitation pattern (N-ESF and S-ESF). This indicates that habitat complexity is a key determinant of species composition and that complex environments are responsible for the occurrence of the largest fraction of non-parasitic species in the region. Besides that, at least four of the nine species found exclusively in the undisturbed forest (N-ESF) are considered rare or exclusive of the neotropical region, e.g. *Auplopus militaris*, *Eufrisea nordestina*, *Isodontia costipennis*, *Priochilus* sp. (Silveira et al. 2002; Buschini and Wolff 2006; Buschini and Woiski 2008; Matos et al. 2016). With these findings, we highlight the importance of conservation units encompassing highly complex environments to maintain wasp and bee diversity.

The low beta diversity found between undisturbed and disturbed woodland areas can be explained by the relatively small difference in habitat complexity between the two areas (see Fig. 2). Undisturbed woodlands are physiognomically more open and less stratified than forest areas (ESF) (Ferraz et al. 2003; Rodal et al. 2008). Low-impact human activities (e.g. subsistence agriculture), very common in the DTW region, may have a small effect on habitat complexity. Hence, resource availability will remain similar in disturbed and undisturbed woodlands. Moreover, the most common species in the woodland areas (*Trypoxylon* sp. 1 and sp. 2, *Podium* sp. *Pachodynerus* sp. 1 and sp. 2) are habitat generalists and prey on spiders, cockroaches and Lepidoptera larvae, which are often more abundant in open areas (Camillo et al. 1996; Buschini and Buss 2010; Uehara-Prado et al. 2007; Gavish et al. 2012; Matos et al. 2013; Petcharad et al. 2016).

In the partitioning of beta diversity across the region, species turnover was higher than nestedness, as in the pairwise comparison between forest areas (N-ESF vs. S-ESF). In the latter, however, turnover was caused by two cleptoparasitic and one parasitoid species found in S-ESF. The occurrence of these species in the disturbed forest is potentially a consequence of the high abundance of their host species, *Trypoxylon* spp. and *Pachodynerus* spp. in simplified areas. When cleptoparasitic and parasitoids were removed from the analysis, nestedness became the main component of beta diversity, i.e. the non-parasitic species in S-ESF are a sub-group of the species found in N-ESF. In addition to the overall reduction of nesting resources, the loss of bee species in the disturbed forest (S-ESF) may also be linked to a reduction in floral resources. Even generalist species of bees have plant preferences and may depend on specific plant species to feed their brood (Schlindwein 2004; Dorea et al. 2010; Kleijn et al. 2015). Hence, the removal of food sources can lead to a local extinction of bees (Severns and Moldenke 2010).

Thus, we conclude that habitat simplification has adverse effects on the diversity of bees and wasps that nest in pre-existing cavities. However, the intensity of these effects depends on the type of physiognomy. Structural changes in vegetation have a larger effect on species composition (e.g. N-ESF vs. S-ESF and S-ESF vs. S-DTW) than species richness (e.g. N-ESF vs. N-DTW). Considering the whole assemblages of species that use pre-existing cavities, both disturbed and undisturbed areas should be preserved for maximizing species richness in the region. However, for non-parasitic bee and wasp species that provide ecosystem services, complex habitats support a large diversity and may act as a source of species for adjacent areas, simplified by human activities. Hence, the conservation of humid mountain ranges within the semiarid domain is fundamental for the maintenance of the diversity of bees and wasps.

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