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Trap-Nesting Hymenoptera and Their Network with Parasites in Recovered Riparian Forests Brazil

GJ Araujo[1], R Fagundes[1,2], Y Antonini[1,3]

[1]Depto de Biodiversidade Evolução e Meio Ambiente, Univ Federal de Ouro Preto, Ouro Preto, Minas Gerais, Brasil
[2]Depto de Ecologia, Univ Federal de Uberlândia, Uberlândia, Minas Gerais, Brasil
[3]Lab de Biodiversidade, DEBIO, ICEB, Univ Federal de Ouro Preto, Ouro Preto, MG, Brasil

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Correspondence
Y Antonini, Lab de Biodiversidade, DEBIO, ICEB, Univ Federal de Ouro Preto, Campus Morro do Cruzeiro, s/n, CEP: 35400-000 Ouro Preto, MG, Brasil; antonini.y@gmail.com

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Abstract

Different aspects of human activities can cause environmental change that endanger species persistence, alter species distributions, and lead to changes in antagonistic and mutualistic interactions, whereas deforestation and flooding of riparian forest results in landscapes consisting of patchily distributed riparian forest fragments in a matrix of pastures, plantations, and urban areas. Therefore, we assessed the richness, abundance, and trophic interactions of trap-nesting Hymenoptera and their parasites at four patches of restored riparian forest and at one reference natural fragment, of different sizes and ages, located at the Volta Grande Reservoir, in Minas Gerais and São Paulo states to answer the following questions: (1) Does the richness and abundance of cavity-nesting bees and wasps differ in riparian forest fragments according to the seasonal periods? (2) Does the composition of cavity-nesting bees and wasps vary among restoration and reference sites and between climate seasons (wet and dry)? (3) How do the degrees of specialization of the parasites vary among the patches of forest? We recorded 12 species of wasps, eight of bees, and nine species of parasites. Areas with longer time since restoration (reference site) showed higher species richness. However, the abundance was higher in most recent areas. The composition of bee and wasp assembly has not significantly changed between the climate seasons, although it is different between sampling areas. The richness and abundance were higher in warmer and rainy periods. The rate of bee and wasp mortality was high. The degree of specialization of parasites varies among sampling units, and the network of host-parasite interaction has a modular configuration with generalists and specialists. We concluded that the restored areas with more complex habitat could provide better conditions for the reestablishment of ecological interactions among these insects, the local flora, and other invertebrates, which together contribute to the success of the restored environments.

Introduction

Different aspects of human activities can cause global environmental change that endanger species survival, alter species distributions, and lead to changes in antagonistic and mutualistic interactions (Stangler *et al* 2015, Barlow *et al* 2007). Deforestation and resulting fragmentation are regarded as a major threat to biodiversity, since they result in landscapes consisting of patchily distributed forest fragments in a matrix of pastures and plantations (Fahrig 2003). But, we still miss how this kind of human impact affects interspecific interactions, such as plant-pollinator

(Cane *et al* 2006), predator-prey, and parasite-host (Klein 2006).

Riparian forests of the *Cerrados* of Brazil share faunistic and floristic elements with the Atlantic forest (Gibbs and Leitão-Filho 1978, Oliveira-Filho and Ratter 2009). Riparian forests have a highly variable structure, composition, and distribution of species, contributing to different ecological formations based on physiognomy and floristic and structural features (Kageyama *et al* 2001). From the association between riparian forests and adjacent vegetation formations emerged mixed forests with species characteristic of the two physiognomies (Kageyama *et al* 2001). Therefore, riparian forests are very flexible to changes in environment. However, some species are too specific to riparian forests and may suffer landscape modification. For example, species adapted to the riparian forest conditions and living in constant shade cannot easily adapt to higher temperatures and lower air moisture in open habitats and do not have many options to escape from rising temperatures and lower humidity (Morato and Campos 2000, Stangler *et al* 2015). This is the case of species of trap-nesting bees and wasps, which have narrow thermal tolerance and specific requirements for nesting resources (Deutsch *et al* 2008, Stangler *et al* 2015).

The assemblage of trap-nesting bees and wasps respond to habitat disturbances in different ways because they have different levels of sensitivity to habitat disturbance (Tscharntke *et al* 1998, Klein *et al* 2006, Tylianakis *et al* 2006). This is very concerning, because bees and wasps fulfill important tasks in ecosystem functions. Specifically, bees are the most important pollinator group of plants (Didham *et al* 1996, Kremen *et al* 2007) and wasps are important predators and parasitoids, with considerable economic and agricultural relevance (Tylianakis *et al* 2005). Their variety of functional niches makes insects and other invertebrates important for the maintenance of vital ecosystem processes (Didham *et al* 1996). Studies conducted in Neotropical forests have demonstrated that trap-nesting bees are very sensitive to habitat changes that causes reduction on the abundance and diversity. The assemblage of bees is more complex in continuous forest and natural gaps, while wasps seem to prefer small forest remnants and cleared areas (Morato & Campos 2000, Stangler *et al* 2015). Both groups rely heavily on nesting site availability (Potts *et al* 2005), specific materials for nest construction (Taki *et al* 2008), and pollen or arthropod as food resources (Tscharntke *et al* 1998). The nesting frequencies of trap-nesting Hymenoptera are also known to respond to climate factors such as temperature, precipitation, humidity, and microclimate variables (Morato 2001, Tscharntke *et al* 1998, Thiele 2005).

Data on communities of trap-nesting bees and wasps and their natural enemies have been used in research on habitat quality (Tscharntke *et al* 1998), the effects of habitat fragmentation and of landscape complexity on community composition and predator-prey interactions (Steffan-Dewenter *et al* 2002, Klein *et al* 2006, Steckel *et al* 2014, Stangler *et al* 2015) There is a lack of studies done inside riparian forests that combine the effects of climate and habitat size on communities of trap-nesting bees and wasps since most studies have investigated influences of tropical forests in adjacent agro-ecosystems (Klein *et al* 2002, 2006) or along land-use gradients (Tylianakis *et al* 2005, 2006, Batista Matos *et al* 2013). Moreover, there is a lack of studies investigating the possible interactive effects of small fragments and microclimate on solitary Hymenoptera and their parasitic interactions in tropical restored riparian fragments. Therefore, we assessed the richness and abundance and the network of interactions with its parasites of trap-nesting Hymenoptera at five locations in different sized and aged secondary forests. This was done in order to answer the following questions: (1) Does the richness and abundance of cavity-nesting bees and wasps differ in patches of restored riparian forest according to the seasonal periods? (2) Does the composition of cavity-nesting bees and wasps vary among restoration and reference sites and between seasons (wet and dry)? (3) How do the degrees of specialization of the parasites vary among the patches of riparian forest?

Material and Methods

Study Area

This study was carried out between November 2013 and September 2014 in the Volta Grande Reservoir region in Minas Gerais and São Paulo states (20°01′54″S/48°13′17″W), Brazil. The average annual temperature was 23°C and the average annual precipitation was 1506 mm. According to Alvares *et al* (2014), Volta Grande belongs to the Tropical AW Köppen climate (with a dry winter) (Fig 1). The landscape consists mostly of pastures and monocultures (sugarcane and rubber tree plantation) (see Martins & Antonini 2016 for more details). We selected five riparian forest fragments (average 17.7 ha ± 4.86; range 3–40 ha), at least 15 km between each, and with similar forest cover in the matrix (approx. 30%). The fragments were created in a single planting event that included between 30 and 40 species of native and exotics trees. Hereafter, following Martins & Antonini (2016), each fragment will be referred to as sampling units (SUs) (Table 1).

Sampling Design

In each of the five sampling units (hereafter SU), 12 plots of 100 m^2 were installed in the central area of the fragment. The woodblocks (two by each plot) were placed 1.5 m high in

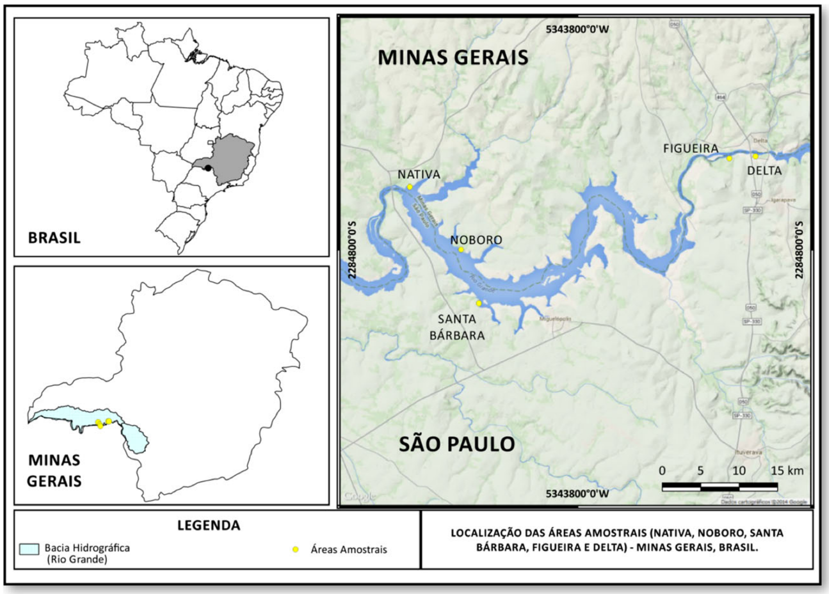

Fig 1 Location of the five areas of restored riparian forest around the Volta Grande Reservoir, Brazil.

the most central tree, forming a sampling point (hereafter Pt), totaling 120 blocks and 5400 nesting sites in total. Trap nests were black cardboard tubes inserted in holes drilled into wood blocks with a total of 45 holes arranged linearly (Camillo *et al* 1995). Trap nests were uniform in length (120 mm) but varied in their inner diameters (6–12 mm). The number of trap nesting, in each diameter, was the same.

Occupied cardboard, those closed with soil or plant materials, indicating completed nest construction (Krombein 1967), were collected and taken to the laboratory. New empty cardboards were used to replace those collected. In the laboratory, cardboards brought from the field were kept in a glass assay tube plugged with a cotton wad and kept in the laboratory at room conditions (ca. 15–25°C). Cells that remained closed for a long time were opened to investigate whether a juvenile had died (egg or pre- or post-defecating larvae) or whether it was diapausing. The number and identity of parasites and cleptoparasites also were recorded. Insects were identified and deposited with their nest material in the Entomological Collection of the Laboratório de Biodiversidade, of the Universidade Federal de Ouro Preto.

Analyses

Following Klein *et al* (2006), we calculated the accumulation curve of species richness of trap-nesting bees and wasps for each SU. Expected values of accumulated richness were obtained from the number of occupied trap nests found in each of the 12 collecting points, inside each SU, using 100 randomizations, with the Jacknife I estimator.

A generalized linear model (GLM) was used to test the relationship between the number of cells built by bees and wasps as well as the richness, abundance, and composition of bees and wasp assemblage with the temperature and precipitation among four seasonal periods following Martins & Antonini (2016). For this, the data were grouped into four categories—start and end of the dry season and the start and end of the wet season. We also tested if the rate of mortality changed between the SUs.

Permutational analysis of variance (PERMANOVA) was used to test the hypothesis that the composition of the bee and wasp assemblage varies between seasons (dry and wet) and between SUs. To test the composition of the bee and wasp assemblage between SUs, the data were grouped into five categories according to the sampling units presented in

Table 1 Geographic location and characterization of sampling units by age, width, forest cover and the surrounding matrix. Data of land use and cover were gathered evaluating a circular buffer of 3 km from the center of each sampling unit.

Sampling Unit	Location (UTM)	Age (years)	Width (meters)	Matrix
1	23 K—205,429/7,786,874	20	100	Sugarcane
2	23 K—208,838/7,787,209	10	100	Sugarcane + households
3	22 K—800,294/7,768,027	10	30	Sugarcane
4	22 K—798,082/7,775,015	20	30	Rubber trees
5	22 K—791,531/7,783,262	30	400	Cerrado

Table 1. The measure of dissimilarity used was that of Bray-Curtis with 1000 permutations, and to measure the dispersion of the data, multivariate analyses of permutation distance (PERMDISP) were performed. The graphical representation of the variation in the composition of solitary bees and wasps between the five sampling units was shown by analysis of non-metric multidimensional scaling (NMDS). All the statistical analyses were performed using the R software (R Development Core Team 2013).

Host-Parasite Network

We built one host-parasite network for the five fragments. Each network was built by an adjacency matrix A, where "a_{ij}" is the number of nests of an individual host species (bee or wasp) "i" parasitized by a parasite species "j." Then, we evaluated if selective parasite species would parasitize a subset of wasp or bee species parasitized by the generalist parasites (i.e., nested pattern of host-parasite interactions). For this, we estimated nestedness using the NODF metric (Almeida Neto *et al* 2008) in the ANINHADO program, a program developed by Guimarães and Guimarães (2006). The values of this metric range from 0 (non-nested) to 100 (perfectly nested). In addition, we tested if there were groups of parasite species strongly associated with a particular set of host, as expected in a modular network and less connected to other groups (Guimerá *et al* 2004). For this, we used the modularity index (M) based on simulated annealing (SA) (range 0–1) (Guimerá *et al* 2004) using the software MODULAR (Marquitti *et al* 2014). To characterize the degree of specialization or partitioning, between two parties in the network, we used the H2′ index (Bluthgen *et al* 2006) that range from 0 (highly generalist) to 1 (highly specialized). We tested the significance of H2′ using Monte Carlo. We used GLM to test whether the number of parasite species has a positive relationship with richness and abundance of hosts.

Results

Trap-Nesting Bee and Wasp Assemblage

During 11 months, 1271 brood cells were constructed by solitary bees and wasps. The community consisted of eight host bees and 12 host wasps that interacted with three parasitic bees and three parasitic wasps (Table 2). The majority of brood cells (81.5%) were constructed by wasps, while only 18.5% were constructed by bees. In total, 109 cells (8%) were parasitized, being 23 bee cells and 86 wasp cells. The rate of mortality of juvenile was 49.14% for bees and 46.78% for the wasps. Three nests were used both for *Centris tarsata* and *Pachodynerus grandis*. The cells of *C. tarsata* were built first and were located in the end of nest. In these nests, adults of *C. tarsata* failed to emerge from the nest.

The species accumulation curve indicated that the sampled richness is still somewhat lower than expected (Fig 2). The lower estimated richness was recorded in SU5 (S = 22) with 59.38% of total species. However, SU2 registered 83.10% of the expected species (Table 3).

In SU5 (S = 13), SU2 (S = 12), and SU1 (S = 11), we registered the highest richness of bees and wasps and in SU2 and SU1 the highest abundance (*n* = 125 and 124 nests built, respectively). In the SU3 and SU4, we found lower richness, but the lower abundance of bees and wasps were observed in the SU4 and SU5 (Table 3).

The composition of trap nesting bees and wasps was different between SUs (PERMANOVA: F = 2.6989, R^2 = 0.45368, *P* = 0.001; PERMIDISP: F = 2.7324, *P* = 0.0752) (Fig 3). Only *P. grandis* was found in all five SUs and *Trypoxilum nitidum*, *C. analis*, and *Megachile* (*Melanosaurus*) sp. were found in four out the five SUs (Table 2). For *P. guadulpensis*, *Megachile* sp., *Tetrapedia* sp., and *Epanthidium* sp., they were found only in one sampling unit (SU4, SU1, and SU5, respectively) (Table 2).

Seasonal Periods

There was no difference in species composition among dry and rainy seasons (F = 1.5732; R^2 = 0.08037; *P* = 0.172). However, abundance of bees and wasps was higher all over the rainy season (F = 10,331, *P* < 0.0001) (Fig 4(a)). The highest value for total richness was found at the end of the rainy season (F = 9.4704, *P* < 0.0001) (Fig 4(b)).

Some wasp species (*P. grandis* and *Penepodium* sp.1) were recorded throughout the sampling period, but the number of constructed cells varied throughout the seasons (Fig 5). Other species such as *P. anodontus* Willink & Roig-Alsina 1998, *Minixi brasilianum*, and *Penepodium* sp2 nested only at the end of rainy season, *Hypancistrocerus* sp. only at the end of dry season, and *P. guadulpensis* only at the start of rainy season. Despite the low abundance of *Pepsis* sp., this species has been recorded in almost all seasonal periods.

Centris (*Heterocentris*) *analis* (Fabricius 1804) was the bee species that constructed the higher number of cells (*n* = 76) and also the only one registered during the entire sampling period (Fig 6). The other bee species showed a pattern of more "seasonal" occupation. *Centris tarsata* for example was recorded only at the end of dry season, *Megachile* sp. only at the end of rainy season, *Euglossa melanotricha* during the end of rainy and start of dry period, *Tetrapedia* sp. only at the start of rainy season, and *Epanthidium* sp. only at the start of dry season and *C. terminata* only being absent at the start of rainy season.

Table 2 Number of cells built by trap-nesting bees and wasps at the Riparian forest of Volta Grande Reservoir from November 2013 to February 2014 and from May to September 2014.

Species	Sampling units				
	SU1	SU2	SU3	SU4	SU5
Apidae					
Centris (*Heterocentris*) *analis* (Fabricius 1804)	22	41	0	5	8
Centris (*Heterocentris*) *tarsata* (Smith 1874)	0	6	0	0	24
Centris (*Heterocentris*) *terminata* (Smith 1874)	11	3	0	0	9
Euglossa (*Euglossa*) *melanotricha* Moure 1967	0	1	3	0	1
Tetrapedia sp.	0	0	0	0	4
Mesocheira sp.[a]	0	0	0	0	2
Megachilidae					
Epanthidium sp.	0	0	0	0	2
Megachile (*Melanosarus*) sp.	32	4	28	0	9
Megachile sp.	12	0	0	0	0
Coelioxys sp1[a]	0	0	2	5	2
Coelioxys sp2[a]	0	0	2	0	0
Crabronidae					
Trypoxylon nitidum (Smith 1856)	167	92	99	0	4
Trypoxylon (*Trypargilum*) *lactitarse* Saussure	33	17	0	1	0
Chrysididae	0	0	0	0	0
Chrysis sp.[a]	0	2	11	7	7
Eulophidae					
Melittobia sp.[a]	2	0	9	14	14
Mutilidae					
Mutilidae sp.[a]	1	0	0	0	0
Pompilidae					
Pepsis sp1	0	0	3	6	0
Sphecidae					
Penepodium sp1	11	35	0	0	5
Penepodium sp2	5	0	0	0	5
Vespidae (Eumeninae)					
Ancistroceroides sp.	8	0	42	0	0
Hypancistrocerus sp.	0	9	12	0	0
Minixi brasilianum (de Saussure 1875)	0	2	1	0	3
Pachodynerus anodontus Willink & Roig-Alsina 1998	0	6	0	0	1
Pachodynerus guadulpensis (de Saussure 1853)	0	0	0	11	0
Pachodynerus grandis Willink & Roig-Alsina 1998	75	137	106	16	14
Pachodynerus pannus Willink & Roig-Alsina 1998	1	0	1	0	0
Diptera					
Bombyliidae					
Anthrax sp1[a]	0	2	4	6	2
Anthrax sp2[a]	4	0	0	0	1
Coleoptera					
Macrosiagon sp1[a]	0	0	2	7	6

[a] Nest parasites.

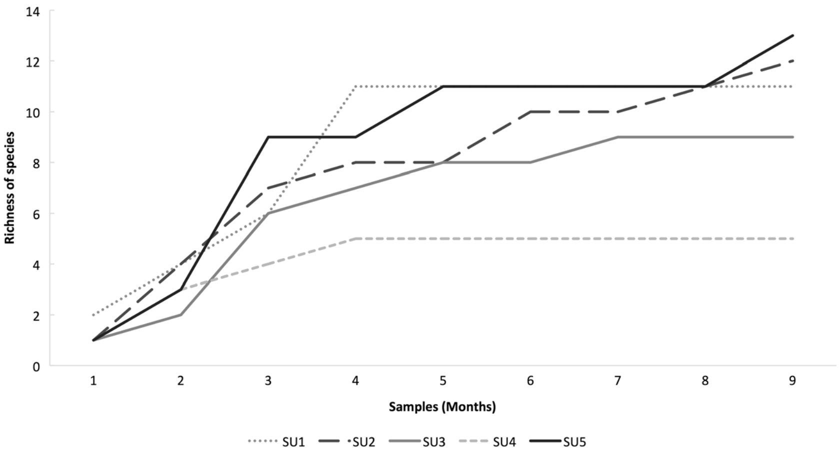

Fig 2 Expected richness of trap-nesting bees and wasps recorded from September 2013 to November 2014 on the five sampling units of the Volta Grande reservoir, Brazil.

Host-Parasite Interaction

Nine parasitic species were recorded, and there was more than one species in seven trap nests. Wasp species of *P. grandis* (*n* = 35), *T. nitidum* (*n* = 22), and *Penepodium* sp1 (*n* = 10) were the most parasitized species. However, for *Penepodium* sp1, we found only one parasite species. We found 25 host-parasite interactions, 23% of the possible interactions. The average number of interactions was 1.2. Parasite species overlap interactions with hosts in 23%, while host species overlap in 22%.

The network was more modular (M = 0.56; *P* = 0.05) and less nested (NODF = 29.6; *P* = 0.30) than expected by chance. Four groups were identified in the host-parasite network (Fig 7); two groups were formed by one parasite species (*Melittobia* sp. and *Coelioxys* sp.) each with three interacting host species, a group formed by one host species (*C. tarsata*) interacting with two species of parasites, and a group formed by several species of parasite sharing various hosts. Although the most abundant parasites (*Chrysis* sp., *Anthrax* sp1, and *Mellitobia* sp.) have shared most abundant hosts (*P. grandis* and *T. nittidum*), there was a higher preference of *Mellitobia* sp. for *Penepodium* sp1 and *Macrosiagon* sp. for *P. grandis*. The parasite *Coelioxys* sp. formed, together with their host bees, a module. Although modular, the network showed low specialization (H′obs = 2.71; H′ran = 3.2; $p < 0.001$). On the sampling units SU2 and SU4, we registered more specialized parasites to hosts (H2 = 1.000 and 0.75, respectively). For sampling unit SU3, the value of H2 was 0.56 and for SU1 was 0.45. For sampling unit SU5, we do not find any specialized parasites to hosts and the value of H2 was 0.

Discussion

Bee and Wasp Assemblage

The number of trap nests occupied by solitary bees and wasps quantified in this study was relatively high compared with data from other studies in Brazilian Forests (e.g., Aguiar & Martins 2002, Alves-dos-Santos 2003, Buschini *et al* 2006, Loyola & Martins 2006, Aguiar *et al* 2005, Pires *et al* 2012), which is not expected for recovered riparian forests. The abundance of trap-nesting wasps in recovered riparian forests was much higher than that of bees. Wasp dominance was also observed in previous studies in Costa Rica (Stangler *et al* 2015), Central Amazon (Morato & Campos 2000), and Northern (Batista Matos *et al* 2013, Melo & Zanella 2012, Aguiar *et al* 2005) and Southern Brazil (Loyola & Martins 2006).

Our results are in accordance with some studies that show that bees are commonly found in continuous forest and natural gaps, while wasps are common to small forest remnants and cleared areas (Oliveira & Campos 1996, Morato & Campos 2000). The characteristics of the matrix that surround patches of habitat have significant effects over the

Table 3 Values of Jacknife for trap-nesting bees and wasps for the five sampling areas of riparian forests of Volta Grande Reservoir, Brazil.

Sampling units	Richness	Abundance of nests	Jacknife 1 (±SD)	Percent
SU1	11	124	15.56 ± 1.41	77.12
SU2	12	125	14.44 ± 2.35	83.10
SU3	9	73	12.56 ± 1.94	71.65
SU4	5	15	6.78 ± 1.18	73.74
SU5	13	34	21.89 ± 3.64	59.38

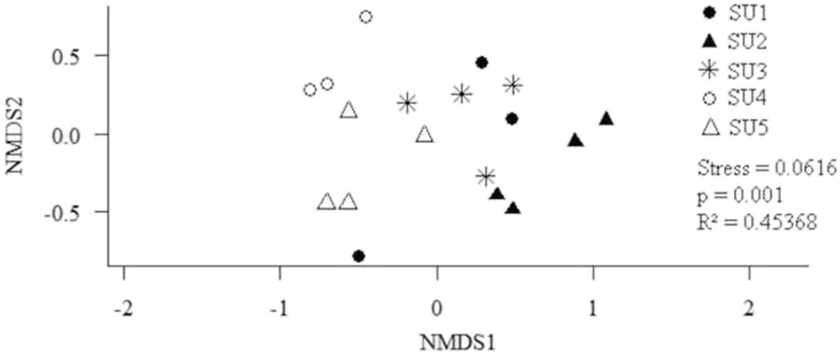

Fig 3 Analysis of non-metric multidimensional scaling (NMDS) for sorting and graphical visualization of the PERMANOVA and PERMDISP analyses of bees and wasps among the sampling areas. The Bray-Curtis dissimilarity index was used.

biodiversity in different types of landscapes, spatial scales, and taxonomic groups (Martins & Antonini 2016). There is evidence that the type of matrix influences individual survival and reproduction as well as the structure and dynamics of communities, especially interspecific relationships (Prevedello & Vieira 2009). The matrix around the sampling units also could explain the dominance of wasps. The sampling units were located in a very anthropogenic matrix formed mainly by grasslands and sugarcane plantations. After 30 years of recovery, the landscape naturally became a mosaic of environments that strongly influenced the restoration of the riparian forest fragments. According to Fried *et al* (2005), field edges provided connectivity and facilitated wasp movements between trap nests and source habitats where dispersal started. It is important to notice that species of the subfamily Eumeninae (most representative group in this study) also showed more preference for open places (Jennings and Housewart 1984). According to these authors, the presence of ruderal plants improve the availability of resources (nectar and prey).

The curves of species accumulation showed that the expected bee and wasp richness in all of the five sampling units is higher than that observed. However, for equal sampling effort, we trapped greater species richness in the more “complex” area (SU5), possibly reflecting resource availability. The habitat heterogeneity of SU5 may support more potential niches and is likely to support food webs with greater range (Lassau *et al* 2005, Stangler *et al* 2015). However, in SU5, we observed lower abundance of nests of bees and wasps in traps. Besides that cavity-nesting bees and wasps depend on nesting sites in natural habitats, they can forage in multiple habitats including crop fields (Fye 1972). So, the lack of nesting sites could explain the higher abundance of occupied trap nests, in the SU1 and SU2, where the forest was recovered recently (10 years).

The most abundant species of wasps occurred in almost all sampling areas, especially species of *Trypoxylon nitidum* and *P. grandis*. It is important to notice that this is the first record of *P. grandis* in Cerrados of Brazil. The high abundance of potter wasps reflects greater availability of preys (Klein *et al* 2002), which is higher for areas of intense land use. So far, the occurrence of this species in trap nests had been recorded only in Atlantic Rainforest (Teixeira 2011).

We did not expect lower abundance of *C. tarsata*, which was considered numerical dominant species both in Atlantic Forest (Aguiar & Garófalo 2004) and in Cerrado (Mesquita *et al* 2009, Pires *et al* 2012). *C. tarsata* is able to successfully nest if the proper nest sites are available, even in areas of open vegetation. However, the number of nests founded by this species

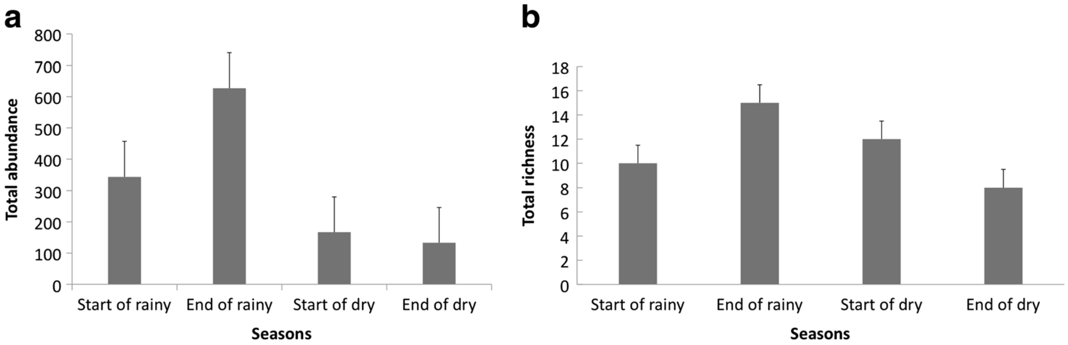

Fig 4 Total abundance (*a*) and richness (*b*) of trap-nesting bee and wasps for the sampled climate periods in the riparian forests of the Volta Grande Reservoir, Brazil. *Ds* start of dry season, *De* end of dry season, *Rs* start of rainy season, *Re* end of rainy season. *Bars* are mean, *different letters* represents statistical differences.

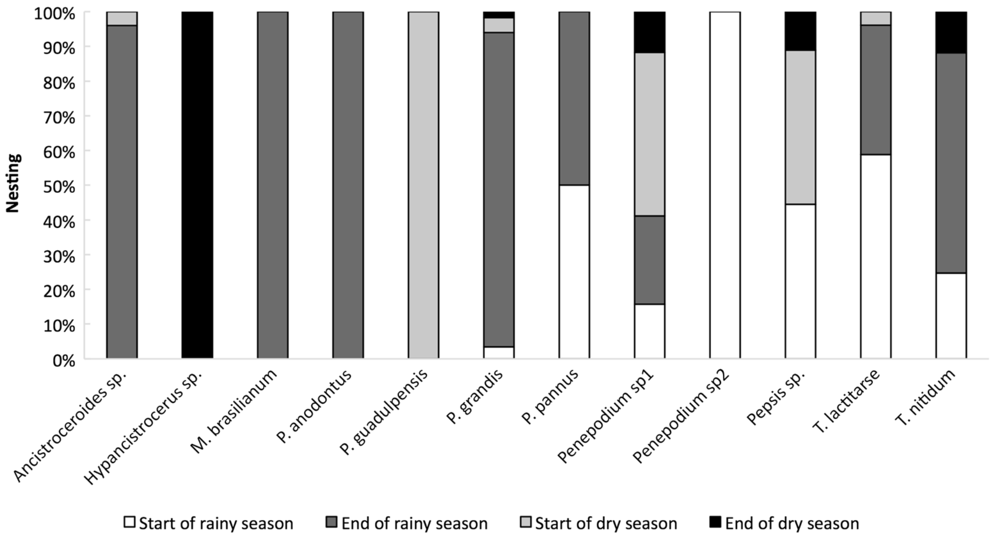

Fig 5 Frequency of nests built by the trap-nesting wasps at the Riparian Forest of Volta Grande Reservoir, Brazil, throughout the four sampling season period: start of rainy season, end of rainy season, start of dry season, and end of dry season.

was much lower compared to *C. analis*. At the sampling units studied, *C. analis* seems to be more efficient in resource use "cavity," as well as having founded more nests in four of the five areas and nests during the entire sampling period.

Seasonality

Nest occupation seems to be directly associated with climatic factors since higher temperatures led to an increased breeding activity of bees and wasps. According to Stangler *et al* (2015) and Batista Matos *et al* (2013), rainfall and temperature are key conditions regulating bees and wasps nesting through the availability of resources, mainly prey and pollen for the supply of the cells. In fact, the more abundant species occupied fewer trap nests when the temperature and rainfall were lower. Wasps are known to markedly respond to relative humidity and temperature (Batista Matos *et al* 2013). For example, *Ancistroceroides* sp., *Hypancistrocerus* sp., and *P. guadulpensis* were also affected by seasonality and nested in a single period. These Eumeninae species prey upon Lepidoptera larvae that are common in agroforests (Buschini & Buss 2010).

No significant correlation was found between temperature, rainfall, and nesting abundance of bee species in our study, probably because they obtain access to complementary resources such as nesting materials or nutrients (Ries & Sisk 2004). Another possible explanation is that the species composition, in our riparian forest fragments, shifted in favor of species adapted to environmental disturbances (Stangler *et al* 2015).

Host-Parasite Interaction

Parasitoid species richness and abundance were well explained by both bee and wasp species richness and

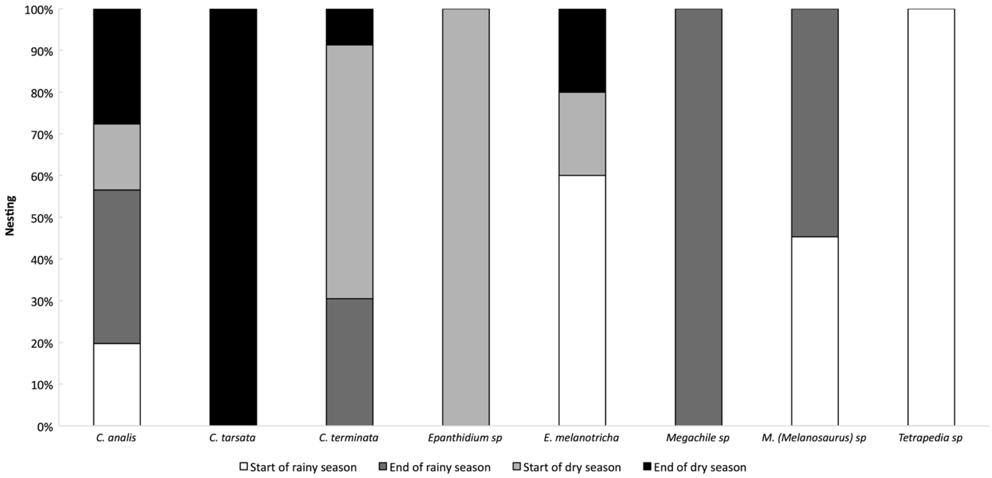

Fig 6 Frequency of nests built by the trap-nesting bees at the Riparian Forest of Volta Grande Reservoir, Brazil, throughout the four sampling season period: start of rainy season, end of rainy season, start of dry season, and end of dry season.

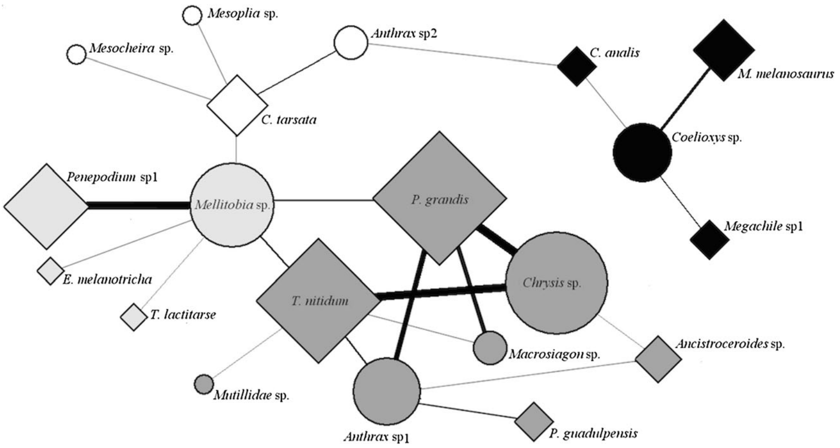

Fig 7 Network of interactions between parasites and their hosts. The *squares* represent the hosts and the *circles* represent parasites, *form sizes* is related to the number of interactions that each species and *thickness of the lines* represents the number of times that these interactions have been carried out. Names of parasites and hosts according to Table 2.

abundance, and a higher number of parasitized nests were found in SU5, SU4, and SU3 where the most abundant species were also recorded. Bees and wasps formed, together with its associated parasites, an interactive network, with some species-specific interactions previously reported besides some new associations. More specialist species as *Mesocheira* sp. only parasitized nests of *C. tarsata*, and this association has been previously recorded (Aguiar & Garófalo 2004, Aguiar *et al* 2005, Gazola and Garófalo 2009). *Anthrax* and *Coelioxys* are generalists and parasitized nests of *C. analis*, *Megachile* (*Melanosauros*) sp., and several species of wasps (Gazola & Garófalo 2009). *Macrosiagon sp.* parasitized only nests of wasps. According to Krombein (1967) and Callan (1981), this genus usually parasitizes the nests of Eumeninae, being rarer in Sphecidae, which confirms our results. This preference may be related to the type of resource used by the host to feed the immature.

The most abundant parasitic genus (*Melittobia*, *Anthrax* sp1, and *Chrysis* sp1) also presented the higher number of hosts, as *T. nitidum* and *P. grandis*. Although *Anthrax* sp1 had presented preference for parasitize *P. grandis* and *Mellitobia* sp. for *Penepodium* sp1.

In this study, the interaction network formed by the parasites and their hosts seems to follow the hypothesis of asymmetric abundance proposed by Vazquez *et al* (2007). According to this hypothesis, the abundance of species in the community determinates the frequency and the power of interaction networks, resulting in asymmetric structures.

The formation of sub-groups (modules) on the network of host-parasite interaction observed in this study is expected in communities where morphological, functional, and phylogenetical constraints determined by evolutionary history prevail (Lewinsohn *et al* 2006). Somehow, the modular presentation in a network of interactions may be related to the evolutionary history of the community and the pressures suffered by these species (Poulin 2010, Lewinsohn *et al* 2006).

An increased specialization of the parasites to their hosts was observed in the SU2 area (H2 = 1.000), but this may not be representing greater specialization, as both the richness and abundance in this area were low, compared with the other sample units. However, in SU4, we found a level of specialization slightly lower than in SU2 but the richness and abundance were higher. According to Vazquez *et al* (2007), the abundance of species within the community could be a major factor mediating the frequency and power of interactions in the network. Also, according to Pereira-Peixoto *et al* (2016), isolated habitats have less specialized natural enemies because generalist species are likely to survive in structurally poor isolated habitats, because they are able to reproduce on a variety of available host species. The specialized parasitoid species are dependent on their specific host species and thus are more likely to benefit from habitats that are structurally more diverse. This is similar to our results for SU5 compared, e.g., with SU2 and SU4.

We can conclude that the restored riparian forests constitute important areas of habitat for bees and wasps that nest in pre-existing cavities. In addition, that the seasonality strongly influences the richness and abundance of these insects and their associated parasites is probably due to differences in the amount and types of habitat features offered. Finally, we can conclude that the community establishment of these Aculeata was possibly also linked to the vegetation structure (type of surrounding matrix, width, and growth) which plays an important role in the group's occupation of riparian forests.

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