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Living in the sunlight: micro-environments with higher exposure of sunlight have more abundance and diversity of Hymenoptera in a Brazilian Atlantic Forest fragment

Camila Cristina Ferreira da Costa[1]*, Rodrigo Barbosa Gonçalves[1]

[1]*Universidade Federal do Paraná, Departamento de Zoologia, Laboratório de Abelhas, Curitiba, PR, Brasil.*

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ABSTRACT

Tropical forests are three-dimensional with the presence of numerous micro-environments formed by horizontal and vertical gradients. Such micro-environments can affect the nesting preference of organisms, including the trap-nesting Hymenoptera. Bees and wasps are key elements in ecosystems and are considered as sensitive to environmental changes, and trap-nests sampling methodology is widely used in their ecological and conservation studies. However, many uncertainties remain about nesting site preferences. From this perspective, our aim is to assess the diversity descriptors of trap-nesting Hymenoptera in different micro-environments. The sampling was conducted on three micro-environments (canopy, understory and treefall gaps) replicated on ten permanent plots within a Brazilian Atlantic forest hotspot. In each micro-environment, we installed trap-nest stations made by a set of twenty bamboo artificial nests. We found 762 brood cells from ten wasp and five bee species. The rarefaction curves indicate the lower species richness in understory stations, while treefall gaps and canopy stations were not significantly different. We analyzed abundance, mortality and parasitism rates using generalized linear models, but only abundance varies significantly among micro-environments. Our data indicates that trap-nesting Hymenoptera prefer to nest in micro-environments with higher exposure of sunlight. Canopy and treefall gap assemblages are consistently more abundant and diverse than understory probably due the higher temperature and lower humidity. On the other hand, mortality, parasitism rates, and the species composition were similar among environments. Our hypothesis is that the species composition was not affected as these species have a foraging range that encompasses nearby micro-environments.

Introduction

Species distribution in tropical forests is three-dimensional in space, occurring along the horizontal and vertical gradients (Basset et al., 2015) which are considered a key feature of tropical forest complexity (DeVries et al., 1997; Basset et al., 2015; Nice et al., 2019). Such gradients create different micro-environments with specific biological and climatic features within vertical and horizontal space (Oliveira-Santos et al., 2022). The vertical strata are strongly structured in tropical forests (Basset et al., 2003; Weiss et al., 2019), particularly due to different abiotic conditions (temperature, humidity and light) in small scales, between canopy and understory (Richards, 1983; Ashton et al., 2015). Biotic and abiotic factors require smaller spatial distances to vary on vertical rather than horizontal dimension (Basset et al. 2015; Nice et al., 2019). Also, understory disturbance, such as forest edges and natural treefall gaps, introduces important spatial heterogeneity in the horizontal dimension (DeVries et al., 1997; Rocha-Filho et al., 2017; Perry et al., 2018; Torretta and Marrero, 2019).

There is an expectation that arthropods are more diverse in the forest canopies than in understories (Basset et al., 2012, 2015). Fogging techniques were extensively used in the past to sample tropical forests, revealing compelling evidence of a huge diversity of insects, such as beetles and treehoppers in the canopies (see Erwin, 1989 for a review). However, further evidence have shown that different arthropods groups have particular responses to stratification (Whitworth et al., 2016; McCaig et al., 2020; Amorim et al., 2022; Oliveira-Santos et al., 2022). The trap-nesting bees abundance and richness, for instance, can be evenly distributed between understory and canopy (Stangler et al., 2016). Nonetheless, individuals are not restricted to a single stratum and turnover can occur in vertical spatial scales (Oliveira and Campos, 1996; Thiele, 2005; Torretta and Marrero, 2019). Even ground-nesting bees, for example, can be highly abundant on canopy during mass-flowering foraging (e.g. Urban-Mead et al., 2021). The distribution of floral resources is seasonal, and it varies among different vertical strata throughout the year, affecting flower-visiting insects (Silva et al., 2021). Still, the life stage is also crucial for insect distribution on space, adults and immatures can rely on different habitats within the forest, with adults being more common on the canopy (Basset et al., 2015).

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*Corresponding author.
E-mail: ccfdacosta@gmail.com (C.C.F. Costa).

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Treefall gaps are considered as canopy secondary openings caused by the death of one or more trees (Schliemann and Bockheim, 2011). This disturbance affects light availability, humidity and cover of understory vegetation, soil moisture levels, and leaf litter cover, thereby improving abundance and diversity of arthropods compared to undisturbed understory (Shelly, 1988; Schnitzer and Carson, 2001; Perry et al., 2018)). These novel environments create resources heterogeneity that allows resource partitioning and niche differentiation among species with differing responses to light (Kern et al., 2013; Blonder et al., 2018; Perry et al., 2018). As reported for vertebrates (Fuller, 2000; Horn et al., 2005; Siri et al., 2019) and invertebrates (Gorham et al., 2002; Horn et al., 2005; Perry et al., 2018), including wasps (Taki et al., 2008b; Costa, 2015), the abundance and diversity main trend is to increase at treefall gaps in comparison to undisturbed habitats.

Hymenoptera offers relevant ecosystem services in two main ways: while bees are the most important pollinators in the world (Michener, 2007), for both native plants (Ollerton et al., 2011) and crops (Klein et al., 2003), wasps are predators and parasitoids, regulating arthropod natural populations and also controlling agricultural pests (Harris, 1994; Brock et al., 2021). Trap-nests are a relevant tool to study those insects, bringing information on their ecological interactions and natural history, thus this methodology is widely used in studies regarding community structure, conservation, and crop management initiatives (Tylianakis et al., 2006; Buschini and Woiski, 2008; Batista-Matos et al., 2013; Steckel et al., 2014). More important here, these trap-nests can access the nesting site preference in forest micro-environments. However, we were able to find only three studies showing vertical stratification of bees and wasps' nests (Morato, 2001; Sobek et al., 2009; Stangler et al., 2016), and one study showing no stratification (Torretta and Marrero, 2019). It is worth emphasizing that no study compared the three micro-environments investigated here.

Our objective is to understand how trap-nesting Hymenoptera is associated with different micro-environments in a tropical forest, and also discuss which factors could be driving these ecological patterns. For this purpose we assessed the abundance, richness, diversity, parasitism and mortality rates of trap-nesting assemblages from treefall gaps, understories and canopies in ten plots of Brazilian Atlantic Forest.

Material and Methods

Study area and sampling design

Trap-nesting Hymenoptera and their parasites were sampled from October 2016 to May 2018 in an Atlantic Forest fragment (Reserva Natural Guaricica, 25º19'15"S and 45º42'24"W), city of Antonina, State of Paraná, southern Brazil. The local climate is humid subtropical with average annual temperature of 22 °C, average annual rainfall 2,545 mm, and the altitude varies from 0 to 600 m (Ferretti and Britez, 2005). The study site includes 10 permanent plots (250 × 40 m each) following the isocline established according to the RAPELD method (RAP=Rapid Assessments, PELD=Long Term Ecological Research) (Magnusson et al., 2005). The plots were distributed in a 1 × 5 km rectangle and are placed 1 km distant from each other. A central corridor with 1.5 m was established in each plot, and from this corridor, in the middle, we established a subplot of 20 × 250 m (Figure 1A). This plot design and the present study are part of project *PPBio Mata Atlântica Paraná* that was carried out from 2013 to 2018 (Oliveira et al., 2019).

We installed three trap-nests groups in each plot (Figure 1B), up to 100 m away from each other. A first station was placed in the understory, on a tree branch at approximately 1.5 meters height; a second station was place in a treefall gap fixed in a wooden post at 1.5 meters height; and a third station was placed in the canopy suspended with nylon thread in a tree branch (maximum height 19.0 m, minimum height 9.1 m).

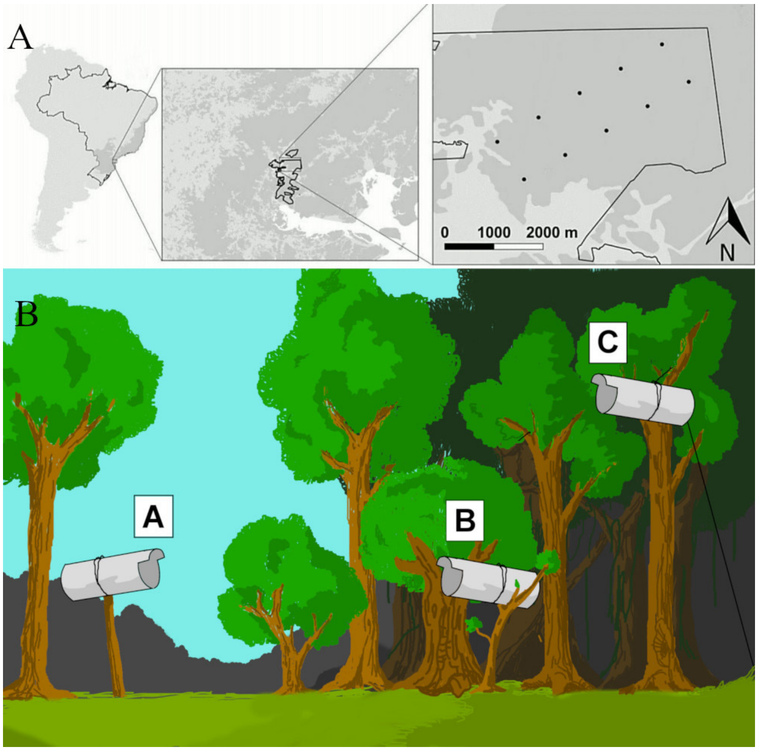

Figure 1 Sampling site and stations. 1A) Study area including the RAPELD modules. Each black point represents a permanent plot. 1B) Trap-nest stations and selected micro-environments: treefall gap (A), placed in wooden post at 1.5m height; understory (B), placed in a tree branch at approximately 1.5 meters height; canopy (C), suspended with thread in a tree (height between 19.0 and 9.1 meters).

Table 1
Abundance of brood cells, richness of wasps and bees, mortality rate (ratio of brood cells per number of cells where any adult emerged) and parasitism rate (ratio of brood cells per number of parasitized cells) in trap-nests of the three studied micro-environments in Atlantic forest, Paraná, Brazil.

	Abundance	Wasps richness	Bees richness	Mortality rate	Parasitism rate
Gap	289	7	3	19.4%	13.1%
Canopy	395	9	2	22.6%	30%
Understory	78	4	1	30.6%	5.5%
Total	762	10	5	24.2%	16.2%

We decided to not standardize height among canopy trap-nest stations because the tree's height was quite variable within the sampling plots. Thirty trap-nest stations were installed in total. Each station consisted of a modified PVC tube (diameter 15 cm, length 30 cm) filled with 20 bamboo internodes of different diameters (0.3 – 3 cm). The bamboos were cut longitudinally, and then held together with adhesive tape to allow further inspection.

Trap-nests were inspected monthly and completed nests, defined by the presence of the closing plug, were replaced by empty traps of similar diameter. The inhabited traps were taken to the laboratory (city of Curitiba, 80 km west of sampling site) and moved to plastic bottles closed with cotton wool. They were kept in a growth chamber whose temperature was adjusted based on the weekly historical mean temperatures of the city of Antonina, with a relative humidity of 50-75%, and photoperiod of 12:12 hours until adult emergence.

Wasps were identified at genus level using the key from Menke and Fernández (1996), and bees with the provided by Silveira et al. (2002). Species level determination was carried out by comparison with individuals previously deposited in the museum collection, and also by specialists listed in the acknowledgments section. Voucher specimens were deposited at the Coleção Entomológica Pe. Jesus Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba (DZUP).

Data description and statistical analyses

For every nest, we recorded the number of brood, vestibular and intercalary cells. We consider the number of brood cells as a measure of species abundance, following previous authors (Tylianakis et al., 2006; Stangler et al., 2014, 2016;). After the adult emergence, we recorded the number of dead cells and parasitized cells. The parasitism rate is here considered as the ratio of brood cells per number of parasitized cells, and the mortality rate as the ratio of brood cells per number of cells in which host or parasite adults emerged.

We calculated species richness curves (Hill numbers 0, 1, 2) for the three micro-environments using the package iNext version 2.0.19 (Hsieh et al., 2019). Individual-based rarefaction curves were estimated with interpolation, having their endpoints defined at the lowest observed abundance (65 brood cells), and extrapolation, with their endpoints at the double of the highest observed abundance (790 brood cells).

Non-metric multidimensional scaling (nMDS) and analysis of similarity (ANOSIM) were used for testing differences on species abundance among micro-environments. These analyses were conducted using Hellinger transformation for reducing the impacts of rare species (Legendre and Gallagher, 2001), and the Bray-Curtis distance based on abundance was used as the similarity index. The nMDS and ANOSIM were computed using the package vegan version 2.5-5 (Oksanen et al., 2019) and the graphics were plotted using the package ggord version 1.0.0 (Beck, 2017). The nMDS ordination was generated only for species sampled more than once and with sampling frequency of at least twenty percent (Marchant, 1999).

We tested the range abundance, parasitism rate, and mortality rate on micro-environments with a general linear model (GLM) using the package *stats* version 3.5.2. We used functions with different families depending on residual distribution and overdispersion, abundance was analyzed with a Gaussian model, while parasitism and mortality rates were analyzed with a binomial model. To test spatial autocorrelation we performed a Mantel test based on Pearson correlations, using a distance matrix from geographic coordinates (Euclidian) and abundance (Bray-Curtis). We found no spatial autocorrelation (Gap: r= -0.10 and p= 0.66; Canopy r= -00.5 and p= 0.58; Understory: r= 0.02 and p= 0.37). All statistics analyses were computed in R version 3.5.2 (R Development Core Team, 2019).

Table 2
Results of generalized linear effects models relating abundance, parasitism rate and mortality rate to the explanatory variable micro-environments.

Response variable	F-statistic	p-value
Abundance	4.9616	0.016**
Parasitism rate	2.6919	0.08
Mortality rate	0.5308	0.595

***P<0.01*

Results

We recorded 762 brood cells belonging to ten wasp species (Crabronidae and Sphecidae) and five bee species (Apidae) (Table 1 and S1). Wasps were far more common than bees, summing up to 730 brood cells. The most common species were *Podium* sp.1 (248 brood cells), followed by *Trypoxylon lactitarse* Saussure, 1867 (180), and *Trypoxylon agamemnon* Richards, 1934 (117). These species were more abundant on canopy stations, except for *T. agamemnon* that was more abundant on treefall gaps. In summary, canopy stations had higher brood cells abundance followed by the treefall gap stations, and wasps were more abundant on canopy and bees on treefall gaps stations (Table 1). Trap-nesting abundance differed significantly among micro-environments according to the GLM analysis (Table 2).

Interpolation and extrapolation curves gave similar results: richness and diversity were lower in the understory than in the treefall gap and canopy stations, without overlap in the confidence intervals (Figure 2 and Figure S1). Richness values were similar between canopy and treefall gaps, but diversity (q=1 and q=2) was higher in treefall gap stations; however, all the curves overlap, indicating no significant difference. The only diversity curves that reach the asymptote were those from the understory stations, suggesting that we sampled a substantial proportion of the species only on this micro-environment.

From the colonized nests, adults hadn't emerged from 184 (24%) of brood cells, and 123 (16%) of brood cells were parasitized (Table 1). Mortality rate was higher in the understory followed by canopy stations, while the parasitism rate was higher in the canopy followed by treefall gap stations. However, both response variables did not differ significantly among micro-environments (Table 2). Ordination analysis did not separate the stations from the micro-environments, indicating that species composition did not vary among micro-environments (Figure S2; k=3, stress =0.077; ANOSIM: R= 0.14, p= 0,07).

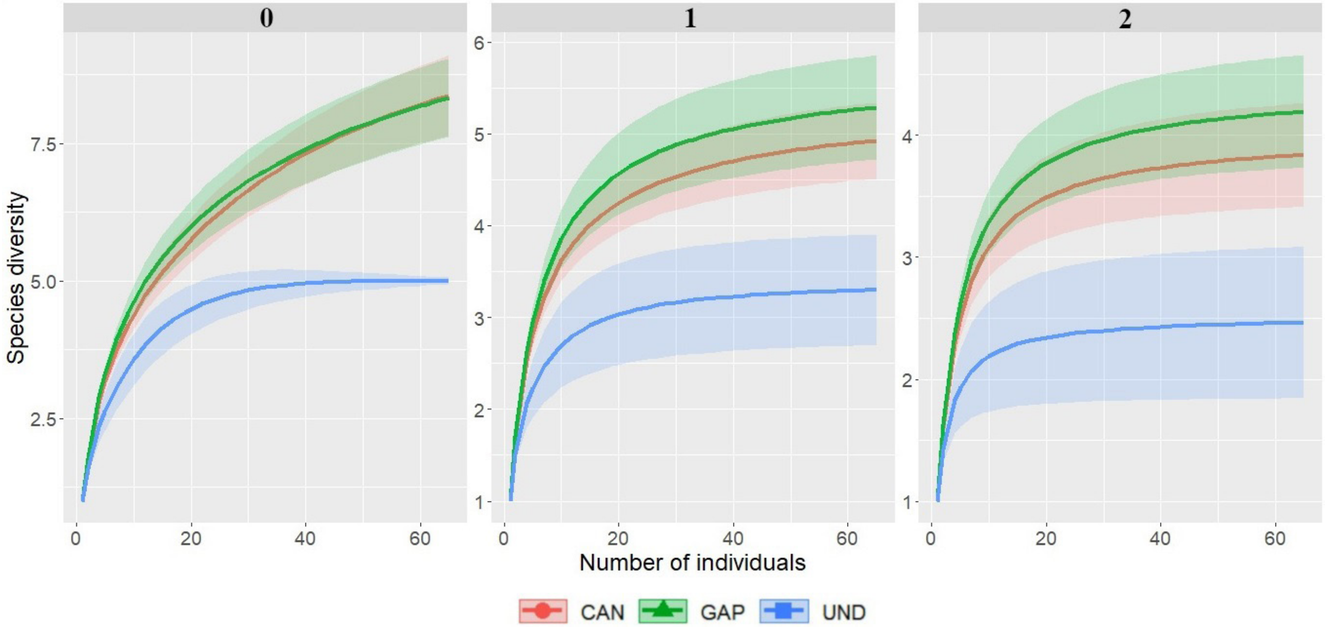

Figure 2 Interpolation curves of the richness and diversity of trap-nesting Hymenoptera (Atlantic forest, Brazil) in relation to the lowest observed abundance brood cells sampled and assessed for three Hill numbers (0, 1 e 2). CAN= canopy; GAP= treefall gap; UND= Understory.

Discussion

We found that trap-nesting Hymenoptera abundance, richness and diversity were lower in understory stations compared to treefall gap and canopy stations, micro-environments with higher sunlight exposure. This suggests that sunlight availability plays a crucial role in shaping the community composition and dynamics of trap-nesting Hymenoptera in tropical forests. Previous studies in Neotropical region have already reported that trap-nesting bees and wasps are more abundant in open and sunnier sites. This preference was explained as a response to factors such as lower humidity (Stangler et al., 2016; Rocha-Filho et al., 2017; Araújo et al., 2020), greater accessibility to floral resources (Oliveira and Campos, 1996), and also due to the thermal tolerance and flight activity (O'Neill, 2001; Loyola and Martins, 2006; Stangler et al., 2016). More sunlight exposition promotes high temperatures, low humidity and other environmental and biological conditions (Denslow et al., 1998; Warrant et al., 2004; Morato and Martins, 2006). The sunlight incidence also creates nutrient hotspots by promoting a high density of young leaves which attracts herbivorous (some wasps' prey) (Richards and Coley, 2007; Brock et al., 2021) and a mass flowering which attracts a huge sort of visitors (Urban-Mead et al., 2021).

The dissimilar abiotic conditions on the understory can also be evoked to explain the difference of the diversity descriptors. In tropical forests, the understory is typically characterized by limited sunlight, resulting in darker and wetter environments compared to treefall gaps and the canopy (Kern et al., 2013; Nakamura et al., 2017). It is well-established that trap-nesting Hymenoptera colonization responds negatively to moisture (Taki et al., 2008a; Costa, 2015; Stangler et al., 2016; Rocha-Filho et al., 2017; Prendergast et al., 2020), preferring to nest in waterproofed substrates (Rauf et al., 2022). Moreover, we have noticed that wasps and bees females avoid nesting within very wet bamboo internodes, choosing nests in the center of each station. Even if a significant difference in mortality rate was not reported here, higher humidity is usually linked to higher activity of fungi that could increase the offspring mortality (Morato and Martins, 2006; Stangler et al., 2014).

Sunlight intensity is definitively an important factor influencing Hymenoptera visual ability (Warrant et al., 2004), despite this effect being poorly studied for solitary bees and wasps. The homing is guided mainly by sight, and visual marks next to the nest entrance are used to proper location (Fauria et al., 2004; Warrant et al., 2004). In this sense, it might be more difficult to find the nest entrance in micro-environments with less sunlight exposure.

Some studies have investigated the vertical distribution of trap-nesting Hymenoptera, demonstrating differences between understory and canopy (Morato, 2001; Sobek et al., 2009; Stangler et al., 2016). In tropical rainforests, arthropods have been shown to be equally or more diverse in the canopy than in the understory (Basset et al., 2015; Nakamura et al., 2017), but this pattern is not recovered in all Hymenoptera studies (Sobek et al., 2009; Torretta and Marrero, 2019; Amorim et al., 2022). Morato (2001), in tropical rainforests of Brazil, and Sobek et al. (2009), in German temperate deciduous forests, both found higher abundance and diversity in canopy. On the other hand, Stangler et al. (2016) found higher abundance and diversity of bees in Costa Rica understory. Finally, Torretta and Marrero (2019) observed no difference between canopy and understory in riparian forests and savannas from Argentina. These different responses could be explained by local characteristics modulating nesting preference other than stratification, mainly climate and vegetation structure (Urban-Mead et al., 2021; Oliveira-Santos, et al., 2022).

Previous studies focused on to measure differences between assemblage structure of canopy and understory arthropods (Basset et al., 2015; Stangler et al., 2016; Amorim et al., 2022; Oliveira-Santos et al., 2022;) or treefall gap and understory (Perry et al., 2018; Saiful and Latiff, 2019). Herein we also compared canopy and treefall gap, which did not show significant differences, indicating that sunlight could be the main driver of trap-nesting Hymenoptera diversity, despite vertical and horizontal distance.

We did not find differences in species composition when examining the common species which were present in all micro-environments stations. Only infrequent or singleton species such as *Megachile* spp, *Podium* sp.2, *Trypoxylon basirufum* Muniz & Melo, 2021 and *Auplopus pratens* Dreisbach, 1963 were specific to micro-environments.

By contrast, previous studies have reported differences in arthropod species composition between canopy and understory (Stangler et al., 2016; De Smedt et al., 2019; Amorim et al., 2022; Oliveira-Santos et al., 2022). In Euglossini bees, species occur only in specific strata, with some species occurring only in understory while others are found in higher heights (12 meters) (Oliveira and Campos, 1996). According to Thiele (2005) and Stangler et al. (2016), *Centris labrosa* Friese, 1899 (Centridini) is also a bee strata-specific, since their nests occur only in the understory.

The similar composition of common species among micro-environments can be associated with the short distance among stations. Foraging distance is correlated to the intertegular distance for bees (Greenleaf et al., 2007), and probably the same mechanisms may also apply for solitary wasps. Most of trap-nesting Hymenoptera sampled in this work is medium-sized and have a foraging range of approximately 1,000 meters (Zurbuchen et al., 2010), a distance that exceeds the plot area. Resources such as larval food and nest building-material availability are important to the nesting activity (Morato and Martins, 2006), and the distance between the resources and the nesting site is important to be considered (Klein et al., 2004; Morato and Martins, 2006). Wasps and bees nest near their resources, as showed by the correlation between brood-cell density and foraging time (Klein et al., 2004). For example, *Podium* sp.1 was the most common species overall and more abundant in the canopy, even though important resources are located in understory, such as their larval food (cockroaches, Blattaria) (Schal and Bell, 1986), and nest-building material (mud).

Mortality and parasitism rates did not differ among micro-environments. Mortality rate is a very popular measure in trap-nest studies (Stangler et al., 2014, 2016; Rocha-Filho et al., 2017; Torretta and Marrero, 2019), although, we suppose this is a vague ecological indicator because death causes are not easily addressed (Tepedino and Frohlich, 1982; Garcia and Adis, 1995), being impossible to properly correlate mortality with any biotic or abiotic factors without specific tests. Another important issue is that the laboratory rearing conditions also can influence the mortality rate (Torretta and Marrero, 2019). For parasitism rate, previous studies also showed conflicting results. If Sobek et al. (2009) found the higher rates in canopy, and Stangler et al. (2016) found in understory, Torretta and Marrero (2019), on the other hand, observed no difference, the same as here.

Conclusions

Based on our findings, sunlight exposure is an important factor in trap-nesting Hymenoptera colonization, since significant difference was found only between understory and the other micro-environments. On the other hand, species composition, mortality, and parasitism rates do not bring conclusive responses. Literature on trap-nesting responses to micro-environments is scarce and published data shows conflicting results, especially for tropical forests. Despite the inherent differences among sites, two trap-nest methodological problems can explain these conflicting results. Firstly, most studies sample only two years or less (MacIvor, 2017), so that temporal fluctuations cannot be fully addressed. Secondly, the trap-nests frequently sampled a few individuals and species when compared to other sampling methods and this frequently leads to inconclusive data. Therefore, we recommend that further trap-nesting studies should prioritize temporal replication and sampling size to answer questions such as micro-environment preference.

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Conflicts of interest

The authors declare no conflicts of interest.

Author contribution statement

CCFC and RBG designed the study. CCFC carried out the fieldwork and data analyses. CCFC and RBG wrote the manuscript.

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Supplementary material

The following online material is available for this article:

Table S1 – Number of brood cells of trap-nesting wasp and bee species (Hymenoptera) sampled in the three micro environments in ten sites at an area of Atlantic Forest from October 2016 to May 2018. G= Treefall gap; C= Canopy; U= Understory.

Figure S1 – Extrapolation curves of the number of species of trap-nesting Hymenoptera found in relation to the double of the highest observed abundance brood cells sampled asses for three Hill numbers (0, 1 e 2). CAN= canopy; GAP = gap and UND= understory

Figure S2 – Non-metric multidimensional scaling (nMDS) ordination for most frequent trap-nesting Hymenoptera species (Atlantic forest, Brazil). Number of dimensions = 3; stress = 0.077. CAN= canopy; GAP = gap and UND= understory.